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RESEARCH

Factors limiting kererū (*Hemiphaga novaeseelandiae*) populations across New Zealand

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Abstract: Kererū declined rapidly following European settlement in New Zealand, and they remain at a reduced density. We assessed three sources of information to test the hypothesis that predation by introduced mammals and abundance of food resources are the two major factors determining kererū abundance across New Zealand. First, we reviewed the literature on factors affecting the vital rates of kererū. This analysis showed that predation is the cause of most nest failures and deaths in kererū. Second, we examined data from a major database of bird sanctuary outcomes across New Zealand to evaluate long-term responses of kererū to intensive pest control at local scales. Kererū detections did not always increase following predator control, which suggests that food supply or forest area may be more important limiting factors at some sanctuaries. Third, to understand the factors underlying temporal and spatial kererū distribution patterns at a national scale, we assessed changes and patterns in kererū local occupancy through time using data from the 1969–1979 and 1999–2004 editions of the *Atlas of Bird Distribution in New Zealand*. Specifically, we asked (1) whether there have been declines in kererū occupancy between the two Atlases, and (2) how patterns of kererū occupancy relate to indigenous forest cover, temperature, urbanisation, and forest type (podocarp or beech dominated). Kererū occupancy remained stable across the North Island between the two time periods but declined in the South Island. Across both islands and time periods, kererū occupancy decreased significantly as forest cover decreased, which suggests that forest availability is still a major limiting factor across some parts of New Zealand. Overall, our results support previous studies showing that predation by introduced mammals is the primary limiting factor for kererū in forests, but also highlight the importance of forest area and food supply for kererū recovery.

Keywords: density impact function, distribution, food limitation, habitat loss, nesting success, New Zealand wood pigeon, occupancy, predation

Introduction

Ecologists have long debated the relative importance of top-down (e.g. predators) versus bottom-up (e.g. food) processes in regulating avian populations (Newton 1998). Often, however, the relative importance of these processes is conditional: for example, the introduction of a novel predator may result in top-down processes primarily regulating a population, whereas in other situations habitat degradation may lead to bottom-up processes dominating. Teasing apart which processes dominate across different situations is important for conserving and recovering endangered species.

The kererū (kūkupa; New Zealand wood pigeon; *Hemiphaga novaeseelandiae*) is a large, fruit-eating pigeon endemic to Aotearoa/New Zealand. Their distensible gape and diverse diet allow them to consume the foliage and fruit of many plant species, and they are important dispersers of New Zealand's six largest seeded plant species (McEwen 1978; Kelly et al. 2010). Kererū are a special bird for many New Zealanders, but especially Māori, who consider the species a taonga (treasure) and have complex cultural relationships with them (Lyver et al. 2008; Timoti et al. 2017). Therefore, kererū are both an ecological and a cultural keystone species within Aotearoa.

Kererū used to be abundant across New Zealand, but the population declined rapidly following European settlement due to habitat loss, mammalian predation, and hunting (Clout et al. 1995). Anecdotal reports suggest that their populations stabilised or recovered in some areas in the late 20th century (Mander et al. 1998), but studies in Northland and Marlborough reported ongoing declines (Pierce et al. 1993; Carpenter et al. 2017). Currently, the International Union for the Conservation of Nature lists them as 'near threatened', with a population that is suspected to be increasing. The Department of Conservation

(DOC) lists them as not threatened but conservation dependent, with an increasing population (Robertson et al. 2017), although it is unclear what data were used to derive this assessment. Results from the New Zealand Garden Bird Survey (a large-scale citizen science project which collects annual data on bird detections from people's gardens) and the Great Kererū Count (a large-scale citizen science project which collects annual data on kererū specifically) suggest that kererū detections increased significantly over recent years (Brandt et al. 2020; Hartley 2020), but these data are spatially biased towards urban environments. Therefore, little is known about recent trends in kererū distribution and abundance on a national scale.

Several factors that drove initial declines in kererū populations are still present and could be having an ongoing impact on the species. Innes et al. (2010) state that predation by introduced mammals remains the primary cause of decline or limitation in New Zealand forest birds, including kererū, at a national level in large, intact forests. Kererū can suffer high levels of nest predation by introduced mammals such as ship rats (*Rattus rattus*), brushtail possums (*Trichosurus vulpecula*), and stoats (*Mustela erminea*) (e.g. Clout et al. 1995; Clout et al. 1995; Innes et al. 2004; Schotborgh 2005). Understanding the relationship between the density of these pests and the impact they have on kererū (density-impact functions, or DIFs) would give valuable insights into the vulnerability of kererū to introduced mammals, and the level of pest management required to effectively protect kererū (Norbury et al. 2015). Innes et al. (2004) has suggested that suppressing rats to tracking rates (the percentage of inked cards that have tracked a rat) below 5% and possums to a residual trap catch index (RTCI; the percentage of trap-nights in which a possum is captured) below 5% is required for managers wishing to boost kererū nesting success to maximum levels. However, no studies have examined whether the relationship between pest abundances and kererū densities is linear or non-linear (e.g. whether benefits only accrue with very low pest numbers; Norbury et al. 2015). In addition, several studies have shown increased kererū nesting success when introduced mammals are intensively controlled (Clout et al. 1995; Innes et al. 2004), but very few have examined long-term responses of kererū populations to intensive pest control (but see Fea et al. 2020; Binny et al. 2020).

Kererū may also be particularly susceptible to the effects of food limitation because their breeding efforts are highly variable and appear to be correlated with food supply (Clout et al. 1995; Powlesland et al. 2003), with food limitation reducing breeding attempts. Insufficient food supply could also increase mortality of both adults and fledglings directly through starvation, and indirectly by increasing predation risk (e.g. hungry birds are less attentive at nests; Chalfoun & Martin 2007), and higher susceptibility to parasites (e.g. Knutie 2020) or disease (e.g. Hoi-Leitner et al. 2001). Introduced mammals interact with food supply because several introduced mammals are omnivores (e.g. possums and rats), which both kill kererū and consume kererū foods. Thus, disentangling the primary drivers of decline can be difficult (Innes et al. 2010). Food limitation also increases with habitat loss and forest degradation, as deforestation and browsing by pest mammals both reduce food supply for kererū.

Here we test whether predation and food resources are the two key factors that combine to shape kererū populations in the forests, production landscapes, and urban areas of New Zealand. We assess three sources of information. First, we review the literature on factors affecting the vital rates (nesting success and adult mortality) of kererū to give insights into possible agents of decline or limitation. Second, we examine a major database of bird abundance within sanctuaries across New Zealand (Binny et al. 2020; data from 1996 to 2016) to evaluate long-term responses of kererū to intensive pest control at local scales and calculate pest density-impact functions. Third, to understand the factors underlying temporal and spatial kererū distribution patterns at a national scale, we assess changes and patterns in kererū local occupancy through time using data from the 1969–1979 and 1999–2004 editions of the Atlas of Bird Distribution in New Zealand (Bull et al. 1985; Robertson et al. 2007). Specifically, we ask (1) whether there have been declines in kererū occupancy between the 1970s and 2000s across New Zealand, and (2) how patterns of kererū occupancy relate to indigenous forest cover, temperature, urbanisation, and forest type (podocarp or beech dominated).

Methods

Literature review on factors affecting vital rates

We collated data from published and grey literature on kererū nesting success, causes of nest failure, and adult mortality to identify agents contributing to decline and limitation. Where possible, we extracted from relevant articles the number of nests studied, the number of successful nests, causes of nest failure, mammalian pest control regimes, mammal abundance indices, estimates of adult survival, number of dead adult kererū found, causes of adult mortality, and when and where the study was done.

We first wanted to understand what factors contribute to nest failure based on the reported number of failed nests and reasons for failure. It was not always possible to determine cause of nest loss unless it was captured on camera. However, if authors stated explicitly how many nesting attempts were ended by predation and reported scat or hair or post-mortem identifications on carcasses identifying a predator, we accepted that claim.

Next, we assessed how the control of pest mammals affected kererū nesting success. Using the literature data on nesting success, we categorised four different regimes of mammalian pest control: no control; only ship rats controlled and rat tracking rates < 10%; only possums controlled and RTCI < 12%; and both rats and possums controlled and rat tracking rates and RTCI < 12%. These numbers reflect the relative abundance of rats and possums achieved by the control operations over the kererū breeding season. We used a binomial generalised linear mixed model with the proportion of successful nests (defined as the proportion of nests that produced a fledgling) of the total number of nests monitored as response. We did not attempt to calculate daily survival rates from nest data, because actual length of exposure was not reported in any of the studies (although almost all nests were found by radio tracking individuals, leading to high detectability even early in the incubation). The type of pest mammal control was the only fixed effect, because the total number of studies was low ($n = 20$). We included study ID as a random effect to account for non-independence among repeatedly used study sites (e.g. before–after experimental designs) and site-specific attributes.

Finally, we assessed factors affecting adult kererū survival based on the number of dead kererū found (radio tracked and unmarked) and reasons for death. As for nest failure, one limitation of these data is that the ultimate cause of death might be different from other contributing factors leading to

death. Again, if the reported causes of death were based on post-mortems, we accepted those claims by the authors.

Responses of kererū to intensive pest control, and density impact functions

We used data from a major database of sanctuary outcomes (Binny et al. 2020) to illustrate the long-term responses of kererū populations to intensive pest control. We aggregated these restoration projects into "major control regimes" (ring-fenced ecosanctuaries, peninsula-fenced ecosanctuaries, and unfenced "mainland islands"; Byrom et al. 2016; Innes et al. 2019), which each have characteristic residual pest mammal outcomes. We only used data from sites where kererū had been monitored using 5 min bird counts (5MBC) in order to make results more comparable among sites. We present these data as time-series graphs, with kererū counts in non-treatment areas included where they existed (see Appendix S1 in Supplementary Materials for distances between treatment and non-treatment sites). We also include rat, possum, and stoat indices of abundance when these were monitored.

We also calculated rat, possum, and mustelid DIFs for kererū using data from Boundary Stream Mainland Island, which is an unfenced mainland island in Hawke's Bay, established in 1996. For rats, we plotted mean autumn kererū 5MBC against the mean rat tracking rate, averaged over the spring–summer immediately prior, or autumn if no rodent monitoring was conducted in spring–summer. For possums, we plotted the mean autumn kererū 5MBC against possum RTCI in the same year. The possum RTCI surveys were conducted mainly in winter, with a few in summer or autumn. Hence in most years the possum RTCI value was taken from a survey conducted in the season immediately following the kererū count. For mustelids, we plotted the mean number of kererū per 5 min in autumn against the maximum value of mean mustelid tracking rate (the percentage of inked cards tracked by a mustelid over a three week period) over all surveys conducted in the 12 months prior to the kererū count. We fitted curves to the data by first fitting linear models to kererū counts with a single predictor for tracking rate or RTCI and assessed model fit using R^2 and plotting residuals. Where linear models were a poor fit, we compared three non-linear models: exponential, logarithmic, and power curve. The model with the lowest Akaike Information Criteria (AIC) was selected as the best model, so long as AIC differences were > 2. Best-fit models are reported for DIFs with ship rats and possums. For mustelids we did not fit a curve to the data, as a linear model was a poor fit to the data ($R^2 = 0.085$) and AIC differences were < 2 for the other models.

Occupancy analysis

Data and hypotheses

We used standardised estimates of probability of occupancy for kererū derived by Walker and Monks (2018) from data in two editions of the Atlas of Bird Distribution in New Zealand. Occupancy is the outcome of underlying processes that generates presences or absences of a species in a landscape. It is defined as the proportion of area, patch or sample units that is occupied. Estimates were made for each of 2155 10 × 10 km grid squares (hereafter 'squares') across New Zealand's three main islands, in each of two measurement periods (1969–1979 and 1999–2004). The 2155 squares exclude all locations not sampled in one or both atlases, and all squares with < 25% land, but include alpine squares above regional treelines. Walker and Monks (2018) used a Bayesian model-fitting process to derive estimates of probability of occupancy for kererū in each square

(local occupancy) in each measurement period, and we use 1000 draws from the posterior distributions of these estimates in our analyses.

Binary factor variables were used to represent measurement period and island (North or South, the latter combining the South Island and Rakiura / Stewart Island). Environmental predictors (i.e. percentage indigenous forest cover, hereafter indigenous forest cover) and median mean annual temperature across squares (hereafter temperature) were derived as set out by Walker et al. (2019). To represent density of human settlement, we used relative road density, which was calculated as the length of all roads contained in the Land Information New Zealand 1:250k road centrelines 2011 data set (which is the earliest dataset available; National Topographic Office 2020), divided by land area in the square and transformed by taking the square root. Percentage of indigenous forest cover dominated by (1) podocarp and/or broadleaved trees and (2) beech trees was derived from the classes of forest recognised in the EcoSat forest type classification (Dymond & Shepherd 2004). Classes considered dominated by podocarp and/or broadleaved trees were coastal forest, kauri forest, podocarp forest, podocarp-broadleaved forest, broadleaved forest, and podocarp-broadleaved / beech forest. Classes considered dominated by beech were beech forest, beech / broadleaved forest, and beech / podocarp-broadleaved forest.

We had three hypotheses about the mechanisms driving differences and changes in local occupancy and the consequent relationships we would expect to see in the data:

(1) Kererū occupancy would be highest in forested squares. Although kererū occur in non-forested environments, we expected that they were nevertheless likely to have mainly inhabited forest and forest edges in pre-settlement New Zealand, and that forest loss would compromise occupancy. In the model, percentage indigenous forest cover was assumed to be a proxy for primary forest habitat available to kererū (Innes et al. 2010).

(2) Temperature would have an indirect effect on kererū occupancy by acting as a proxy for predation rates and food supply. Mean annual temperature and forest type are two key predictors of both mammalian pest densities and food availability (Walker et al. 2019). Warmer, podocarp-dominated forests may provide more food resources (fruit, flowers, and foliage) than cold, floristically simpler forests, and therefore may be capable of supporting more kererū, although this has not been tested. However, podocarp-broadleaf forests also generally support higher median densities of brushtail possums and ship rats throughout the year than cooler beech forests (Efford 2000; Forsyth et al. 2018; Walker et al. 2019), which may affect food supply for kererū. Densities of ship rats and possums are low much of the time in cooler, floristically simpler forests dominated by beech (Nothofagaceae species), although ship rats do irrupt to very high densities intermittently following synchronised heavy seeding (masting) (Walker, et al. 2019). If predation is still causing declines in kererū populations and there is abundant indigenous forest, kererū occupancy should be lowest and more stable in cold sites, where food is either the primary limitation or limits population recovery following periodic outbreaks of predators. Conversely, in warmer, forested sites, where food is less limiting and median pest densities are highest, kererū should be decreasing most rapidly over time.

(3) Lastly, we hypothesised that kererū occupancy would be stable or increasing in urban areas due to nutritional supplementation and/or lower abundance of ship rats, possums, and stoats. Urban areas contain a different suite of pests to

forest areas (Morgan et al. 2009) and the resources provided by floristically diverse urban parks and gardens (Baranyovits 2017) might promote kererū fecundity, outweighing the potential negative effects of urbanisation (e.g. an increased risk of collisions with windows and vehicles) on kererū survival.

We fitted a linear mixed effects model to assess the relationships between the local occupancy of kererū and indigenous forest cover, temperature, and road density across the whole of New Zealand.

New Zealand model

To test the above hypotheses, we fitted a model of kererū local occupancy with a full four-way interaction between island, measurement period, indigenous forest cover, and temperature as fixed-effect predictors. We included island (North and South) as a predictor because we believed it would encompass variation in factors likely to affect kererū occupancy (e.g. human hunting, different timing of possum invasions, generally higher median possum and rat densities in the North Island cf. the South Island; Fraser et al. 2004; Forsyth et al. 2018; Walker et al. 2019) that we could not capture otherwise. Local occupancy was logit-transformed to satisfy linear modelling assumptions (Warton & Hui 2011), and indigenous forest cover and temperature predictors were centred and scaled. A basis function (a generalised additive model with a 3 df regression spline smooth) allowed slopes of occupancy on forest cover to be non-linear. Grid square was a random effect to account for spatial non-independence of records from the same square in the different measurement periods. We then added an interacting term for relative road density (also scaled and centred) to represent density of human settlement and compared the AIC of the two sets of 1000 replicate models.

New Zealand forests model

We also modelled local occupancy of kererū within forests only (which we defined as grid squares with > 50% indigenous cover), aiming to identify whether forest composition (specifically, beech-dominated forests and those dominated by podocarp and/or broadleaved trees) had an effect that was independent of mean annual temperature. We tested whether podocarp-broadleaved forest had higher floristic diversity (and therefore presumably more food resources as well as more stable food supplies for kererū; Cardinale et al. 2011; Garcia et al. 2013) than beech forest using plot data counted in the first measurement cycle of the Land Use and Carbon Analysis System program (LUCAS indigenous forests and shrublands; 1246 plots, over the period 2002–2007; see Holdaway et al. 2017 for details of methods), and present these results in the supplementary material. We hypothesised that their requirements for abundant food resources would mean that kererū would be less likely to occupy beech forests but would have declined more rapidly in more-diverse podocarp forest between Atlases due to the higher median predator densities.

To test the hypothesis, we fitted a model of (logit-transformed) kererū occupancy in forested squares (defined as squares with 50 to 100% indigenous cover) on each of the main New Zealand islands with two composite predictor terms. The first term was a four-way interaction of forest type, temperature, measurement period, and island. The second term was included to account for the effect of forest cover, and was a three-way interaction between forest cover, measurement period, and island.

Results

Factors affecting vital rates

Causes of nest failure

We collated reports of 397 kererū nests from 20 studies and 10 sites with differing levels of mammalian pest control across mainland New Zealand (Appendix S2). The causes of nest failure were reported for 194 nests. With or without pest mammal control, nest failure causes, in declining order of importance, were predation of eggs and chicks, then desertion (Fig. 1a). The identity of the predator was determined for almost half (53 of 113) of all depredated nests at managed and unmanaged sites. Most eggs were eaten by either ship rats (50.0%, $n = 42$) or possums (38.1%, $n = 42$), while most chicks were killed by stoats (72.7%, $n = 11$).

Nest success and predation

The proportion of kererū nests that successfully fledged a chick differed depending on what kind of management regime was used (Fig. 1b). Nest success increased significantly compared to no management if pest mammal control was targeting rats ($P = 0.03$; Appendix S3) or rats and possums simultaneously ($P < 0.001$). The proportion of successful nests was not significantly influenced by control of possums alone ($P = 0.16$). It should be noted that data for the rat and possum control treatment derive from only two sites (Whirinaki Forest Park 2001–2002 and Motatau 1998–1999).

Adult survival

Kererū are expected to have a mean longevity of 20–30 years given their large size and slow reproductive rate (one egg per clutch, not breeding every year; Clout et al. 1995; Clout & Robertson 2021). The mean life expectancy estimated from five sites where kererū were radio tracked (Clout et al. 1995; Powlesland et al. 2003; Powlesland et al. 2011; R. Powlesland unpub. data) was much shorter, ranging from 1.55 years at Whirinaki (Powlesland et al. 2003) to 5.4 years at Pelorus Bridge and Taranaki (Clout et al. 1995; R. Powlesland, unpub. data).

Most recorded deaths were attributed to predation, although for most cases the predator could not be identified (Fig. 1c). Stoats and cats were the only mammalian predators that were identified killing adult kererū. In urban areas, mortalities caused by impact injuries were common (Appendix S4; Gill 2006). Small numbers of kererū deaths were attributed to other causes such as disease, starvation, and electrocution (Fig. 1c). Most studies did not record the sex of dead birds, but Gill (2006) noted a sex ratio of 1.7:1 in favour of females in 104 kererū found dead in the wider Auckland region between 1985–2004.

Responses of kererū to intensive pest control, and pest density-impact functions

We were able to use data from 11 sanctuaries to examine the response of kererū to long-term pest control. Two sanctuaries were ring-fenced with complete eradication of rats, stoats, and possums (Fig. 2), two sanctuaries were peninsula-fenced with complete eradication of rats, stoats, and possums (Fig. 3), and the remaining seven sanctuaries were unfenced mainland islands that attempted to continually suppress rats, possums, and stoats to very low levels (Fig. 4). Kererū detections did not always markedly increase in response to pest control or eradication (e.g. Figs 2a, 3a, 4b,d). Only one site appeared to show a steady increase of kererū over time since management began (Tāwharanui; Fig. 3b), with most sites showing an initial
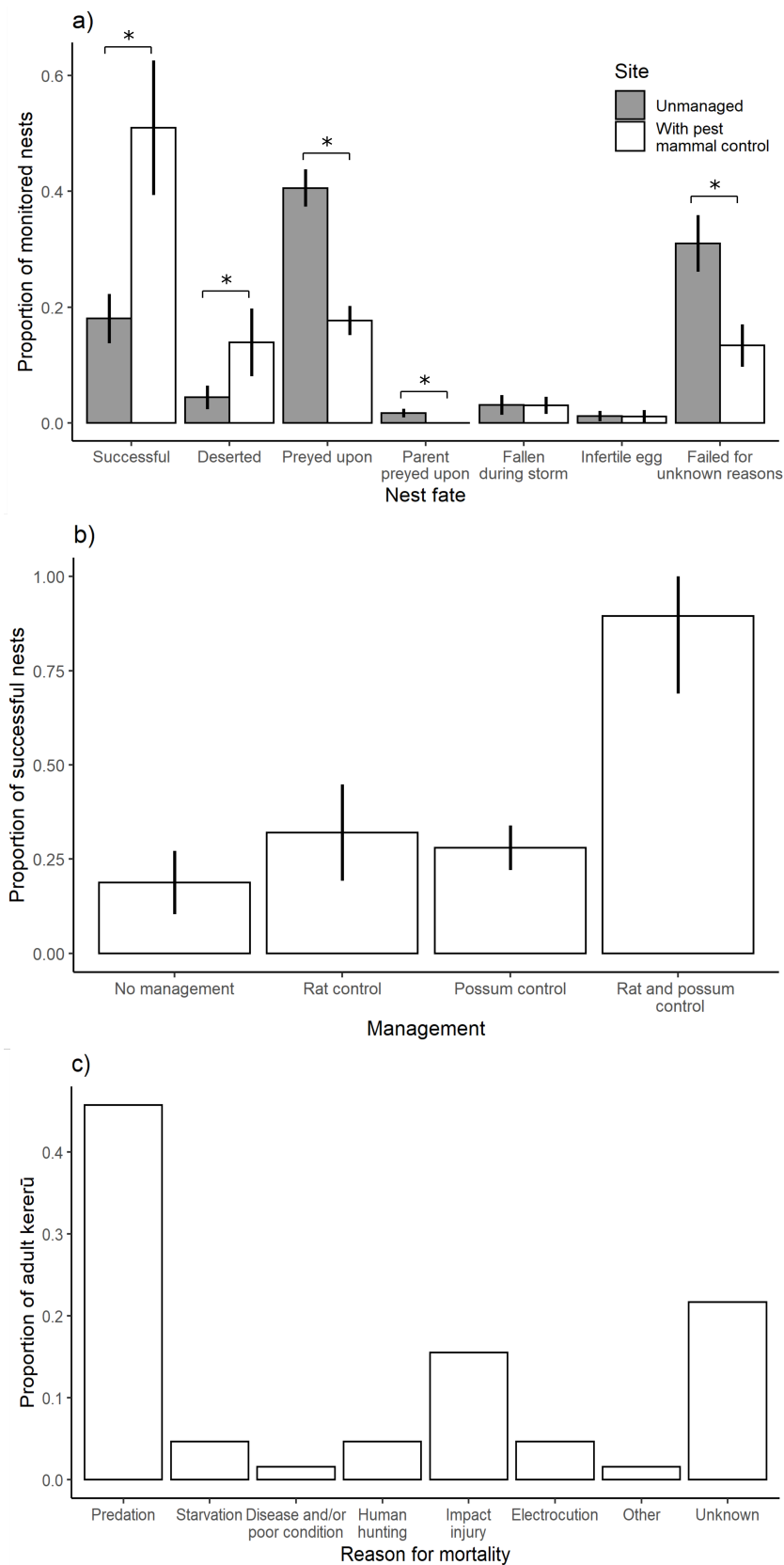
Figure 1. (a) Mean proportion (± SE) of the fate of kererū nesting attempts at sites that were unmanaged ($n = 303$ nests) or with different levels of pest mammal (ship rat, possum or both species) control ($n = 94$ nests) from throughout New Zealand. Differences in the proportion of fates between sites were assessed using a Fisher's test, with significance denoted by * if $p < 0.05$. Proportions do not add to 1 because they are averages. b) Nest success rate (mean ± SE) for kererū with no pest mammal control ($n = 13$ studies), with ship rat control ($n = 3$), possum control ($n = 2$), and rat and possum control ($n = 2$). Depicted are raw data of populations based on the literature review, ignoring differences due to site-specific effects (which in the analysis is accounted for by the random effect). c) Reasons for mortality of radio-tagged or unmarked adult kererū ($n = 137$) from across New Zealand. Depicted are raw data.

Orokonui Ecosanctuary (307 ha)

Sanctuary Mountain Maungatautari (3400 ha)
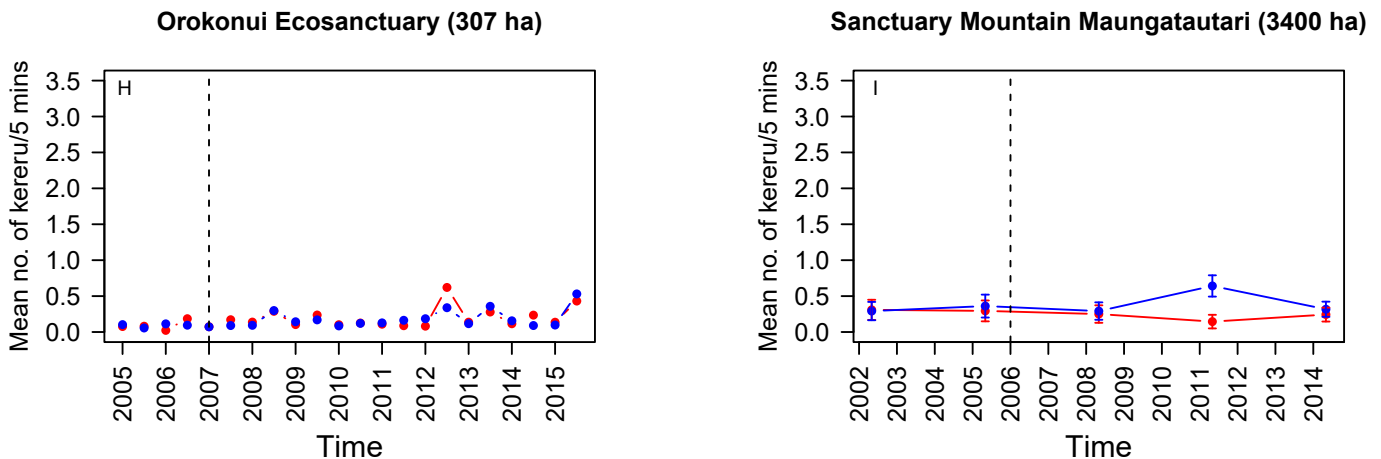
Figure 2. Long-term responses of kererū in ring-fenced ecosanctuaries. The blue points are kererū counts from the sanctuary site, and the red points are kererū counts from a nearby non-treatment site. Vertical dotted lines show when eradication occurred. Error bars are 95% confidence intervals.
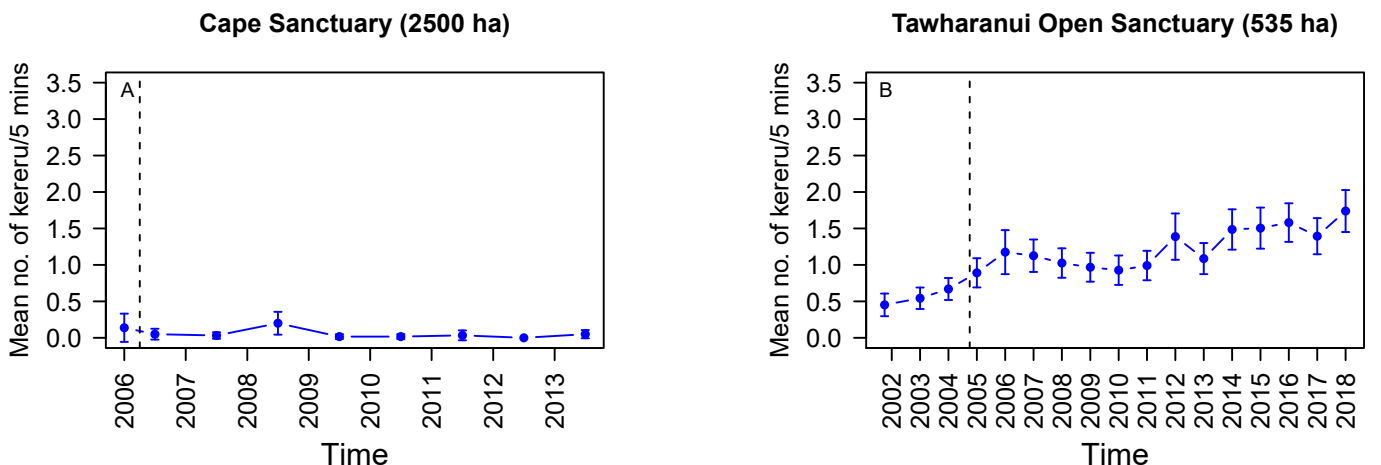
Cape Sanctuary (2500 ha)

Tawharanui Open Sanctuary (535 ha)

Figure 3. Long-term responses of kererū in peninsula-fenced ecosanctuaries. The blue points are kererū counts from the sanctuary site. Vertical dotted lines show when eradication occurred. Error bars are 95% confidence intervals.

increase in kererū in response to pest management that either plateaued or declined over time. Most of the sites that had eradicated rats, possums, and stoats did not have obviously better outcomes for kererū than the unfenced mainland islands. In general, detectability of kererū in five-minute bird counts was relatively low compared to other bird species (Binny et al. 2020).

Non-linear relationships best describe rat and possum density impact functions for kererū from one treatment and two non-treatment sites in the vicinity of Boundary Stream Mainland Island, and demonstrate that few kererū were detected when rats were above approximately 5% tracking (Fig. 5), and when possums are above approximately 5% RTCI (Fig. 5). However, kererū detections were still highly variable, even when rats and possums were below these thresholds. The shape of the curves suggested a "highly vulnerable" relationship (as opposed to "moderately resistant" or "proportionate"; Norbury et al. 2015) between kererū and rats and possums.

Kererū occupancy

Kererū occupancy across New Zealand
In the North Island the average probability of kererū local

occupancy within a square increased slightly (but not significantly) from 0.37 during the first survey (1969–1979) to 0.40 in the second survey (1999–2004; Fig. 6). By contrast, mean probability of occupancy in the South Island fell significantly from 0.36 to 0.27 (Fig. 6).

In the better of our two models (AIC 10 703 vs 10 775), indigenous forest cover, temperature, measurement period, island, and road density together explained 47.5% of the variation in kererū local occupancy. Because of the multiple high-order interactions, we use plots of the fitted effects of the predictors on the probability of occupancy as our primary tool to interpret the model (Fig. 7). These plots and parameter estimates (Appendix S5) show that time, forest cover, temperature, and road density were all significant and interacting predictors of kererū occupancy between 1969–1979 and 1999–2004. On both islands, and in both measurement periods, kererū occupancy decreased significantly as forest cover decreased.

In the North Island, kererū probability of occupancy decreased between the two periods only in the warmest areas, with both moderate forest cover and moderate densities of human settlement (Fig. 7c). There was little change in either warm urban centres (medium to high road density) with
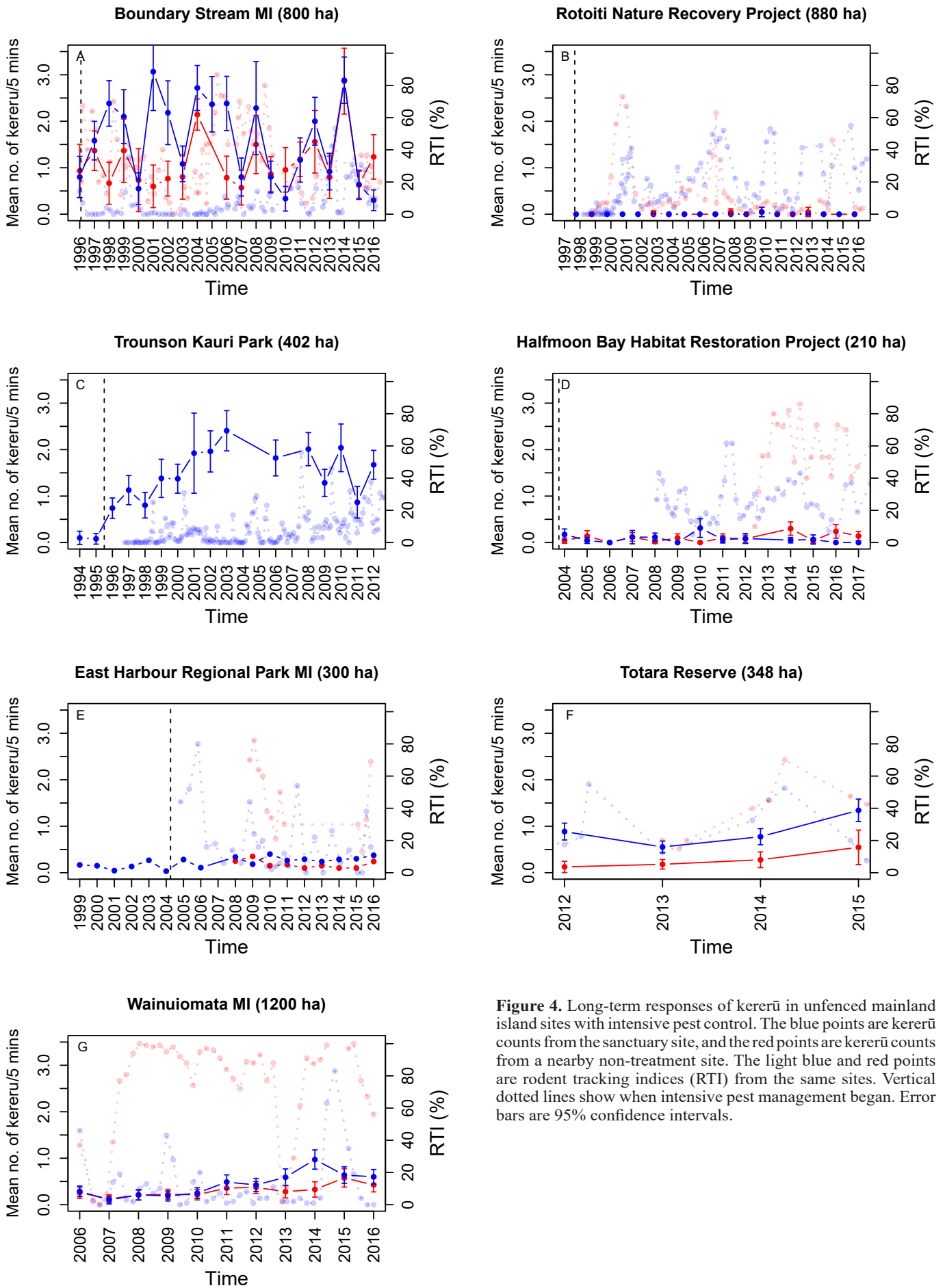
Figure 4. Long-term responses of kererū in unfenced mainland island sites with intensive pest control. The blue points are kererū counts from the sanctuary site, and the red points are kererū counts from a nearby non-treatment site. The light blue and red points are rodent tracking indices (RTI) from the same sites. Vertical dotted lines show when intensive pest management began. Error bars are 95% confidence intervals.
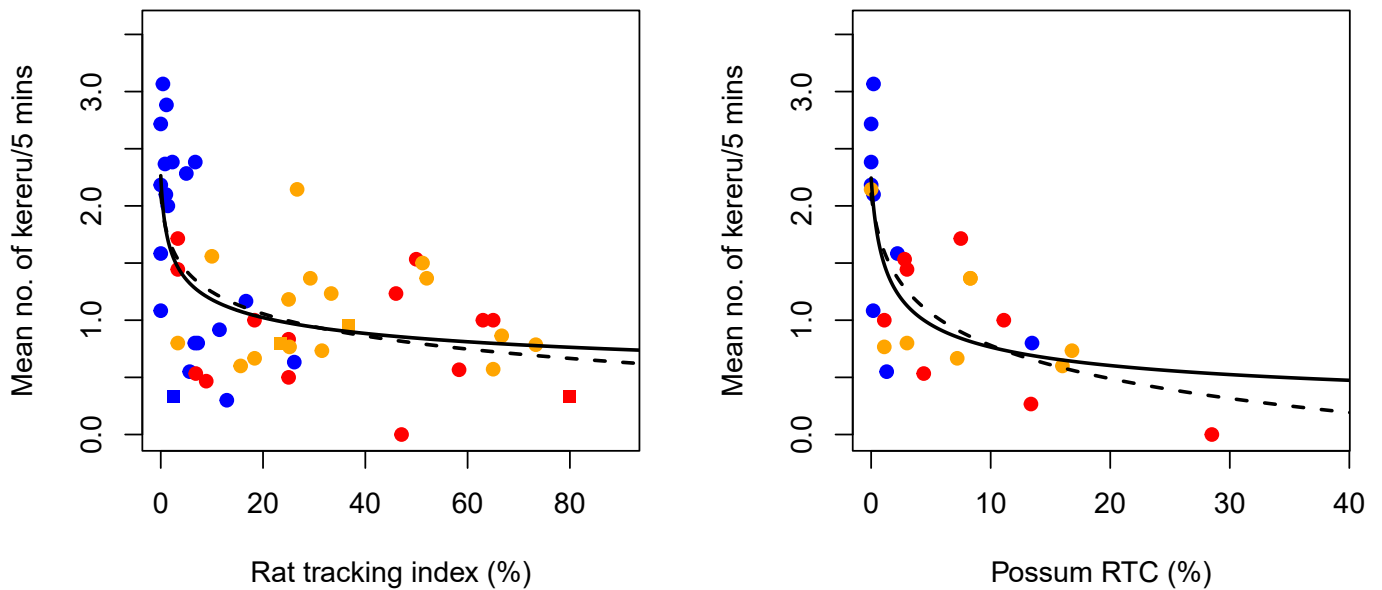
Figure 5. Relative kererū abundance versus (left) ship rat abundance; and (right) possum abundance at Boundary Stream Mainland Island (BSMI) derived from three sites (one treatment site within the mainland island (blue dots) and two non-treatment sites (red and orange dots). Best-fit models (solid lines) and models that were also plausible (ΔAIC < 2) (dashed lines). Left: A power curve (AIC = 96.78; solid line) and logarithmic curve (AIC = 97.64; dashed line) had substantially better performance compared with a linear model (AIC = 108.75) and exponential model (AIC = 106.81). Right: Again, a power curve (AIC = 43.23; solid line) and logarithmic curve (AIC = 44.67; dashed line) out-performed a linear (AIC = 51.15) and exponential model (AIC = 49.45).
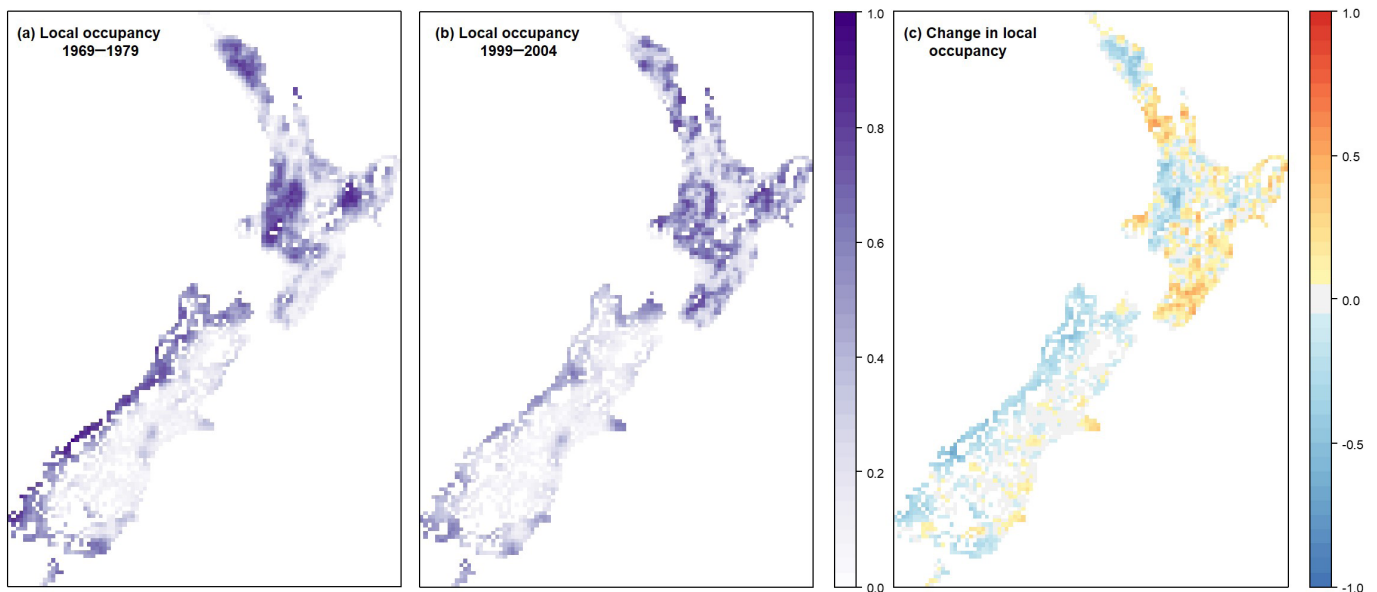
Figure 6. Mean probability of occupancy for kererū in 10 × 10 km grid squares: a) Atlas 1 (1969–1979); b) Atlas 2 (1999–2004); and c) the change in the probability of occupancy between the Atlases (calculated as occupancy in Atlas 2 minus occupancy in Atlas 1). Probability of occupancy is the probability that each 10 km × 10 km grid cell contains kererū.

little or no forest (Figs 7a,c), or in cool, remote forests (Fig. 7e). We could not assess how kererū occupancy changed in remote forests with the warmest temperatures because there are no remote forests left in the areas of New Zealand with the warmest temperatures.

In the South Island, kererū probability of occupancy decreased almost everywhere between the two periods, but most rapidly in places with moderate to high forest cover and medium to low road densities, across the full range of temperatures represented by these conditions (Figs. 7d,f). Kererū occupancy remained unchanged in urban centres

(medium to high road density) with little or no indigenous forest (Fig. 7b).

Kererū occupancy in forested squares only

Our model of kererū occupancy in forested squares explained 41.7% of the variation in the data. This model indicated that time, island, forest cover, temperature, and forest type were all significant and interacting predictors of kererū occupancy within forested squares (Appendix S6). As we predicted, kererū had higher probabilities of occupancy in podocarp-dominated forests compared to beech-dominated forests across both
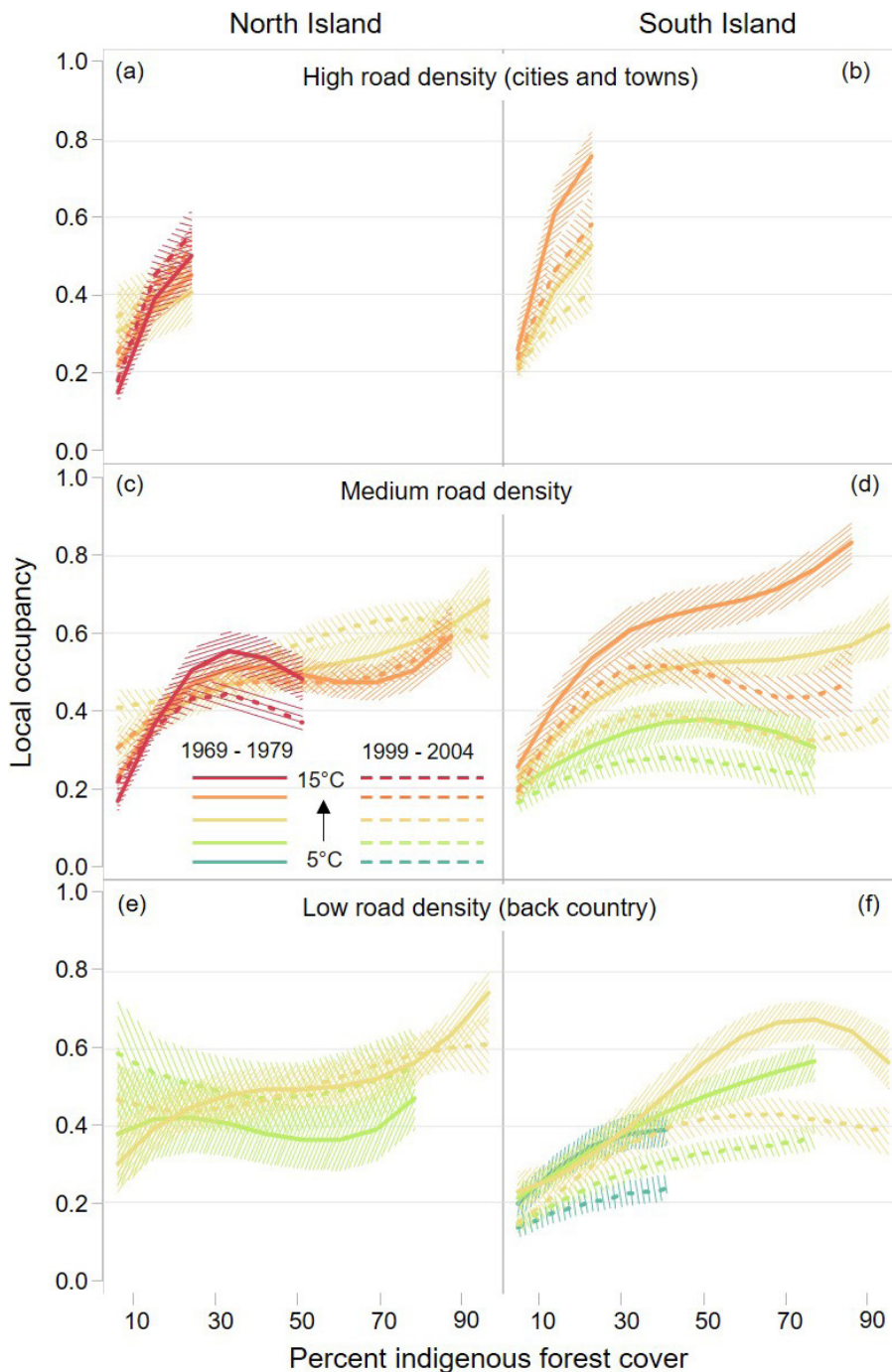
Figure 7. Fitted probability of occupancy of kererū (a–f) in the North and South islands, at different levels of indigenous forest cover, temperature, and road density from a linear mixed effects regression model. Effects and effect changes are plotted only for realistic combinations of environmental variables.

islands (Fig. 8), and podocarp-dominated forests had higher floristic diversity (and therefore presumably more food for kererū) than beech forests (Appendices S7 and S8). Between the two survey periods, kererū occupancy did not significantly decrease across forested squares of any type in the North Island (Figs 8 a,c,e,g). In the South Island, kererū occupancy declined significantly across all forest types (Figs 8b,d,f,h); most notably in the forests that are most dominated by podocarps (Fig. 3b). but also in mixed podocarp-broadleaved-beech forests (Figs 8d,f) and in the warmest of the South Island's pure beech forests (> 10 °C MAT; Fig. 8h). The coldest pure beech forests (left-hand side of Fig. 8h) were those that kererū were least likely to occupy, and the only places in the South

Island where kererū occupancy remained unchanged across the two time periods.

In the North Island, kererū were more likely to occupy squares with higher levels of indigenous forest cover across both measurement periods (Fig. 8i), but especially in the first period. In the South Island, kererū were equally likely to occupy squares with > 50% indigenous forest cover regardless of the actual level of cover in both measurement periods. Occupancy decreased between the first and second measurement periods across all levels of South Island indigenous forest cover (Fig. 8j).
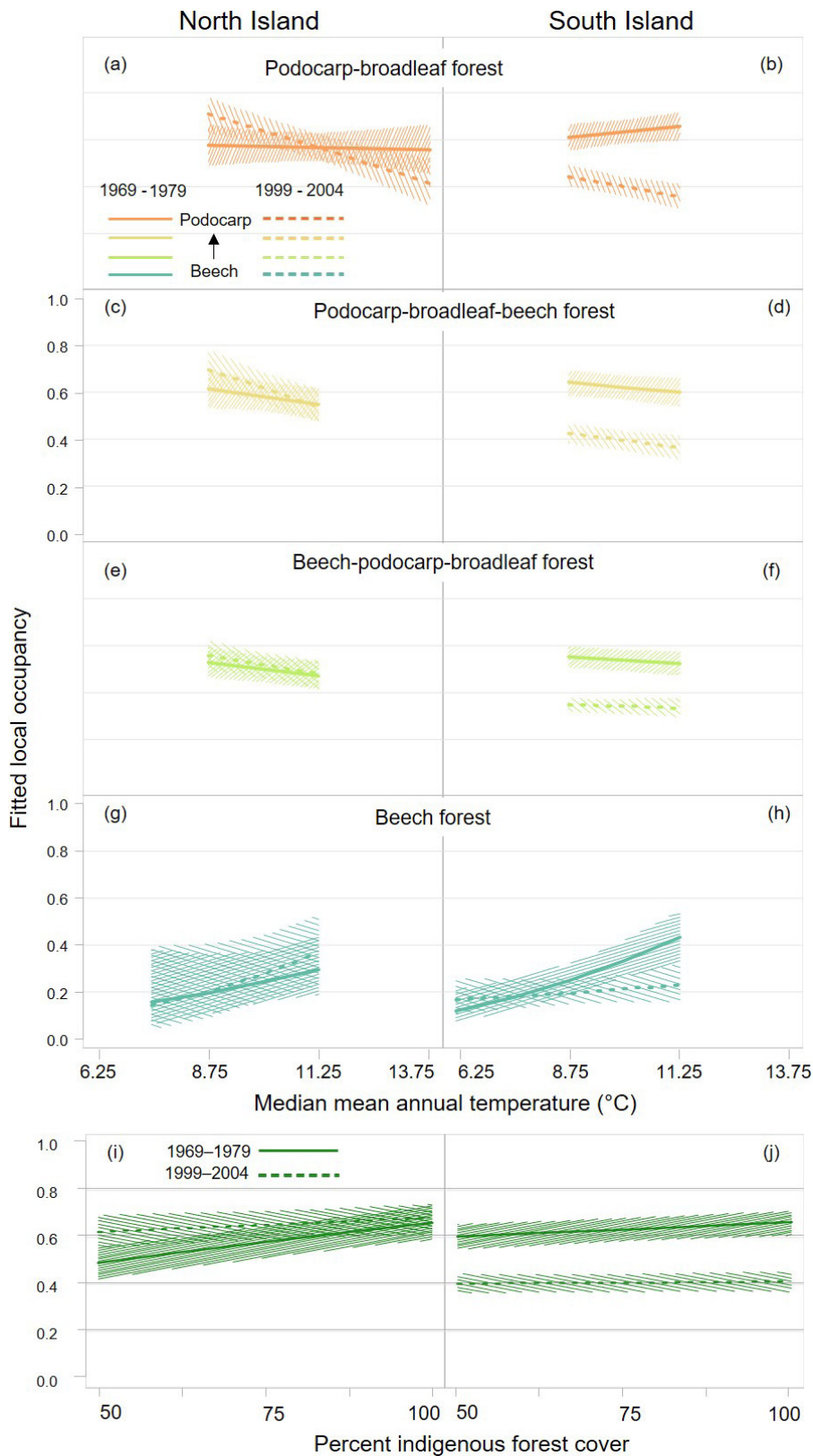
Figure 8. Fitted estimates of probability of kererū occupancy in squares with > 50% forest cover in the 1969−1979 and 1999−2004 measurement periods plotted against temperature, from the forest type model. Estimates are shown for the North (left) and South (right) islands at three different levels of podocarp/broadleaved dominance (from podocarp-broadleaved forest with no beech component (a, b) to beech forest with few or no podocarps (g, h). Subplots i and j show the interacting effects of forest cover and measurement period on each island, which were accounted for in the second composite term in the model.

Discussion

Limiting factors

Newton (1998) suggested that the primary limiting factor for a bird species is the one that, once removed, allows the greatest increase in numbers. Our literature review of factors affecting

vital rates in kererū support the argument that predation by introduced mammals (i.e., top-down processes) is the primary factor limiting kererū in areas with sufficient habitat (e.g. intact forests). Vital rates such as nesting success and adult survival are important population parameters, and our literature review demonstrates that predation by pest mammals severely reduces

both. The cause of most kererū nest failures when mammalian pests are not controlled is predation of the egg by possums and rats, and predation of chicks by stoats. Our results show that controlling possums and rats together boosts kererū nesting success significantly. However, for a K-selected species like kererū, the loss of adult females may have far more effect on population trends than the loss of eggs and young (Lyver et al. 2009). The cause of most adult deaths is predation by stoats and cats, although the predator identity cannot always be determined. While some predation of kererū nests and adults by endemic predators would have occurred in prehuman times (e.g. by Eyles' harrier (*Circus eylesi*); Carpenter et al. 2021), population viability modelling suggests that the rates of failure we have summarised here would lead to populations declining (Lyver et al. 2009).

If food limitation was the primary limiting factor for kererū, we would expect this to be evident in vital rates, which record starvation of chicks or adults, and egg desertion. Yet although some adult kererū mortalities have been attributed to starvation, our collated data show this causes an insignificant number of deaths in comparison to predation, while starvation of chicks and desertion of nests was infrequently observed. Food limitation could also exacerbate the susceptibility of kererū to predation through several mechanisms: hungry birds take more risks, and food limitation can increase the time it takes for chicks to fledge, thereby increasing the time in which chicks are most vulnerable (Mander et al. 1998). Predators such as possums and ship rats are also potential competitors of kererū because both also eat fruits (Innes et al. 2010). While it is important to acknowledge all these possible interactions, the vital rate data suggest that the removal of mammalian pests is still likely to result in the largest population increases in kererū, consistent with predation being the primary limiting factor in intact forests.

The long-term kererū count data from 11 sanctuaries suggest that bottom-up (e.g. food limitation) processes have a part to play in regulating kererū populations outside of intact forest. While intensive management of rats, possums, and stoats often resulted in increased kererū detections, a relationship also demonstrated on pest-free offshore islands such as Motutapu (Spurr et al. 2011) and Tiritiri Mātangi (Graham et al. 2013), this relationship was not always consistent. In an analysis of the full database, Binny et al. (2020) demonstrated that kererū increased significantly at unfenced sanctuaries, but not at fenced sanctuaries. Similarly, our timeseries show that at some sites kererū did not appear to increase compared to non-treatment sites, and at some sites kererū only increased marginally. The rat and possum density impact functions we calculated for kererū at Boundary Stream Mainland Island suggested that although kererū were rarely abundant above 5% rat tracking or 5% possum RTCI, keeping rat and possum indices below these thresholds did not guarantee high kererū numbers, as kererū detections were highly variable at low pest abundances. We propose several explanations for these results. First, many of the sanctuaries only encompass a small area of protected habitat, and that habitat is not always rich in food for kererū. At these sites, factors other than predation – probably food or habitat scarcity – may be secondarily limiting, or co-limiting, kererū. For example, Rotoiti Mainland Island is comprised entirely of beech forest, which is not high-quality habitat for kererū (Burge et al. 2021). Supplementary feeding experiments at these sites would test this hypothesis. Second, the low reproductive rate of kererū means that there may be a considerable lag before increased numbers of kererū are

observed in sanctuaries. Finally, kererū are highly mobile, with home ranges as large as 31 732 ha (Powlesland et al. 2011) and excellent ability to cross habitat gaps (Burge et al. 2021). These factors make the interpretation of responses to management difficult: the kererū detected at non-treatment sites may be the same individuals detected in sanctuaries. Alternatively, increased numbers of kererū at a managed site may simply reflect immigration into the site rather than a net increase of kererū in the wider landscape.

Kererū occupancy

Nationwide occupancy patterns offer mixed support for the role of predation as the primary limiting factor of kererū populations. Under this hypothesis we expected kererū to have declined most in the warmest, most productive forests, where year-round median densities of ship rats and possums are highest (Walker et al. 2019). This is the trend seen for several of New Zealand's forest birds, which are being increasingly confined to thermal refuges in cool, higher-elevation forests (Walker et al. 2019). Instead, we saw different patterns in the North and South Islands. Kererū occupancy across the North Island remained stable between the two time periods, despite higher predicted median rat and possum densities in these forests. In contrast, kererū occupancy declined almost everywhere across the South Island, including for isotherms equivalent to those in the North Island, and most dramatically in warmer podocarp-dominated forests.

We consider several explanations for these patterns. First, higher reproductive rates in the North Island could be offsetting the effects of predation. Kererū in Northland may lay eggs at any time of year (except when moulting during March–May; Pierce & Graham 1995), whereas in Pelorus Bridge (Nelson) there is a more restricted egg-laying season between December and January (Clout et al. 1995). This means there is more opportunity for laying second or subsequent clutches in the North Island should the nest fail. This mechanism would have to be driven by day length or a temperature measure other than mean annual temperature to explain our data, given that the differences between islands are observed for the same mean annual temperature isotherms.

Second, predation risk may be higher for the same isotherm in the South Island than in the North Island. While rats and possums probably have higher median densities in the North Island compared to the South Island (Fraser et al. 2004; Forsyth et al. 2018; Walker et al. 2019), rats are more irruptive in the South Island (Walker et al. 2019). These irruptive rodent dynamics (which often result in irruptions in stoats too; King 1990) may have a bigger impact on kererū than higher median, but less variable, rodent densities. We found that stoats were a major cause of death for adult kererū, so if stoat densities are higher or more irruptive in the South Island, this could have driven the observed declines in kererū occupancy.

Third, the North–South difference could be an artefact of the relationship between abundance and occupancy. While abundance is at some level expected to correlate with occupancy (Gaston et al. 2000), at large spatial scales occupancy will saturate at comparatively low density. Under this scenario, declines in abundance in the South Island could drop the population below the threshold at which significant changes to occupancy are observed, but not have a similar effect in the North Island. The data are lacking to dismiss this hypothesis. However, Great Kererū Count data, corrected for numbers of observers, suggest that kererū density is not lower in the South Island than in the North Island (Hartley 2020). Finally, it is

possible that there is some as-yet-unidentified mechanism, such as disease, that is affecting kererū in the South Island but not the North Island.

Our occupancy results suggest that in deforested regions of New Zealand (e.g. Hawke's Bay, Manawatu, and Canterbury; Ewers et al. 2006), forest scarcity probably trumps mammalian pests as the primary limiting factor for kererū. Kererū occupancy was typically much higher in forested squares compared to non-forested squares, and within forested squares occupancy was highest in podocarp-dominated forests compared to beech forests. Podocarp-dominated forests have higher plant species richness than beech forests and may therefore provide more food for kererū. As a large bird (one of the largest pigeons in the world), kererū are likely to have high energy needs (Jetz et al. 2004), necessitating extensive areas of habitat, or habitats with higher food resource productivity to sustain them. Kererū are capable of living in highly modified habitats such as farmland shelterbelts, urban parks, and rural and suburban gardens, but these habitats only support low numbers. Kererū are probably able to live in these modified habitats due to their high mobility, which allows them to move from fragment to fragment in search of food (Powlesland et al. 2011). As a result, kererū home range size and movements are directly linked to the availability and distributions of food (Clout et al. 1986; Clout et al. 1991; Pierce & Graham 1995; Schotborgh 2005; Campbell 2006).

Kererū occupancy in urban areas remained low, yet stable, over the two time periods, which suggests that the factors that drove kererū declines across forested and rural areas of the South Island are less influential in urban landscapes. Results from the Garden Bird Survey support this argument, as kererū detections have undergone a shallow increase since the survey began in 2007 (Brandt et al. 2020). Urban landscapes typically have lower numbers of mustelids and ship rats than forests (McCulloch 2009; Morgan et al. 2009; Balls 2019), and the diversity of exotic and native plantings may provide a more constant stream of food for kererū through the year. For example, kererū in Auckland were frequently observed consuming exotic plant species in the winter months (Harwood 2002).

Implications for conservation management

Our analyses revealed that while mean kererū occupancy remained stable across the North Island between 1967–1979 and 1999–2004, it significantly declined in the South Island. As occupancy often covaries with abundance (Gaston et al. 2000), this result suggests that kererū abundances also declined in the South Island over this period. This prediction is consistent with the one study we know of that measured kererū relative abundance over a similar time period in the South Island, which found that kererū detections declined significantly between the 1980s and 2000s (Carpenter et al. 2017). However, it differs from expert opinion that kererū populations have been increasing since that time, reflected in the current threat status of kererū as "not threatened" (Robertson et al. 2017) as opposed to the earlier classification of "chronically threatened (gradual decline)" (Hitchmough et al. 2007). Prior to Walker and Monks (2018) estimating the probabilities of occupancy from the two Bird Atlases, comparison was made difficult by different spatial systems and locations of sampling units used between the two atlases, with differing detection probabilities, and differences in levels of effort between and within each of the two surveys. However, crude comparisons of the percentages of grid squares where kererū were detected suggested an overall increase in

kererū distribution between the two surveys, from 46.6% in the 1969–1979 atlas, to 58.1% in the 1999–2004 atlas (Bull et al. 1985; Robertson et al. 2007). These raw calculations (which do not account for variable detectability and effort) may have contributed to the expert assessment that kererū were actually increasing between the two time periods, when, in the South Island at least, the opposite was true.

As with all bird populations, the recovery of kererū requires maximising nesting attempts and their fledging success, and then limiting mortality of the subsequent subadults and adults. Our results suggest that intervention is particularly needed in warm, South Island forests, where Atlas data show that kererū experienced the steepest occupancy declines in recent decades. In aggregate, these steps demand both maximising year-round food supply and minimising predation at all life stages. Large-scale control of the ubiquitous, omnivorous, and arboreal ship rats and brushtail possums will achieve both aims and has been shown to result in increased kererū detections (Fea et al. 2020), but additional actions are also needed. Stoats and feral cats are key predators of adult kererū, while deer, goats, and other browsers limit regeneration of desirable kererū food plants (Husheer 2007), which may affect kererū. In heavily deforested regions, a long-term programme of planting food-providing trees would also be needed to restore sufficient area and connectivity of suitable habitat.

Finally, reanalysing trends in kererū occupancy using the 2018–2023 Bird Atlas data, when they become available, is a logical next step. The last atlas data are now 16 years old and we do not yet know the net outcome for kererū of increased predator management since the 1999–2004 data were collected (Russell et al. 2015; Elliott & Kemp 2016). These data will show how kererū distribution is changing across the country, and whether the declines in the South Island are ongoing.

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Author contribution

All authors conceptualised the idea for the paper. JC, RB, AS, SW, and AM collected and compiled data. AS, SW, AM, and RB carried out data analyses. JC led the writing of the manuscript and all other authors provided editorial input.

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Supplementary Material

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

Appendix S1. Distance between sanctuary sites and non-treatment sites.

Appendix S2. Summary of kererū nesting studies used in literature review.

Appendix S3. Parameter estimates and standard errors from a generalised linear mixed effect model (with binomial error) of nesting success of kererū.

Appendix S4. Details of results from survival studies.

Appendix S5. Parameter estimates for models of kererū local occupancy.

Appendix S6. Parameter estimates from the 'New Zealand forests' linear mixed effects models of probabilities of occupancy for kererū in 2155 10 × 10 km squares across New Zealand.

Appendix S7. Parameter estimates and standard errors from a generalised linear mixed effect model (with poisson error and log link function) of the number of non-fern plant species per plot.

Appendix S8. Fitted estimates of numbers of conifer and angiosperm (non-fern) species per plot in podocarp-broadleaved and beech forest classes (derived from Ecosat classes) plotted against mean annual temperature on the North and South Islands.

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