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RESEARCH

Bird population trends in response to predator management at Waitutu Forest, Fiordland: 2006–2022

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Abstract: New Zealand's native birds are particularly vulnerable to predation from introduced mammals, especially rodents and mustelids. The prolific seeding of trees during mast years triggers rodent irruptions, and the subsequent increase in mustelids can have devastating effects on native bird populations. Waitutu Forest, in Fiordland, New Zealand, has experienced declines in many of its bird populations and has been subject to pest management since 2008 to reverse these trends. A monitoring programme was established to determine the success of this management. Several peaks in seed-rain indicated partial or full mast events, which appeared to drive increases in rodent and mustelid populations. However, with a few exceptions, indices of abundance for mustelids and rats were consistently low (< 10% tracking) for at least 12 months following 1080 operations, indicating that aerial application of 1080 was effective at suppressing these predators. Five indigenous bird species, all with high levels of endemism, responded positively to pest management. Conversely, six bird species (three indigenous, three introduced) showed population declines, potentially the result of inter-specific competition from those species that benefitted most from pest management. The remaining nine bird species monitored showed no significant increase or decrease during the study. There was considerable spatial variation in relative abundances of most bird species. The pattern was different between species, suggesting that variations were due to differences in site characteristics or linked to inter-specific competition. Despite the absence of a non-treatment site for comparison, this study has provided useful time-based insights into the population trends of birds at the study sites. It is recommended that the management and associated monitoring continue, to further increase our understanding of bird population dynamics in response to pest management and to monitor the impacts of future environmental changes.

Keywords: aerial 1080, long-term monitoring, pest control, relative abundance

Introduction

New Zealand's native birds are vulnerable to introduced mammalian predators, such as stoat (*Mustela erminea*), brushtail possum (*Trichosurus vulpecula*) and ship rat (*Rattus rattus*; hereafter referred to as rat), because they have evolved in the absence of these predators and therefore lack appropriate predator defence strategies (Wilson 2004; DOC 2020). Many are flightless or poor flyers, and they are often K-selected, and as such have low reproductive rates and slow growth (King 2019). Cavity-nesting species such as yellowhead | mohua (*Mohoua ochrocephala*), kākā (*Nestor meridionalis*), and yellow-crowned parakeet | kākāriki (*Cyanoramphus auriceps*) are particularly susceptible to stoat predation, as most nests have a single entrance and, therefore, neither adults nor chicks can easily escape these predatory mammals (O'Donnell 1996; Wilson 2004). The problem is exacerbated during mast years, when tree species such as beech (*Fuscospora* spp. and *Lophozonia* spp.) and podocarps (e.g. miro (*Pectinopitys ferruginea*), rimu (*Dacrydium cupressinum*), and *Podocarpus* spp.), seed prolifically. The seeds provide a super-abundant food source which leads to cascading irruptions of mice (*Mus musculus*; e.g. Ruscoe et al. 2004) and, in turn, to a higher abundance of rats and stoats, which prey on both mice and native birds (O'Donnell 1996). Numerous studies have shown that many bird populations suffer significant declines following mast events (Elliott & O'Donnell 1988; Moorhouse et al. 2003; Powlesland et al. 2009; Kemp et al. 2022).

Introduced predators can be eradicated from offshore islands or excluded from predator-fenced eco-sanctuaries such as Zealandia (Miskelly 2018), however conservation management on the main islands of New Zealand usually entails landscape-scale control to reduce predation pressure at critical times (Innes et al. 2024). This has been shown to benefit many native bird populations (James & Clout 1996; Dilks et al. 2003; Kelly et al. 2005; Elliott & Suggate 2007; Malham & Elliott 2023), and various techniques and tools have been developed for doing so (Eason et al. 2017). Aerial

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predator control entails the application of poisoned bait from the air, usually by helicopter, and is often applied in areas that are too large or too remote to effectively cover using ground control methods (DOC 2020). The use of the toxin 1080 (sodium mono-fluoroacetate) in this way has proven most effective for large-scale control of possums, stoats, and rats (and has proven increasingly effective for mice; J. Kemp, DOC Nelson, pers. comm.). However, it has become controversial, with some members of the public rejecting the scientific evidence that supports its use (King 2019). Nevertheless, 1080 currently remains the most practical option for the necessary landscape-wide pest control required to protect a significant portion of New Zealand's wildlife populations (Warburton et al. 2021).

The New Zealand Department of Conservation (DOC) has carried out pest control operations at numerous sites across New Zealand's Public Conservation Lands (PCL), as part of its National Predator Control Programme (NPCP, formerly known as Tiakina Ngā Manu or Battle for our Birds). This programme aims to prevent local extinctions of bird populations and provide some level of protection for threatened species over as large an area as possible of PCL (Elliott & Kemp 2016). Waitutu Forest, situated in south-east Fiordland on New Zealand's South Island (Fig. 1), forms part of the Te Wāhipounamu South West New Zealand World Heritage Area and has been identified as a priority site for predator control by the NPCP. Detailed surveys of the area in the mid-1980s reported the forest to be "outstanding" in terms of its wildlife values (Elliott & Ogle 1985). The area supported high densities of kākā and yellow-crowned parakeet | kākāriki, a distinctive invertebrate fauna, a high diversity and

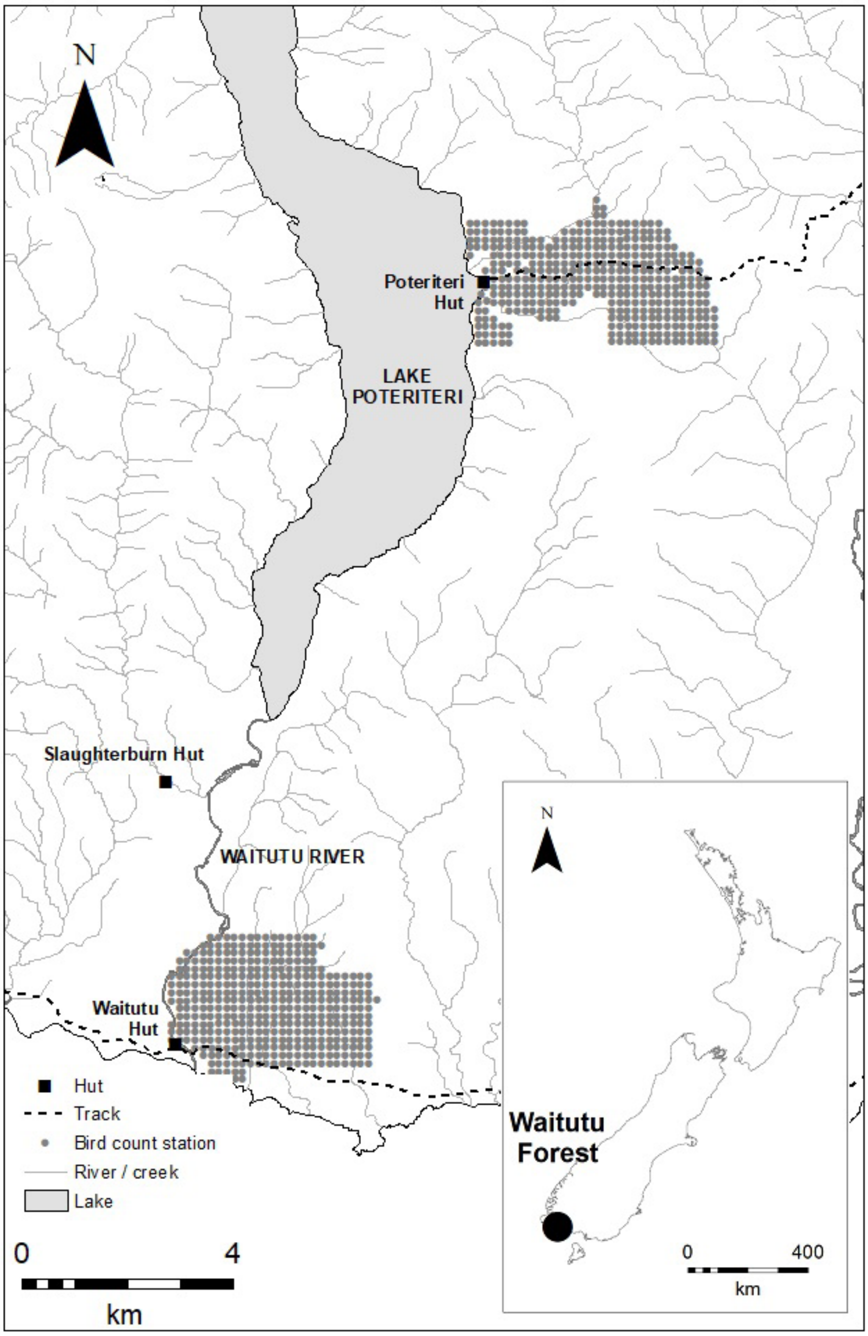

Figure 1. Locations of the two study sites, Lake Poteriteri (northern site) and Waitutu Coast (southern site), as indicated by locations of bird count stations (grey dots).

abundance of freshwater fishes, and populations of several threatened mistletoe (*Loranthaceae*) species (Ledgard et al. 2020). However, the ongoing presence of stoats and rats, and the subsequent invasion by possums (Wildland Consultants 2008), resulted in populations of native fauna and flora being severely impacted (Southey 2000; Wilson et al. 2006; Wildland Consultants 2008). In particular the mistletoe population had been decimated by possum browse (Ledgard et al. 2020), many female kākā were being killed on the nest by stoats (Wildland Consultants 2008), and other formerly abundant bird species such as the South Island robin | toutouwai (*Petroica australis*) and yellowhead | mohua were rarely seen (Greene et al. 2013). Some species (e.g. yellowhead | mohua and kākā) were brought to the brink of local extinction.

To counter the threat from introduced predators, a series of pest control initiatives were established, starting in 1996 with a four-year ground-based possum control programme, covering 3300 ha and centred on Waitutu River. The aim of this was to slow possum movement westwards. Pest control continued to expand in subsequent years. In 2008, an extensive predator trap network was set up at Lake Poteriteri and Waitutu Coast, followed by four aerial 1080 applications between 2010 and 2020 at these sites and across the wider area. Following the introduction of sustained pest control, an ongoing monitoring programme was established to assess the effectiveness of pest control for the target pest species and native wildlife. This initially focused on the Slaughterburn area then expanded to include several other parts of Waitutu Forest. Bird population monitoring began in 2006 and was focussed on two of these areas: Waitutu Coast and Lake Poteriteri. Although the latter was originally established as a control site, to monitor populations in the absence of pest control, it was considered too valuable to leave unmanaged and was incorporated into the pest control area.

In this study we report on results from the first 17 years of forest bird monitoring at Lake Poteriteri and Waitutu Coast. Our aim is to describe the temporal trends and spatial distributions of selected bird species populations at each site and assess the impacts of predator management.

Methods

Study site

Waitutu Forest encompasses 45 000 ha of southern Fiordland National Park, and is a significant part of the largest remaining expanse of lowland forest in New Zealand (Fig. 1). The area consists of a mosaic of forest types growing on largely flat uplifted marine terraces of variable fertility. Coastal terraces and lowland alluvial flats are generally dominated by podocarp species including rimu, miro, totara (*Podocarpus totara*), and southern rātā (*Metrosideros umbellata*). On steeper slopes and at higher altitudes there is frequent silver beech (*Lophozonia menziesii*) and mountain beech (*Fuscospora cliffortioides*). In swampy areas, mountain beech replaces silver beech, and is joined by kahikatea (*Dacrycarpus dacrydioides*) and mānuka (*Leptospermum scoparium*). Kāmahi (*Pterophylla racemosa*) is a common sub-canopy species throughout. For a more detailed description of the area see Greene et al. (2013). The Lake Poteriteri site consists largely of kāmahi/podocarp/beech forest with areas of broadleaved hardwood/beech to the west of the centre and to the far east. There are stands of beech/kāmahi forest to the north-west and around the fringes of the site, and a scattering of broadleaf/tree fern/beech through the centre. The Waitutu Coast site consists of mostly kāmahi/podocarp/beech forest with kāmahi/podocarp forest around the edges and to the east of the centre. When compared to the Lake Poteriteri site, beech is less common and southern rātā more common (E. Wright, DOC Christchurch, unpubl. data).

Pest management

The current mammalian pest control regime consists of: (1) a network of DOC 150 double set predator kill traps to target mustelids and rats, and (2) periodic aerial 1080 poison drops applied over extensive operational areas. Predator traps were established in 2008 at nominal densities of 0.1 traps ha^{-1} (Waitutu Coast) and 0.05 traps ha^{-1} (Lake Poteriteri) and reset quarterly (February, May, August, and November). 1080 operations took place in October 2010 (25 000 ha), August 2014 (30 000 ha), November 2016 (30 000 ha) and March 2020 (63 000 ha), coinciding with mast seeding events, and encompassing all monitoring sites. Specifics of the bait and sowing rates varied between operations: 6 or 12 g RS5 or PCR bait types were used and sowing rates varied between 1 and 2 kg ha^{-1} (DOC 2024).

Monitoring design

To facilitate bird monitoring at the Waitutu Coast and Lake Poteriteri sites, a grid was established, consisting of bird count stations spaced 150 m apart. Within and around this, several tracking tunnel lines were established, along with seed-rain collection traps (Fig. 2).

Seed-rain monitoring

Seed-rain monitoring was established in 2011 and measured using traps, each consisting of a large plastic funnel (0.28 m^2) mounted on a metal frame, with a removable collection receptacle at the base of the funnel. Traps were permanently established on two grids (approximately 0.5–1 ha) in the Waitutu Coast area, each with 15 traps spaced between 10 and 45 m apart. At Lake Poteriteri, three seed-rain traps were established approximately 150 m apart along five of the six tracking tunnel lines ($n = 15$; Fig. 2). The differences in seed-rain trap layout between the Waitutu Coast and Lake Poteriteri sites stem from differences in establishment times, with the Waitutu Coast sites having been established historically, while the Lake Poteriteri sites were newly established as part of this study. Seeds were collected from each trap quarterly (in February, May, August, and November), identified to species, and counted (by the University of Canterbury).

Mammalian pest monitoring

Mammalian predator populations were monitored using quarterly counts of animals caught in the predator traps and tracked within footprint tracking tunnels (Gillies & Williams 2013). Six tracking tunnel lines were established at each study site and monitored quarterly in February, May, August, and November (2006– 2022 at Waitutu Coast, 2007– 2022 at Lake Poteriteri). Each line consisted of 10 tracking tunnels, spaced approximately 50 m apart (Fig. 2). These were set for one night (baited with peanut butter) to monitor rodents, and for three nights (baited with fresh rabbit meat) to monitor mustelids. Possum monitoring was not included in our study, however the results of monitoring associated with pest management operations indicated that post-control possum abundances were lower than pre-control levels (< 5% residual trap catch;

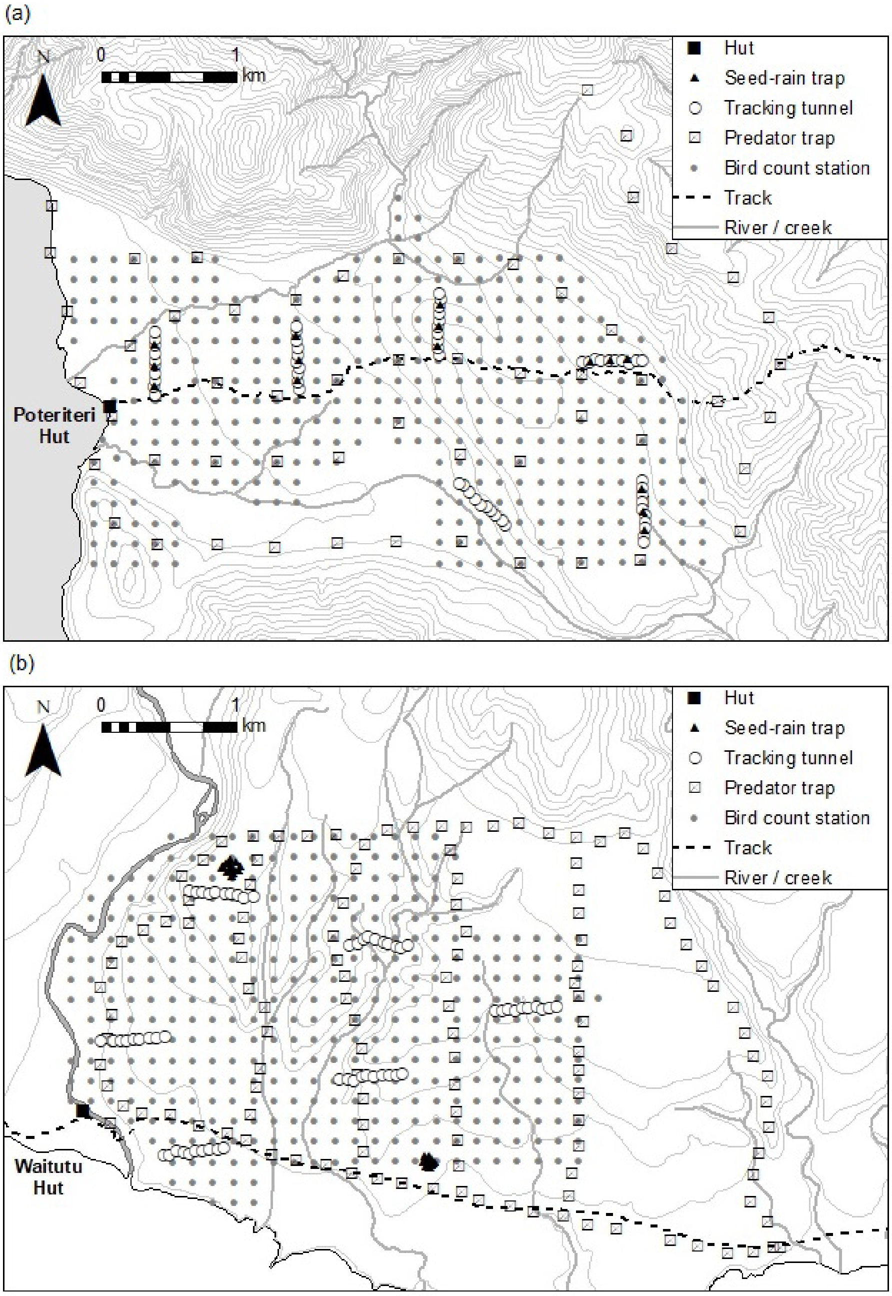

Figure 2. (a) Layout of bird count stations, tracking tunnels, predator traps, and seed-rain traps at the Lake Poteriteri study site. (b) Layout of bird count stations, tracking tunnels, predator traps, and seed-rain traps at the Waitutu Coast study site.

Pestlink database, DOC, unpubl. data), demonstrating that the pest management strategy was successful in suppressing possum numbers.

Bird monitoring

Bird counts were completed annually, in November, from 2006 to 2022. Bird count stations were individually marked and spaced approximately 150 m apart using a systematic grid, established using a random starting point. There were c. 350 stations at the Waitutu Coast site and c. 375 at Lake Poteriteri. A single five-minute bird count was completed at each station in each survey year.

Five-minute bird counts, adapted from Dawson and Bull (1975) were carried out in suitable weather conditions by experienced observers, not less than 1 hour after official local New Zealand sunrise and completed by approximately 1300 hrs, within a six-day period. To minimise bird identification error, we used experienced ornithologists, and whenever possible, those who had previously carried out surveys at these sites (and were therefore familiar with the bird dialects of the region). Most birds were identified to species, with the exception of parakeet | kakariki.

Data analysis

Seeds counted on each survey visit were aggregated for all seed-rain traps within each site (Waitutu Coast and Lake Poteritieri) for the entire calendar year and converted to number of seeds m^{-2}. Seeds were assigned to their taxonomic group: beech, which included mountain beech and silver beech, or podocarp, which included kahikatea, miro, totara, and rimu. Seeds counted from other species (broadleaf | kapuka (*Griselinia littoralis*), red matipo | mapou (*Myrsine australis*), southern rātā, and *Pseudopanax* spp.) were non-masting, relatively few, and were therefore excluded from the analysis.

We decided to use tracking tunnel data to monitor fluctuations in rodent and mustelid population dynamics rather than data from predator traps. The tracking tunnel data provided a snapshot of current activity (tunnels being deployed for a maximum of three days on each survey visit), whereas the predator traps were set and left for an extended period of three months between each survey visit and could therefore trap animals at any time during this period. Tracking tunnels had the additional benefit of being independent from the predator management methods. Rodent and mustelid tracks were identified by experienced ecologists, and the proportion of tunnels tracked for each line calculated. This was then used to produce an index of relative abundance, in the form of mean percentage of tunnels tracked for each site in each quarter.

Because bird counts were relatively intensive, conducted at stations arrayed along transects within two blocks of relatively small spatial extent (c. 1000 ha each), the counts were expected to exhibit strong spatial autocorrelation. We accounted for this by using a spatially structured random effect in our model so that nearby sampling locations were more closely correlated with one another than they were with locations further away. Accounting for spatial autocorrelation in this way reduced the risk of spurious inference resulting from an incorrect assumption of independence between sampling locations. The counts may have included the same individuals measured at a nearby site (due to both animal movement or detection distance) and thus form an index of abundance.

We used a generalised linear mixed model (GLMM) to model the observed five-minute bird count of each species, N_{jt} (s), at site (j) (Lake Poteriteri or Waitutu Coast), time (t), and station location (s). We assumed the counts were a Poisson random variable with a station-site-year specific rate parameter, $\gamma_{jt}(s)$ per 5-minute count:

$$N_{jt}(s) \sim Poisson\ \left(\lambda_{jt}(s)\right) \tag{1}$$

The rate parameter is a log-linear function:,

$$\log \lambda_{jt}(s) = \ \beta_j + \alpha_j t + \ f(s) + \ \varepsilon_{jt} \tag{2}$$

where β_j parameter is a site-specific intercept parameter, α_j is the site-specific annual trend, $f(s)$ is a spatially structured random-effect and ε_{jt} is the site-specific annual random effect. The spatially structured random effect $f(s)$ is a Gaussian Markov random field approximation to a Gaussian random field with Matérn covariance (Lindgren & Rue 2011). This random effect accounted for spatial auto-correlation in counts but not temporal correlation, which was modelled separately. The site-specific annual random effect, ε_{jt}, accounted for site specific random variation from the trend. Importantly, it ensured that the trend was not overly influenced at the beginning or end of the study by a particularly extreme set of observations. Covariates based on seed mast, tree canopy dominants, environmental conditions, or predation were considered as predictors. However, increased predation impacts nesting success and leads to a year or more lag in the number of observed birds. The key variable of interest was the impact of management activity, which has an interaction effect with this relationship. Given that these interacting effects exist at the scale of sites and years, there were too few observations to tease apart these complexities using indices of abundance, which are often impacted by environmental conditions for that particular year. Instead, we focussed on the long-term trend in abundance for each species to reflect the overall effect of management, allowing the random effect structure to account for the site and year differences.

To fit the model, we used the integrated nested Laplace approximations (INLA) approach to approximate Bayesian inference (Rue et al. 2009, Martins et al. 2013) in the program R version 4.4.2 (R Core Team 2024). We implemented the model using "inlabru" (Bachl et al. 2019), a software wrapper and extension of R-INLA that supports spatial modelling applications and facilitates sampling from the posterior distribution for prediction and posterior checking. This approach approximates the marginal posterior of all model parameters and allows sampling from the approximate joint posterior in a computationally efficient way. The INLA approach has been shown to be accurate for the class of latent Gaussian models, which includes GLMMs such as the model used here (Rue et al. 2009). Model outputs are then based on summarising samples from the relevant approximate posterior distributions. See supplementary material S1 for a full description of the model and the prior distributions used.

Model validation was done visually using scaled randomised quantile residuals and the "DHARMa" package (Hartig 2024). We treated each species as independent, running the model for each species separately. We explored alternative joint species distribution models (e.g. such as offered by the R package "Hmsc"; Tikhonov et al. 2022) to incorporate species interactions but found that the flexibility in the spatial model from R-INLA was more important. At such a small spatial scale, all sample locations may be considered equally influenced by any species at that site. Alternatively, combining the counts to the site level obscures species interactions due to their spatial heterogeneity, making the practicality of a more complicated multi-species approach unclear.

The analysis output for each species was provided in three parts: (1) a summary graph displaying the annual trend estimated by the model for each species, (2) graphs for individual species showing the estimated annual trend against the temporal variation in the five-minute bird count at each site, and (3) distribution maps showing how relative abundance varied within each site at two different time points: prior to the commencement of 1080 treatments (2009), and 12 years after 1080 treatment had begun (2022). For summary annual trends, a positive trend is defined as having a mean value and lower credible interval higher than zero; a negative trend has a mean value and upper credible interval lower than zero; and a neutral trend has one of its credible intervals bisecting zero.

Results

Seed-rain

There was considerable variation in annual seed-rain of beech and podocarp species at both sites. Beech ranged from a minimum of 2.1 beech seeds m^{-2} (Waitutu Coast, 2021) to a maximum of 7714 seeds m^{-2} (Lake Poteriteri, 2019), whilst podocarps ranged from 1.9 seeds m^{-2} (Lake Poteriteri, 2021) to 1053.6 seeds m^{-2} (Waitutu Coast, 2019). Beech seed-rain was generally higher at Lake Poteriteri than at Waitutu Coast. Conversely, podocarp seed-rain was usually higher at Waitutu Coast. There were high seed-rain years for beech and podocarp species in 2014, 2016, and 2019 (Fig. 3).

Mammalian pest abundance

Mean indices of relative abundance (unmodelled) were highly variable for mice, rats, and stoats. Tracking indices for mice had the largest range, from 0% (multiple years at both sites)

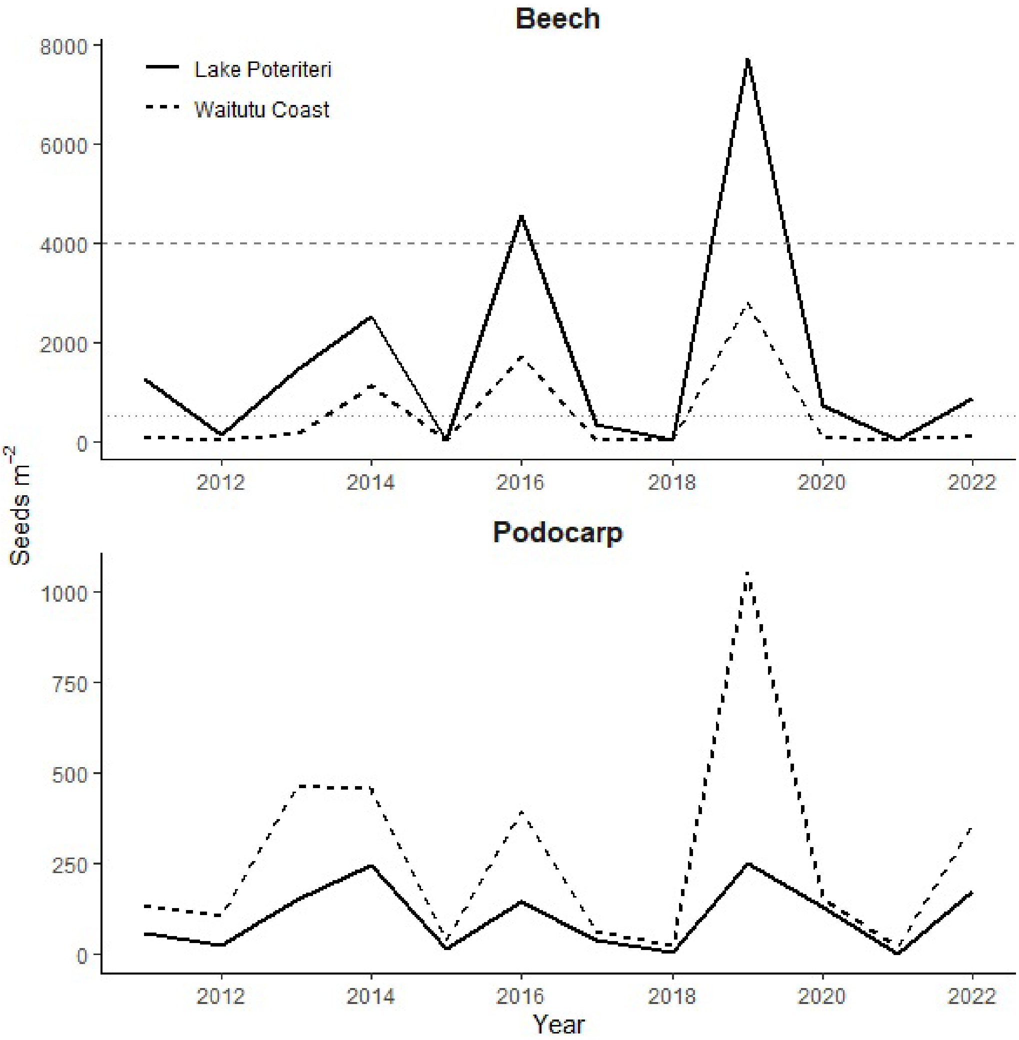

Figure 3. Seed counts (m^{-2}) for beech species (mountain beech and silver beech) and podocarp species (kahikatea, miro, totara, and rimu) at the Lake Poteriteri and Waitutu Coast sites. The dashed horizontal line represents the full mast threshold for beech, and the dotted horizontal line represents a partial mast threshold for beech. Equivalent mast thresholds for podocarp species were not available. Note that y-axes use different scale limits.

to 95% (in the fourth quarter of 2009 at Lake Poteriteri; Fig. 4). Large fluctuations coincided (albeit with a time-lag) with seed production, i.e. an increase in seed counts was generally followed by an increase in mouse tracking indices. For example, a seed mast year in 2019 at both Waitutu Coast and Lake Poteriteri was followed by mouse tracking indices of 78% and 86%, respectively, in the first quarter of 2020. The mouse and mustelid indices were also inter-linked. For example, at Lake Poteriteri the mouse index was relatively high in the second half of 2006, prior to commencement of pest control. As the mustelid index increased throughout 2007, the mouse index decreased sharply to zero. After trapping began in 2008, the mustelid index dropped to low levels, and immediately following this the mouse index increased again.

Mean indices of rat abundance ranged from 0% (multiple years at both sites) to 44% (in the fourth quarter of 2009 at Waitutu Coast). This followed a broadly similar pattern to mouse abundance, though less pronounced, with higher rat indices generally coinciding with higher mouse indices. There were periodic increases between 1080 operations (usually up to around 25–30% tracking), however indices were always low following 1080 operations.

Mustelid indices were highest prior to commencement of pest control (93% in the last quarter of 2007 at both sites) but, following the onset of trapping in 2008, were reduced to undetectable levels by the first quarter of 2009. As with rats, indices were always low immediately following 1080 operations, with some increases between operations (usually 33% tracking or less, except at Lake Poteriteri in the fourth quarter of 2012, when it reached 53% tracking).

Comparisons were made between our results and those from a non-treatment forest site near Lake Hauroko, located c. 17 km to the north-east of the Lake Poteriteri site and monitored intermittently from 2016 onwards. This revealed that the non-treatment site generally had higher mustelid tracking rates (up to 19%), but lower rat and mouse tracking rates (0–18 % and 0–100 % respectively), than our treatment sites (C. Bishop, DOC Invercargill, unpubl. data).

Bird populations

Thirty-four bird taxa were recorded in counts during the study period. All were recorded at Lake Poteriteri, and 28 were recorded at Waitutu Coast. Species with fewer than 40 detections at one or both sites were excluded from analyses

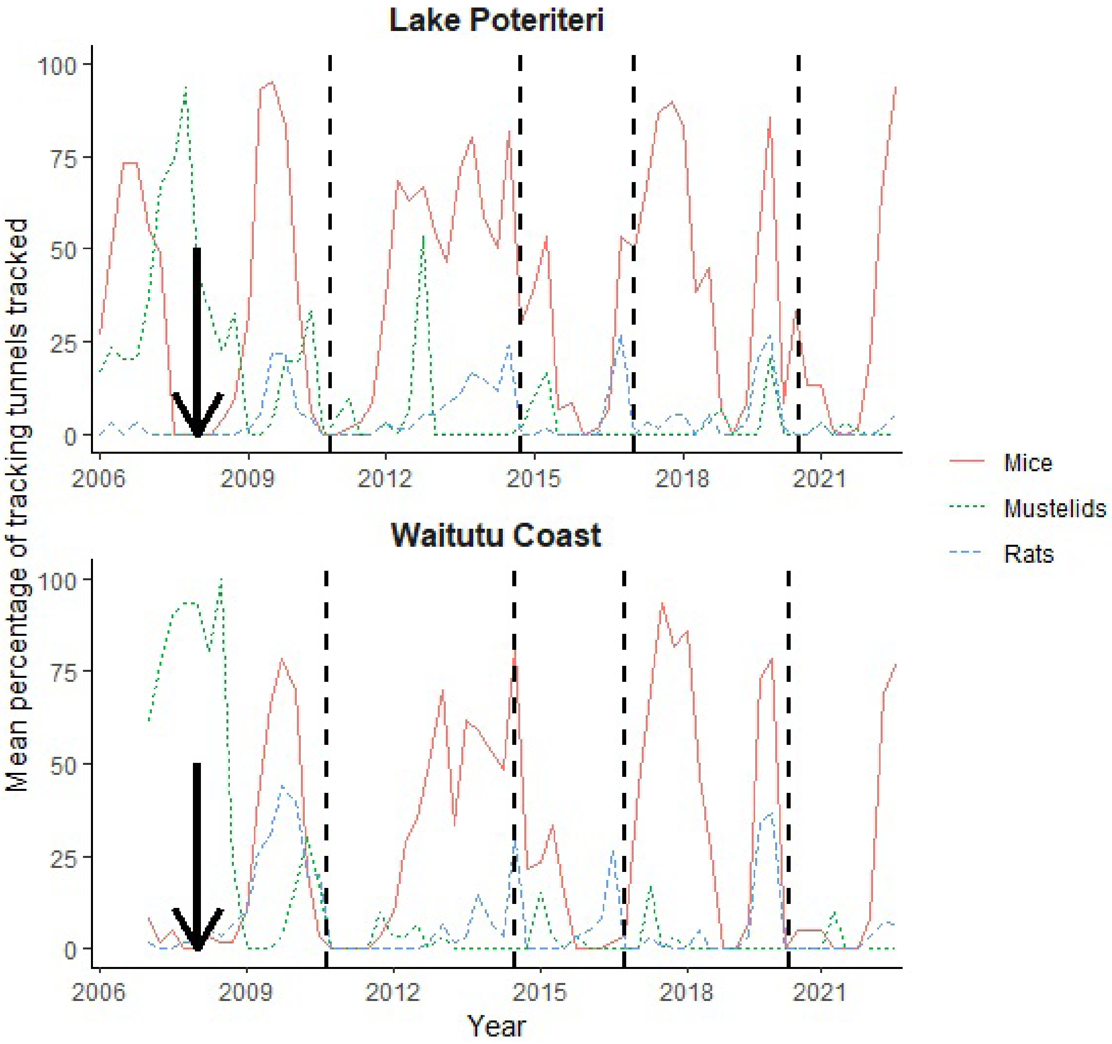

Figure 4. Mean indices of relative abundance for mice, rats, and mustelids, at Lake Poteriteri and Waitutu Coast. The black arrow indicates when predator trapping began, and the dashed vertical lines show the timing of 1080 treatments. Note: there are no data for Waitutu Coast in 2006 because tracking tunnels were not established until 2007.

(yellowhead | mohua, morepork | ruru (*Ninox novaeseelandiae*), goldfinch | kōurarini (*Carduelis carduelis*), European greenfinch (*Chloris chloris*), swamp harrier | kāhu (*Circus approximans*), black shag | māpunga (*Phalacrocorax carbo novaehollandiae*), house sparrow | tiu (*Parus domesticus*), New Zealand kingfisher | kotare (*Todiramphus sanctus vagans*), paradise shelduck | pūtangitangi (*Tadorna variegata*), southern black-backed gull | karoro (*Larus dominicanus*), starling (*Sturnus vulgaris*), Canada goose | kuihi (*Branta canadensis*), shining cuckoo (*Chrysococcyx lucidus*), and yellowhammer | hurukōwhai (*Emberiza citronella*)). Data for the remaining 20 species (Table 1) were analysed further.

Some species were recorded in broadly similar numbers at both sites, for example silvereye | tauhou (Lake Poteriteri = 1399, Waitutu Coast = 1441). However, for many species there was a considerable difference in the total number of birds counted between sites. In these cases, numbers were usually higher at Lake Poteriteri, the exceptions being bellbird | korimako (Lake Poteriteri = 7672, Waitutu Coast = 13 456) and tūī (Lake Poteriteri = 2730, Waitutu Coast = 5190).

Population trends derived from modelled five-minute bird count data varied considerably between species (see Fig. 5 for an overview and Fig. 6 for individual species' temporal trends). Whilst some showed a sharp increase in relative abundance during the study period, others apparently declined or fluctuated but remained stable overall. For many species, the population trend type (positive, negative, or neutral) was the same at both sites (e.g. if there was a decline at Waitutu Coast, there was also a decline at Lake Poteriteri). Exceptions to this general relationship were grey warbler | riroriro (*Gerygone igata*), long-tailed cuckoo | koekoeā (*Eudynamys taitensis*), common redpoll (*Acanthis flammea*), Eurasian blackbird | manu pango (*Turdus merula*), New Zealand fantail | pīwakawaka (*Rhipidura fuliginosa*), and silvereye | tauhou (*Zosterops lateralis*). With the exception of long-tailed cuckoo | koekoeā, the direction of trend was the same at both sites, but one of the trends was classed as neutral due to the credible interval bisecting zero. For New Zealand fantail | pīwakawaka and silvereye | tauhou, the means were very similar and the credible intervals only just bisected zero, suggesting that there was little difference in trend between the two sites.

Five species (all indigenous) had a positive trend at one or both sites: New Zealand falcon | kārearea, South Island robin | toutouwai, tūī, kākā, and New Zealand fantail | pīwakawaka.

Table 1. Total species detections between 2006 and 2022 at each site (LP = Lake Poteriteri, WC = Waitutu Coast), with level of endemism (family, genus, species) and cavity nester (Y/N). Grey shading indicates introduced species.

Common name	**Endemism level**	**Cavity nester**	**Detections**	
			LP	**WC**
Grey warbler | riroriro *Gerygone igata*	Species	N	10673	8685
Tomtit | miromiro *Petroica macrocephala*	Species	N	9007	8828
Bellbird | korimako *Anthornis melanura*	Genus	N	7672	13456
Chaffinch | pahrini *Fringilla coelebs*	-	N	6236	3466
Kākā *Nestor meridionalis*	Family	Y	4440	3481
South Island robin | toutouwai *Petroica australis*	Species	N	3034	1011
Rifleman | tītitipounamu *Acanthisitta chloris*	Family	Y	2890	785
Common redpoll *Acanthis flammea*	-	N	2753	1336
Tūī *Prosthemadera novaeseelandiae*	Genus	N	2730	5190
Eurasian blackbird | manu pango *Turdus merula*	-	N	1908	767
Brown creeper | pipipi *Mohoua novaeseelandiae*	Family	N	1870	1171
Parakeet | kākāriki *Cyanoramphus* spp.	Species	Y	1811	1382
New Zealand fantail | pīwakawaka *Rhipidura fuliginosa*	Species	N	1810	1284
Silvereye | tauhou *Zosterops lateralis*	-	N	1399	1441
Long-tailed cuckoo | koekoeā *Eudynamys taitensis*	Species	N	912	388
New Zealand pigeon | kererū *Hemiphaga novaeseelandiae*	Genus	N	717	190
Song thrush | manu-kai-hua-rakau *Turdus philomelos*	-	N	265	60
Dunnock *Prunella modularis*	-	N	108	123
New Zealand falcon | kārearea *Falco novaeseelandiae*	Species	N	45	42
Kea *Nestor notabilis*	Family	N	44	55

Six species (three native, three introduced) had a negative trend. Grey warbler | riroriro and common redpoll only declined at Lake Poteriteri, long-tailed cuckoo | koekoeā, silvereye | tauhou and Eurasian blackbird | manu pango only declined at Waitutu Coast, and dunnock declined at both sites. The remaining nine species (seven indigenous, two introduced) showed a neutral trend at both sites (Table 1, Fig. 6).

For each species the relative abundance across each site was not uniform. In other words, birds were more abundant at some parts of the site than others (Fig. 7). The distribution of abundance was different for each species, for example New Zealand fantail | pīwakawaka was most abundant in the far south-west of both sites, whereas kākā was most abundant in the central southern and far eastern regions of Lake Poteriteri and the central area of Waitutu Coast. The pattern of relative abundance for each species was assumed to be constant with time, however the relative abundance did change for some species between time periods. For example, at Lake Poteriteri in 2009 grey warbler | riroriro was most abundant in the central areas, but by 2022 relative abundance had decreased overall. The trend was shown explicitly by the mean abundance per year (Fig. 6), which showed an overall downward trend in relative abundance for grey warbler | riroriro at Lake Poteriteri throughout the study period.

The non-uniform pattern of abundance was more pronounced for some species than others. For example, tomtit | miromiro was common throughout both sites, with slightly higher abundance in the western areas of Waitutu Coast. South Island robin | toutouwai, however, was of low abundance or absent in parts of both sites, yet of relatively high abundance in central-southwestern Lake Poteriteri in 2022.

Discussion

Seed-rain and mammalian predator management

There were several high seed-rain years during the study (in 2014, 2016, and 2019), which indicated either full or partial masting for beech and podocarp trees in those years. Beech seed counts were highest at Lake Poteriteri and podocarp seed counts were highest at Waitutu, which reflects the different forest composition of the two sites (E. Wright, DOC Christchurch, unpubl. data).

The abundance of seeds in mast years resulted in irruptions of the mouse population, as described by others (King 1983; O'Donnell & Phillipson 1996; Walker et al. 2019a), with knock-on effects on the rat and mustelid populations, as described by Elliott and Kemp (2016). Although the increased quantity of seeds may have provided additional food for seed-eating birds, without management of introduced mammals the increase in rats and mustelids would have probably offset any potential benefits, either via competition for food or from predation (Innes et al. 2010). Indices of mammal abundance were at their lowest following 1080 operations, with some periods of

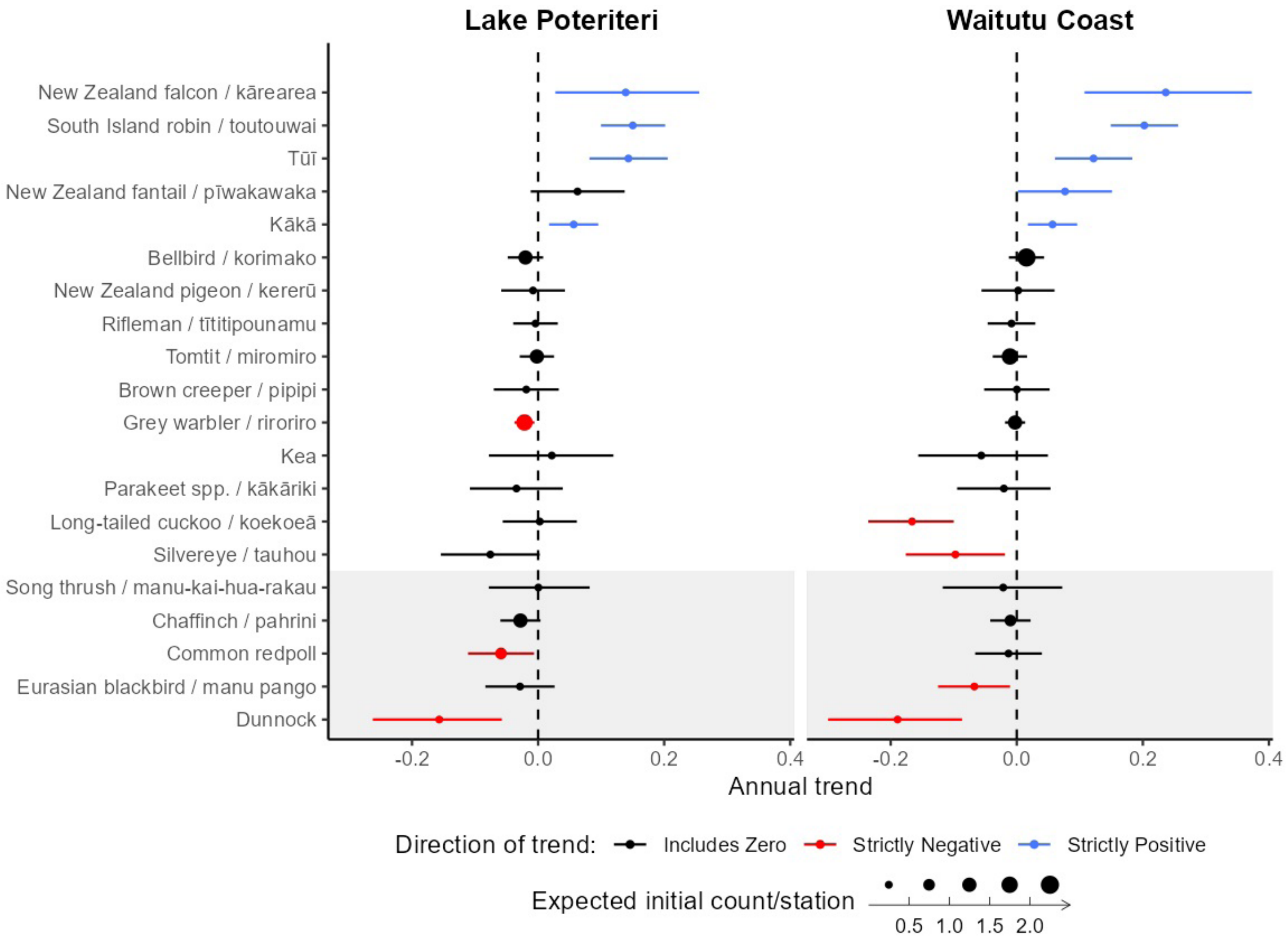

Figure 5. Mean annual population trends of 20 species of bird at Lake Poteriteri and Waitutu Coast, with associated 95% credible intervals. Point colour indicates direction of trend and point size indicates the model-estimated expected count at a single site when monitoring began in 2006 (i.e. indicating how commonly the species was likely to be detected). The grey background shading identifies those that are introduced species.

higher indices between operations. This suggests that trapping alone would not be sufficient to keep the mammal populations suppressed, and that additional periodic 1080 operations are necessary for effective sustained mammalian pest control at these sites. Rat and mouse indices were generally higher at our treatment sites than at non-treatment sites. Griffiths and Barron (2016) also noted this effect, following large-scale pest control in the Tararua Forest Park. Possible explanations include immigration from outside the treatment area, or a meso-predator release effect due to reduced stoat densities (Griffiths & Barron 2016).

Bird population trends

Several species had higher relative abundances and birds were more abundant overall at the Lake Poteriteri site. Also, some species did not display the same population trend at both sites (grey warbler | riroriro, long-tailed cuckoo | koekoeā, common redpoll, and Eurasian blackbird | manu pango). The two sites had the same management regime, which suggests that there are other differences between them. These could include, for example, uneven increases in indigenous species such as South Island robin | toutouwai between sites (and therefore uneven inter-specific competition between these and shallow endemics—those that are endemic to species level—and introduced species; e.g. Miskelly et al. 2021), or differences in pest abundance due to the forest type or other site characteristics. The latter has been explored by Walker et al. (2019b), who noted patterns of decline in bird populations consistent with higher levels of predation by introduced mammals (presumably due to higher predator densities) at warmer sites. Potential differences between our study sites include forest composition and resulting differences in timing of mast seed events, exposure (the Waitutu Coast site is almost immediately adjacent to the southern Fiordland coast, and therefore likely to be more exposed than the Lake Poteriteri site, which could result in higher rates of bird mortality; e.g. Dilks 1999, Greene et al. 2013), water table (Lake Poteriteri has a higher water table than Waitutu Coast and consequently has areas that are regularly flooded or swampy), and topography (Lake Poteriteri is mostly flat, whereas Waitutu Coast has several large gullies running through it). A comparison of site differences is beyond the scope of this study, however it may be worthy of further investigation and highlights the inherently variable nature of forests within the wider landscape and the importance of careful interpretation of analysis from treatment/non-treatment studies. It is worth noting that New Zealand

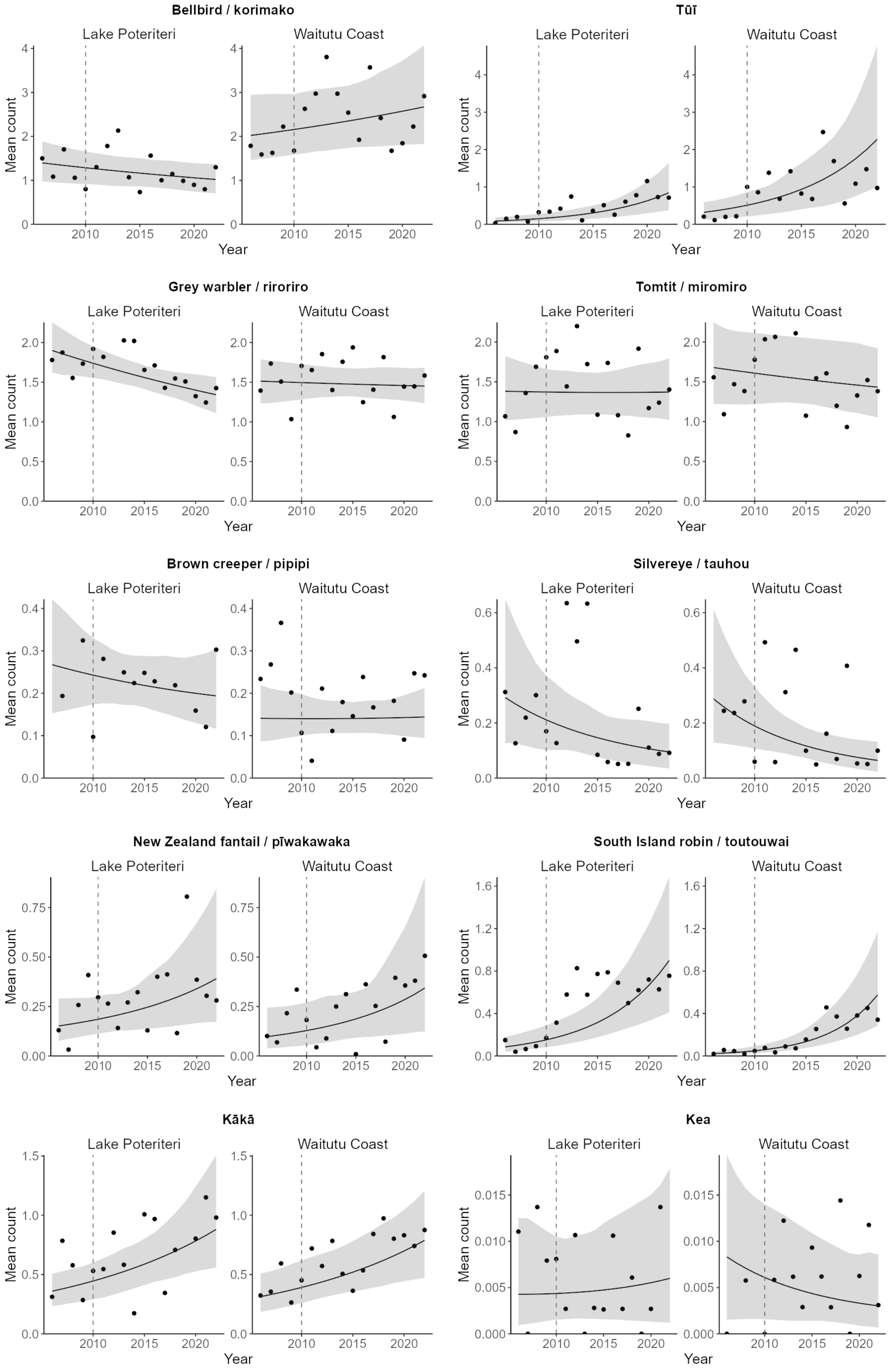

Figure 6a. Temporal trends for 10 / 20 bird species at Lake Poteriteri and Waitutu Coast, between 2006 and 2022. The solid line is the expected count for that time, and the shaded bounds represent a 95% credible interval. The vertical dotted line indicates timing of the first aerial 1080 operation. For the number of detections for each species, refer to Table 1.

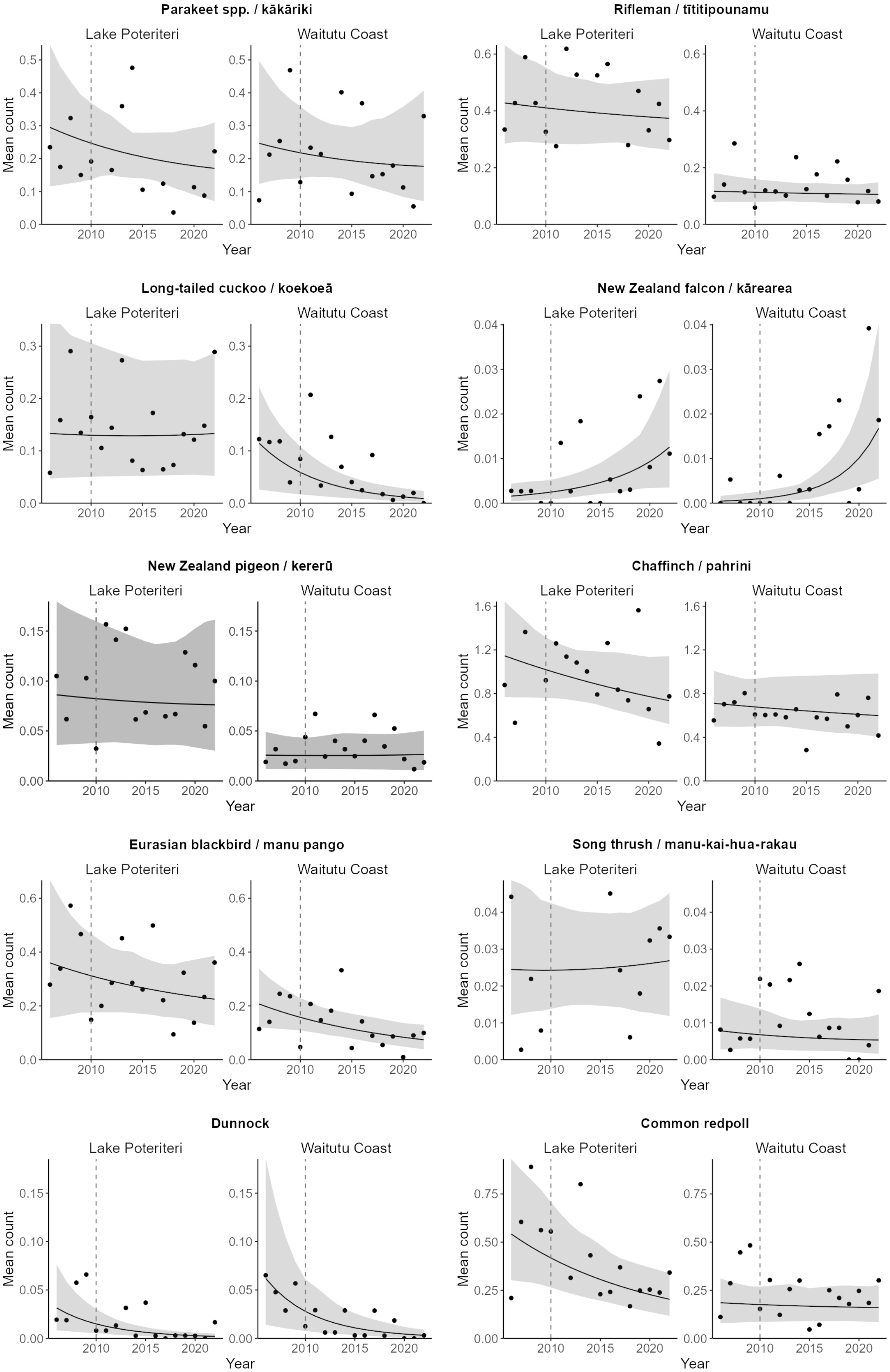

Figure 6b. Temporal trends for 10 / 20 bird species at Lake Poteriteri and Waitutu Coast, between 2006 and 2022. The solid line is the expected count for that time, and the shaded bounds represent a 95% credible interval. The vertical dotted line indicates timing of the first aerial 1080 operation. For the number of detections for each species, refer to Table 1.

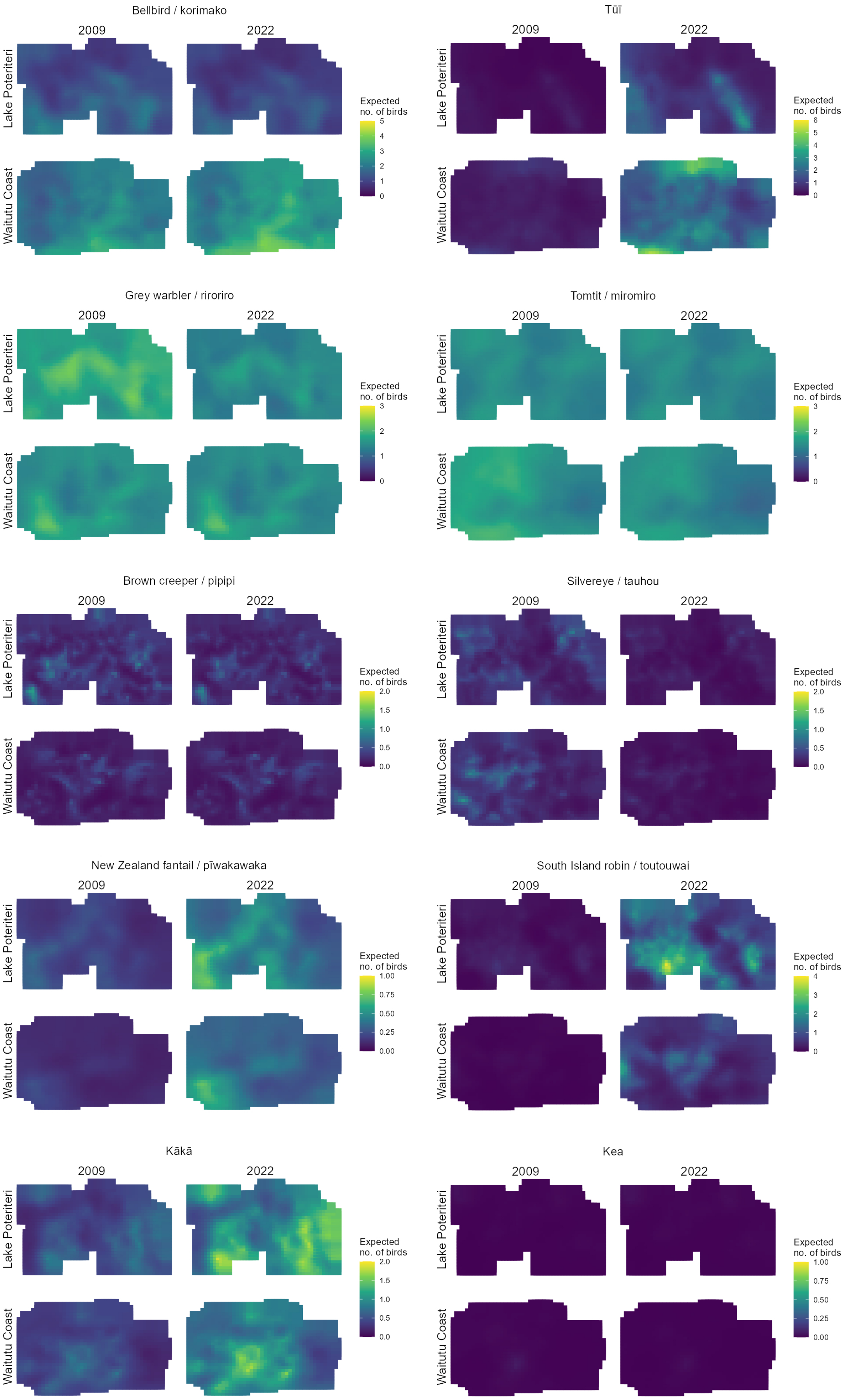

Figure 7a. Spatial variation in abundance (modelled) for 10 / 20 bird species at Lake Poteriteri and Waitutu Coast, before and after 1080 treatment (2009 and 2022 respectively).

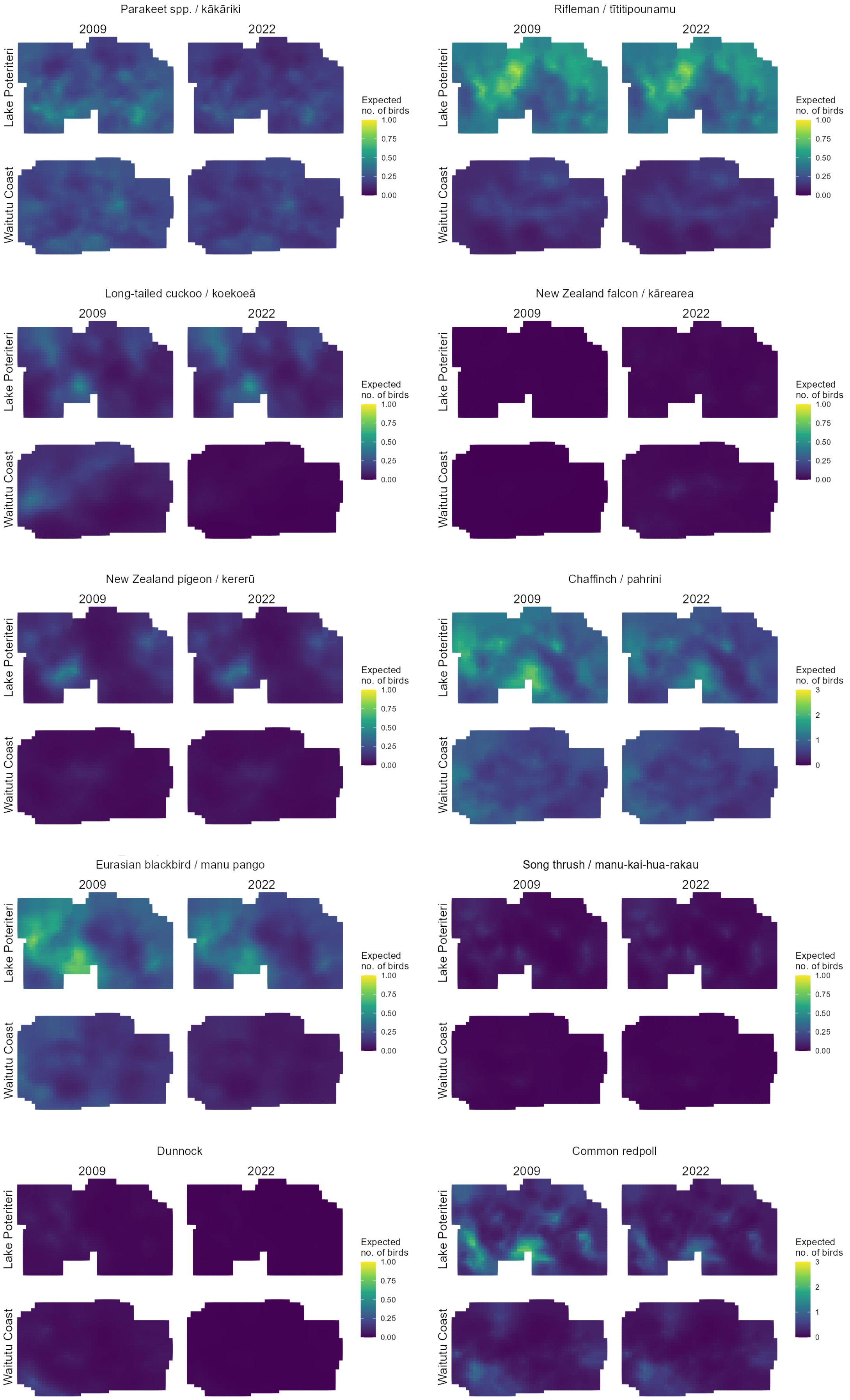

Figure 7b. Spatial variation in abundance (modelled) for 10 / 20 bird species at Lake Poteriteri and Waitutu Coast, before and after 1080 treatment (2009 and 2022 respectively).

fantail | pīwakawaka and silvereye | tauhou also had different trends at each site, however in both cases the credible intervals at Lake Poteriteri only just bisected zero, classifying the trend as neutral. It may be that given additional years of monitoring, the data will show a definite positive or negative trend at this site for these species.

For several species, there was a positive trend in relative abundance at one or both sites (New Zealand fantail | pīwakawaka, New Zealand falcon | kārearea, South Island robin | toutouwai, tūī, and kākā). According to Fea et al. (2020) and Walker et al. (2021), deeper endemics (taxa that are endemic to family or genus level) that are cavity nesters and have relatively large body size are more vulnerable to predation from introduced mammals than birds without these traits and therefore are likely to benefit more from management of such predators. This could explain the increasing populations of kākā (being endemic to family level, large-bodied, and a cavity nester), and to a lesser extent tūī (which is endemic to genus level and has a medium body size). Both these species have been reported to respond positively to pest management in other parts of New Zealand (Fea et al. 2020; Greene et al. 2023; Malham & Elliott 2023). However, the remaining three species with positive population trends are all shallow endemics (species level) and non-cavity nesters. Nevertheless, Seaton et al. (2009) reported that a population of New Zealand falcon | kārearea in pine plantation in the central North Island increased during a period of 1080 pest control due to decreased predation from introduced mammals and an increase in prey, which consisted mainly of small birds. New Zealand fantail | pīwakawaka has also been reported to respond positively to control of mammalian predators by O'Donnell and Hoare (2012) in their 12-year study at the Landsborough Valley. South Island robin | toutouwai has responded positively to pest management in other studies, for example Bell et al. (2021) found that pest control using 1080 at a site in Marlborough Sounds had a large effect on robin nest success through reduction of rat predation. It is also possible that this species is vulnerable to predation not only whilst nesting, but due to its habit of foraging on the ground (Heather & Robertson 2015), and therefore predator suppression could reduce predation whilst foraging. This would be contrary to the findings of Schlesselmann et al. (2024), however, who report that for a range of New Zealand forest birds, predator suppression improves nest survival rates rather than adult survival.

Six species declined within at least one of the study sites: three indigenous (grey warbler | riroriro, long-tailed cuckoo | koekoeā, and silvereye | tauhou) and three introduced (common redpoll, Eurasian blackbird | manu pango, and dunnock). In a 30-year study of bird populations at Nelson Lakes, Elliott et al. (2010) showed that several common species (including grey warbler | riroriro) had significantly declined during their study period. This was attributed to ongoing impacts of rat and stoat predation, an increase in possum abundance, and the introduction of the common wasp (*Vespula vulgaris*). This demonstrated that common and widespread birds, not just rarities, may be vulnerable to these pressures. Several studies have also shown that different bird species populations benefit to varying extents from pest management, and some may even decline. In their meta-analysis of population-level responses of forest birds to mammal control, Fea et al. (2020) found that shallow- and non-endemic species with small body size (which included grey warbler | riroriro and silvereye | tauhou) generally had slight negative or neutral responses to mammal control. They proposed that more recently arrived species such as these are likely to be more resilient in the presence of mammalian predators, since they will have retained some of the behaviours required to avoid predation. They would therefore not benefit from suppression of predators as much as predator-naïve endemics, which are more vulnerable. As populations of deep endemics increase, small insectivores such as grey warbler | riroriro or insect/fruit/nectar feeders like silvereye | tauhou may experience competition from larger birds that also include insects, fruit, or nectar in their diet (e.g. bellbird | korimako or tūī). According to Heather and Robertson (2015) silvereye | tauhou readily eats nectar but is often excluded by bellbird | korimako or tūī. Miskelly et al. (2021) also reported declines in several native and introduced species (tomtit | miromiro, grey warbler | riroriro, silvereye | tauhou, dunnock, and chaffinch | pahrini) on a series of Fiordland islands, surveyed between 1974 and 1986 and then again between 2016 and 2019. The most likely explanation for this was thought to be inter-specific competition in the form of direct aggression from South Island robin | toutouwai, which had increased in abundance following pest management.

A decline in the long-tailed cuckoo | koekoeā population was observed at Waitutu Coast, but not at Lake Poteriteri. Declines have been observed for this species in other parts of New Zealand, especially at the Eglinton and Landsborough valleys (Robertson et al. 2021). A decline could be linked to this species' migratory nature. The long-tailed cuckoo | koekoeā over-winters on tropical Pacific Islands and therefore will be vulnerable to any major habitat changes such as forest clearance (Heather & Robertson 2015), and to the increasing frequency of significant environmental perturbations (e.g. cyclones). However, if either of these drivers were responsible for the decline, we would expect the decline to be observed at both of our study sites. Another explanation would be that populations of the long-tailed cuckoo | koekoeā's preferred host species, yellowhead | mohua, have declined in the Waitutu area. According to Wildland Consultants (2008), the Waitutu yellowhead | mohua population declined fourfold between 1984 and 2000. Sightings have become increasingly rare during the study period (TG, pers. obs.), to the point where it is probably now locally extinct. However, brown creeper | pipipi, which is also parasitised by long-tailed cuckoo | koekoeā (Higgins 1999), has not declined significantly during the study period, and numbers counted at Lake Poteriteri and Waitutu Coast are not dissimilar. Therefore, differences in host species populations also cannot easily explain the differing trends for long-tailed cuckoo | koekoeā in Lake Poteriteri and Waitutu Coast.

The remaining species (i.e. rifleman | tītitipounamu, New Zealand pigeon | kererū, tomtit | miromiro, bellbird | korimako, brown creeper | pipipi, kea, parakeet | kākāriki, chaffinch | pahrini, and song thrush | manu-kai-hua-rakau) did not increase or decrease in overall relative abundance throughout the study period. It could be that these species were entirely unaffected by pest management (resulting in no change in trend), were positively affected (enough to stop a decline but not enough to result in an increase) or were negatively affected (turning a positive trend into a neutral one).

We would expect the parakeet | kākāriki population to increase following reduction in predation pressure, since this species is a cavity nester and vulnerable to predation (O'Donnell 1996), however our results indicate there has been an overall neutral trend (albeit with large annual fluctuations). This could be explained by productivity and mortality being closely related to mast seeding. The parakeets | kākāriki in a study by Elliott et al. (1996) fed extensively on beech seed and consequently the population increased dramatically, only to decline sharply the following autumn, probably due to depletion of seed and also increased predation by stoats. In their study, Elliott et al. (1996) found that although trapping reduced stoat population density, enough stoats remained to prey on accessible parakeet | kākāriki nests. It seems likely that this pattern of rapid increase followed by equally rapid decline mediated by food supply (a classic r-selection response; Rafferty 2025) was repeated in our study, and that the trapping and application of 1080 was insufficient to reduce rat and stoat numbers to produce a sustained positive trend for the parakeet | kākāriki population. In particular, the periodic increases in rat densities in between 1080 operations may have limited the recovery of the parakeet | kākāriki population, due to this species' probable vulnerability to rat predation (Elliott et al. 1996; O'Donnell 1996; Kearvell 2002). A similar rationale might also help to partly explain the neutral trend in the population of rifleman | tītitipounamu, which is also a cavity nester. However, this is not consistent with the positive response exhibited by kākā— the remaining cavity nester— suggesting that here there may be other factors involved, such as differences in the vulnerability of kākā to stoats, rats, or possums, compared to the smaller cavity nesters.

The population trends observed in our study differed somewhat from those in a similar study at Landsborough Valley, South Westland, New Zealand (O'Donnell & Hoare 2012). Although the results indicated that some species had the same trends, most species did not, despite the Landsborough Valley site having a similar pest management regime to Waitutu Forest (continuous trapping to control mustelids and pulsed aerial application of 1080 to control rats and possums). Out of the nine species (mostly indigenous) at Landsborough Valley that had significant population increases, only two had a significant increase at Waitutu Coast | Lake Poteriteri (New Zealand fantail | pīwakawaka and tūī). Similarly, only two out of the four species that declined at Landsborough also declined in our study (silvereye | tauhou and Eurasian blackbird | manu pango). Interestingly, grey warbler | riroriro, which declined in our study, showed an increase at Landsborough Valley. There are many reasons why this might be, including differences in forest composition (for example the Landsborough Valley site canopy consisted largely of silver beech), location (Landsborough Valley is approximately 300 km to the north-east of Waitutu Forest) or presence/abundance of predators. Nevertheless, it serves as a reminder that population trends observed in one area may not be consistent with those at other sites, making assumptions or generalisations risky (Lindenmeyer et al. 2022). In addition, we cannot rely on national monitoring to inform us of local trends. A review of biodiversity metrics at different geographical scales by Leroy et al. (2023) demonstrated that a national decline may not be evident at a local scale, or vice versa. As such, a good latitudinal spread of long-term study sites would be beneficial in determining regional variation in population trends.

At Waitutu Coast and Lake Poteriteri, birds were not uniformly abundant throughout each site, but rather appeared to prefer some areas to others. This is unlikely to reflect differences in predation pressure since, if this were the case, we would expect the patterns of bird abundance to be similar for all species, which they were not. It is likely that each species' distribution is influenced by site characteristics that are beneficial. These could include resources such as food and nesting sites, which would in turn be influenced by the vegetation composition and structure (Ferger et al. 2014), or it could include physical site characteristics, such as aspect or slope. Alternatively, it may be a result of competitive exclusion. There is some evidence to support this in our study, using nectar feeders as an example. At Lake Poteriteri, bellbird | korimako and tūī showed a similar distributional pattern, being generally most abundant in the southern parts of the site. Silvereye | tauhou, however, was more abundant in the central, north-western, and north-eastern parts of the site. The distributions of silvereye | tauhou and the two larger honeyeaters were not mutually exclusive, however clear differences were apparent.

The non-uniform patterns of abundance were more pronounced for some species than others. For example, the relative abundance of tomtit | miromiro was more-or-less even across both sites, however several other species (including bellbird | korimako, tūī, New Zealand fantail | pīwakawaka, kākā, and rifleman | tītitipounamu) had large differences in relative abundance in different parts of each site. These latter species were perhaps more specialist in their habitat requirements, and therefore subtle changes (such as differences in food availability or suitable nesting sites) may have excluded them or made them considerably less abundant in some areas.

Study limitations

A significant limitation of this study was the absence of a non-treatment site (or sites). Although the Lake Poteriteri site was originally proposed to serve this purpose, operational decisions were made that ultimately meant that it was included in the pest management area following apparent area-wide population declines in several bird species and other wildlife. Despite the obvious benefits of a formal before-after-control-impact (BACI) design (i.e. improved inference and assignment of causality; Lindenmayer et al. 2022), there are few examples of such studies in New Zealand pest control. In their review of 32 studies, Fea et al. (2020) discovered that only three included a non-treatment site, and only one of these also included before and after monitoring. Reasons for this were not discussed but are probably a function of the cost of establishing replicate sites at scale, likely habitat and bird community heterogeneity between sites, and the variable application of management methods and the frequency with which they occur. Future monitoring efforts of this scale should, ideally, seek to secure comparable non-treatment site(s) to improve inference. Observational (quasi-experimental) study designs that rely on extended time frames to reveal population trends, particularly when commenced prior to pest management (the before and after component of BACI designs), also have merit providing the limitations of such designs are understood (i.e. reduced potential for inference and assignment of causality) and they have temporal consistency in field protocols (Lindenmayer et al. 2022). Being able to commence a monitoring programme well in advance of intensive management efforts, such as with this study, is also relatively rare.

Methods that produce indices of relative abundance, such as five-minute bird counts, have received much criticism concerning their inability to account for detection probability (Farnsworth et al. 2002; MacKenzie & Kendall 2002; Rosenstock et al. 2002; Buckland 2006). Detectability of birds is influenced by a number of factors including time of year, time of day, weather conditions, presence of an observer, habitat type, and species density (Keast 1994; Gutzwiller et al. 1994; McShea & Rappole 1997). Tracking tunnel indices for relative abundance of mammalian pests are similarly limited by changes in detectability, which varies with changes in behaviour, home-range size, sex, age, season, and density (Vattaito et al. 2023). For example, Christie et al. (2015) found that increased rainfall meant a higher probability of detecting ship rats in tracking tunnels, and according to Gillies et al. (2017) the 3-night tracking tunnel method did not reliably detect stoats when they were present at very low abundances. Therefore, despite our efforts to standardise the surveys, we cannot be certain that species detectability is comparable through time.

For many bird species at Waitutu Forest, the study period (17 years total, 12 since the first 1080 operation) may be of sufficient length to determine whether species have responded to pest management. In a study by Van Vianen et al. (2018), several indigenous bird species showed a positive reaction to 1080 management within four years of treatment, when compared to a non-treatment site. Binny et al. (2021) found that after approximately seven years of sustained control, competition or other factors were strong enough to cause declines for introduced birds. However, for populations of some species (particularly those that are rare or episodic breeders) it could take many additional years before a trend becomes apparent. This will depend partly on the nature of the species (e.g. fecundity, generation time, dispersal abilities) but also on the site characteristics. Many ecosystems require long-term (i.e. multi-decadal) monitoring of bird populations because changes are inherently slow, count data are often noisy or highly variable, and environmental perturbations such as droughts and floods may be infrequent. Long-term monitoring programmes are essential for our understanding of ecosystems and population dynamics. However, despite their obvious benefits, they remain uncommon. There are many reasons for this, including a reluctance for organisations to commit to funding long-duration programmes, with a view that they divert funds from other important activities (McGlone et al. 2020; Wright et al. 2020). Funding streams are vulnerable to changes in government policy and organisational priorities, resulting in tensions between conservation action and monitoring. Even so, the cost of monitoring is generally small compared to the cost of policy implementation (especially in the absence of data), or it can be easily offset by gains in management effectiveness (Lovett et al. 2007). It is essential that the monitoring continues for a sufficient length of time to allow for effects of management on target species populations to become apparent, and to allow for the natural dynamics inherent in ecosystems, communities, and populations to be revealed (Callahan 1984; Lindenmayer et al. 2022).

Conclusions

There are a number of temporal and spatial trends that have become apparent from this study. Several species appear to have benefitted from pest management (New Zealand fantail | pīwakawaka, South Island robin | toutouwai, kākā, tūī, and New Zealand falcon | kārearea), whilst others have remained relatively stable or have declined. The species in decline tended to be those that were either shallowly endemic, non-endemic, or introduced. It is possible that some of these were being out-competed by deeper endemics, who benefitted more from pest management (Miskelly et al. 2021).

Despite its limitations, this study has provided good evidence for the success of the mammalian pest control programme in Waitutu Forest. We therefore strongly recommend that current management continues with associated monitoring (at a minimum), to avoid immediate reversals in trend for the likes of the South Island robin | toutouwai, kākā, and other species. The apparent population declines for some species that are considered common and widespread, such as grey warbler | riroriro, is concerning, and may indicate that the current management regime is not sufficient to control mammalian predators to a low enough level to allow these populations to be maintained in the long term. Alternatively, these species may be experiencing population declines due to increased competition from those species that have benefitted from pest management (Binny et al. 2021).

Many environmental and ecological drivers and specific species responses to them only manifest themselves over long-term (multi-decadal) timescales (e.g. climate change or changing frequency of mast events) and large spatial extents. Continued monitoring will enable us to document responses to environmental change, identify trends that are not yet apparent, determine carrying capacity for those species with currently increasing populations, observe future trends for species currently in decline, inform ecological predictions, and quantify the effectiveness of current and future management regimes. Following on from this study, we may review the management regime and monitoring methods to improve efficiency and effectiveness. For example, it may be desirable to reduce the number of bird count stations surveyed annually and use the cost savings to establish and monitor a non-treatment site.

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Ethics: No ethics approval was required for this study.

Data availability: Data and analysis code are available via Github (https://github.com/paul-vdb/Waitutu-Bird-Response-to-Predator-Management).

Author contributions: TG established and managed the monitoring programme. PvDB and AS performed the analysis. JM wrote the manuscript, with contributions from TG, PvDB and AS.

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Supplementary Material

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

Appendix S1. Analysis methods.

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.