A New Zealand island in change: 38 years of landbird populations affected by habitat restoration and invasive mammalian predator control

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Abstract: Bird abundances on a small island (150 ha) near the mainland of northern North Island New Zealand were studied using a standardised, longitudinal survey through 38 years (1988–2020), a period during which habitat restoration, reintroductions of five native bird species, and control of rats (*Rattus* spp.) and stoats (*Mustela ermina*) occurred. We estimated time-series abundances of 33 bird species and found substantial population shifts shared by many taxa. The unique data set from this restoration project showed that: (1) more species and more individual birds were present at the end of the study than at the beginning; (2) rat control made an immediate and lasting difference, increasing population growth of the typical species 6% per year; (3) boosting ecological succession by habitat conversion and habitat enrichment resulted in a long term population growth of many native bird species; (4) shifts in species composition are still ongoing 20 years after predator control, with both gradual, long-term increases, and declines. In particular, two endemic species, and pōpokotea (whitehead, *Mohoua albicilla*) proved robust competitors in a predator-free environment, increasing in abundance, while most non-native and many native species declined. These gradual, longer-term shifts became clear during "maturation", a period beginning about 13 years after predator control started.

INTRODUCTION

Restoration is urgently needed in New Zealand because several hundred years of human settlement have drastically changed the habitat and brought mammalian predators to an island world previously lacking them. Endemic New Zealand birds, which evolved in the absence of these predators, became easy prey to rats (*Rattus rattus*, *R. norvegicus*, *R. exulans*), mustelids such as the stoat (*Mustela ermina*), common brushtail possum (*Trichosurus vulpecula*), and house cat (*Felis catus*). Innes *et al.* (2010) document thoroughly the role of these mammals and their effects on native birds. The rats and mustelids are the target of an ambitious effort to remove them from the entire country by 2050 (Murphy *et al.* 2019).

The three main tools in conservation and restoration biology in New Zealand are: (1) elimination of pest mammals; (2) revegetation with native plants when the habitat has been radically altered; and (3) reintroduction of formerly present bird species. The first two are required for the success of the third (Parker *et al.* 2020). Islands, both offshore and "mainland" (surrounded by a predator-proof fence), have been essential in the restoration process as manageable-sized pieces of land on which to test predator removal techniques. The few islands where predators never arrived have been the refuges for some bird species which have provided source populations for restoration projects. In addition, recently predator-free islands can serve as nurseries for native species, building populations, increasing chances for cultural or biological acquisition of predator avoidance behaviours, disease resistance, or new foraging strategies.

When two of us (CJR & CPR) joined the shareholders of Moturoa Island in northern New Zealand in 1982, we joined one of the first private ecosystem restoration projects in a country now thickly speckled with them. In the early days that meant fencing the stock out of the bush and somewhat haphazardly planting flax (*Phormium* spp.), kauri (*Agathis australis*), and a few other iconic trees. Planting procedures became more sophisticated as the objectives of the restoration project developed, and rat and stoat controls were implemented on the island. Shareholders, as is often the case with idealistic restorationists, envisioned a lush bush full of native birds. Now, with 38 continuous years of bird counts, 12 years before and 26 after predator control, we are well prepared to ask: have we achieved that; which procedures were effective; and what have we learned about these birds?

MATERIALS AND METHODS
Study area

Moturoa Island is a privately-held wildlife sanctuary in the western part of the Bay of Islands in the far north of New Zealand. Grazed since the 1870s (Spicer 1993), in the last 50 years approximately one third of the 150-ha island has been incrementally fenced to exclude stock, creating areas designated for native wildlife. The remainder of the island is active sheep-grazing paddocks (Fig. 1). The western tip of the island is 0.5 km from the mainland. Twenty houses and six farm buildings scattered over 20 hectares of paddock and planted trees and shrubs are at this end of the island. Throughout the rest of the island, more than 65,000 native trees and shrubs have been planted since 1980 for both enrichment and pasture conversion (P. Asquith *pers. comm.*). Eighty bird species have been recorded on the island and surrounding waters within about 3 km (CJR *unpubl. data*).

The main vegetation of the wildlife areas is regenerating kānuka (rawirinui, *Kunzea robusta*) shrubland ("bush"), 2–5 m tall with abundant mapou (*Myrsine australis*) and scattered pōhutukawa (*Metrosideros excelsa*), especially on the coastal fringe. Kohekohe (*Dysoxylum spectabile*) and legacy puriri (*Vitex lucens*) are notable on the south face. Understorey plants include abundant hangehange (*Geniostoma ligustrifolium*) and *Coprosma* spp. About 450 species of vascular plants are recorded on the island, species typical of the nearby mainland bush areas (CPR & E. Asquith *unpubl. data.*). Over the study period, forested areas grew taller and darker, and the understorey thinned. Grassy areas planted in shrubs and trees achieved solid canopy at 3–6 m in height. A striking increase in native seedlings occurred after rat control, as also reported elsewhere by Allen *et al.* (1994). Five small
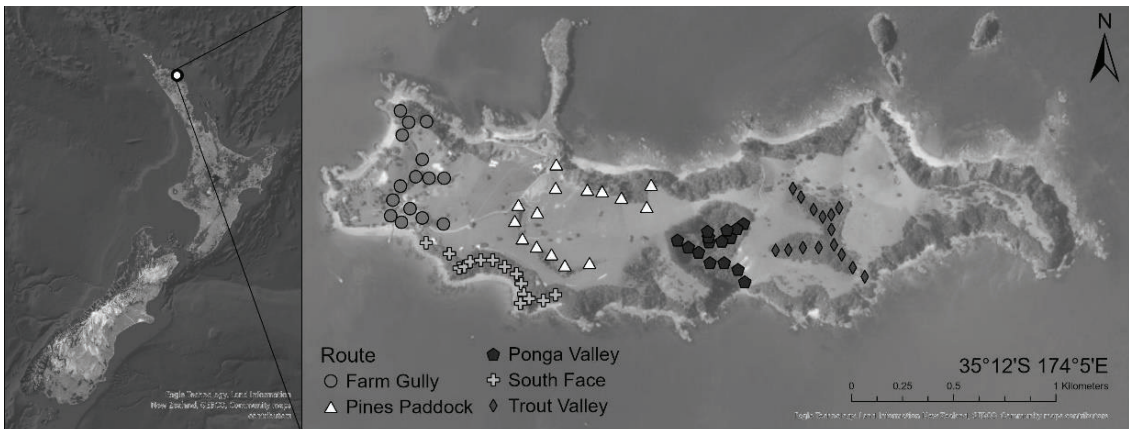

Figure 1. Moturoa Island (North Island, New Zealand) paddocks, bush, and bird counting routes, and stations.

wetlands and ponds were created during the study. Stands of Monterey pine (*Pinus radiata*) that were planted c. 60 years ago have mostly died or felled during the study, and a programme continues to remove the remainder from the wildlife areas. An active control programme involves removal of gorse (*Ulex europaeus*), woolly nightshade (*Solanum mauritianum*), moth plant (*Araujia hortorum*), pampas grass (*Coraderia selloana*), and other invasive plant species as they are found.

Predator control

The introduced mammalian predators found on Moturoa at the beginning of this study were Norway rat (*Rattus norvegicus*), ship rat (*R. rattus*), and stoat. The major rat control effort started in August 1992 with two hand-scattered applications of the second-generation anticoagulant brodifacoum over the entire island. At that time Moturoa was one of the largest islands in the country that had been so treated. Between 12 and 30 bait stations containing poison have been and are still maintained over the island. Trapping for both rats and stoat began informally in mid-1980s, initially only in the western part of the island, closest to the mainland. Wider deployment of traps over the whole island started in the early 1990s, initially with Victor style snap traps. As the Department of Conservation developed trapping equipment and procedures, first Fenn Mark 4 traps, and then DOC 200 traps were adopted, set in custom-built wood-and-screen tunnels. These were usually baited with hen eggs and poison blocks, but occasionally other baits were tried, e.g. peanut butter, fresh or salted chicken wings, possum, rabbit, or tinned pet food. Since 1998, 55 traps dispersed over the entire island have been permanently set and checked monthly. Occasional track tunnels are deployed in areas not well covered by traps, and observations by alert residents supplement the information from trapping and poison. A total of 146 rats have been trapped, making an average of five rats per year. When a rat is found, traps and poison are applied in that area, and if rats appear in more than a single area of the island, such as occurred in 2004, 2006, 2014, and 2018, hand-scattered poison applications were made in all wildlife areas. Fewer than ten stoats and one possible weasel (*Mustela nivalis*) have been seen alive on the island (P. Asquith *pers. comm.*), each briefly. A total of 15 stoats have been captured. The house mouse (*Mus musculus*) is on Moturoa, sometimes abundantly. It is a documented predator of birds on islands (e.g. Cuthbert & Hilton 2004), albeit rarely. Its small home range and size make eradication difficult. Our predator control methods depressed its population but could not eradicate it.

For 18 months from June 1995 to December 1996, 457 common myna (*Acridotheres tristis*), suggested as a competitor and predator of small birds, were trapped using a narcotic bait and decoy birds (Tindall 1996; Tindall *et al.* 2007).

Reintroductions and self-introductions

During the study nine bird species that were presumably present historically were translocated to the island. These species, which we refer to as "reintroduced," were pāteke (brown teal, *Anas chlorotis*) (1983 and later), korimako (bellbird, *Anthornis melanura*) (1983), toutouwai (North Island robin, *Petroica longipes*) (1983 and 1999), kiwi-nui (North Island brown kiwi, *Apteryx mantelli*) (1985 and later), kākāriki (red-crowned parakeet, *Cyanoramphus novaezelandiae*) (1986 and later), moho pererū (banded rail, *Gallirallus phillipensis assimilis*) (1996–1997), tīeke (North Island saddleback, *Philesturnus rufusater*) (1997), tētē-moroiti (grey teal, *Anas gracilis*) (1999), and pōpokotea (whitehead, *Mohoua albicilla*) (2011). Tīeke, kākāriki, korimako, and tētē-moroiti introductions failed. Tīeke rapidly increased over two years, then suddenly declined and disappeared in less than a year. This rapid disappearance could have been caused by a single stoat, which could easily have been undetected without intensive monitoring (N. Fitzgerald *pers. comm.*). Kiwi-nui were abundant throughout the island but, being largely nocturnal, were only rarely detected during diurnal point counts employed in the study. The other four species are addressed in this paper.

Six species have self-introduced to Moturoa during this study, i.e. arrived and bred: spur-winged plover (*Vanellus miles novaehollandiae*) (1988), pūtangitangi (paradise shelduck, *Tadorna variegata*) (1988), pūkeko (*Porphyrio melanotus*) (about 2000), miromiro (tomtit, *Petroica macrocephala*) (2001), rook (*Corvus frugilegus*) (2005), and Barbary dove (*Streptopelia risoria*) (2011). The non-native rook and dove were eliminated by island managers in the year they appeared and bred. Miromiro, despite arriving on the island on three occasions, and known to breed one season, has not persisted.

Evolutionary history of species

As a useful proxy for evolutionary isolation from mammalian predation, we compare species by their level of endemism (Table 1): (1) six **endemics** that occur only in New Zealand; (2) 11 **recent immigrants**, that colonized New Zealand from Australia in the last few thousand years; and (3) 16 **non-native** species, introduced in the past 150 years from outside of New Zealand.

Bird counts

We set up five census routes (Fig. 1) each made up of 15 stations. (1) Farm Route was along edges of small, planted bush patches in a matrix of pasture and

Table 1. Species recorded in study on Moturoa Island (North Island, New Zealand) in order of total abundance (number observed) over the entire study (1988–2020). Origin: E = endemic, R = recent immigrant, N = non-native, I = reintroduced on island, S = self-introduced. Four "Groups" (A through D) are identified according to the population trend they display during the study (see text). "Increase Timing" indicates the number of years before (B) or after (A) rat control a population started to increase, or if there was no relevant pattern (NA). Common and scientific names follow the Ornithological Society of New Zealand list (Checklist Committee (OSNZ) 2022, after Gill et al. 2010). The potential cause of the population increase ("Increase Cause") was: P = possibly population released as a result of rat control; S = possibly succession of habitat; NA = unknown or not applicable. The trend in last 15–20 years of study ("Later Trend") was D = decline, I = increase; S = stable.

Species common name Te reo (English)	Code	Scientific name	Origin	Number	Group	Increase timing	Increase cause	Later trend
Common myna	COMY	Acridotheres tristis	N	8,814	D	NA	S	D
Tūī	TUI	Prosthemadera novaeseelandiae	E	6,721	A	A1	S, P	S
Tauhou (silvereye)	SILV	Zosterops lateralis	R	6,066	D	B2	S	D
House sparrow	HOSP	Passer domesticus	N	5,235	C	B3	S	S
Eurasian skylark	SKYL	Alauda arvensis	N	5,189	D	NA	NA	D
Riroriro (grey warbler)	GRWA	Gerygone igata	R	4,597	D	A1	P	S,D
Pīwakawaka (New Zealand fantail)	FANT	Rhipidura fuliginosa	R	4,338	D	A1	P	D
Chaffinch	CHAF	Fringilla coelebs	N	3,972	C	B5	S	S
European goldfinch	GOLD	Carduelis carduelis	N	3,546	D	A3	P	D
Eurasian blackbird	BLAC	Turdus merula	N	2,780	D	B4	S	S,D
Warou (welcome swallow)	WESW	Hirundo neoxena	R	2,732	B	A1	P	D
Common starling	STAR	Sturnus vulgaris	N	2,662	B	A1	P	D
Song thrush	SOTH	Turdus philomelos	N	2,111	B	A4	P	D
Eastern rosella	EARO	Platycercus eximius	N	1,759	C	A2	P	S
Kōtare (New Zealand kingfisher)	KING	Todiramphus sanctus vagans	R	1,619	D	B5	S	D
Common pheasant	RNPH	Phasianus colchicus	N	1,383	D	B8	S	P
California quail	CAQU	Callipepla californica	N	1,236	D	A2	P	D
Wild turkey	TURK	Meleagris gallopavo	N	1,233	D	B6	S	D
Yellowhammer	YELL	Emberiza citrinella	N	906	B	A3	P	D
Pūtangitangi (paradise shelduck)	PASH	Tadorna variegata	E, S	855	A	A2	NA	I,S
Pōpokotea (whitehead)	WHIT	Mohoua albicilla	E, I	572	A	NA	I	I
Spur-winged plover	SWPL	Vanellus miles	R, S	417	A	A1,8	NA	S
Brown quail	BRQU	Coturnix ypsilophora	N	370	D	A3	P	D
Toutouwai (North Island robin)	NIRO	Petroica longipes	E, I	366	B	NA	I	D
Pūkeko	PUKE	Porphyrio melanotus	R, S	337	A	A15	NA	I
Australian magpie	WBMA	Gymnorhina tibicen	N	298	C	A10	S	D,S
Kāhu (swamp harrier)	HARR	Circus approximans	R	214	C	A2	P	S

Table 1. *continued*

Species common name Te reo (English)	Code	Scientific name	Origin	Number	Group	Increase timing	Increase cause	Later trend
Pīpīwharauroa (shining cuckoo)	SHCU	*Chrysococcyx lucidus*	R	194	A	A8	NA	S
Dunnock	HESP	*Prunella modularis*	N	176	B	A3	P	D
Pāteke (brown teal)	BRTE	*Anas chlorotis*	E, I	141	B	A3	P	D
Moho pererū (banded rail)	BARA	*Gallirallus phillipensis*	R, I	102	A	NA	I	I
Ruru (morepork)	MORE	*Ninox novaeseelandiae*	R	72	C	B6	S	S
Tōrea pango (variable oystercatcher)	VAOY	*Haematopus unicolor*	E	70	A	A12	NA	I

scattered buildings. One small pond, a year-round stream, and foreshore were near some stations. (2) Half of Pines Paddock Route was in or along the edge of paddocks as it followed an intermittent stream, originally with sparse kānuka and an open stand of Monterey pine. The pines were gradually removed, and in 1996 the stream was fenced, planted, and three ponds created. Half the route is along the top edge of a steep, kānuka, pine, and pōhutukawa wildlife area. (3) Ponga Valley Route was in the largest, most mature, and diverse area of native forest, centred on a small, sedge-dominated marsh feeding a year-round stream. (4) Trout Valley Route was in a narrow, young, regenerating native forest along a year-round stream. (5) South Face Route was in a band of mature, native forest, fenced from sheep in 1974, and covering the steep, south-facing side of the island. There were no streams on this route, only a few freshwater seeps along its shore.

To define the summer breeding season more conveniently for analyses, data were divided into "austral years" that begin 1 July and end 30 June. The austral year is named for the calendar year in which summer and autumn seasons occurred. For example, censuses in December 2009 and January 2010 would be in austral year 2010, and predator control in August 1992 occurred in austral year 1993.

We used an intensive point count method, which is used primarily for inventory and adequately samples most diurnal species (Ralph *et al*. 1995; Spurr & Ralph 2006). Counts were all in summer, i.e. November, December, or January. Since abundance and conspicuousness (and hence species detection rates) are likely to change over this period for some species, in some years some routes were repeated, in part to investigate the effect of season (Supplementary Material Table A)[1]. The first two authors conducted all counts except the first year, and some of the 1995–1996 counts were done by David Tindall (Tindall 1996). Most often two observers counted each station together. Each route was counted at least once each summer. From austral summer of 1982 through 2020, 3,536 station point counts of landbirds were conducted along the five routes. Ten-minute point counts were taken at stations positioned 75–100 m apart, 15 per census route, with the aim to obtain abundance indices of birds in areas of largely continuous habitat. Although binoculars were used, most detections were auditory, that is they were heard before seen, or were never seen. Every attempt was made to avoid double counting individuals at a single station. Detections of all birds seen or heard at all distances were recorded, including birds on shorelines, for a total of more than 70,000

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1 See details beneath Acknowledgements for links to online Supplementary Material.

observations. A few individuals were detected from more than one station, but these were a small percentage of all observations, and for purposes of this study we considered each station an independent sample. Censuses were carried out on fine days, and not in rain heavier than a drizzle or in wind greater than 10 kph. Birds flying over, but not foraging or landing within 100 m of the observers, were recorded, but not used in analyses. Censuses began within 20 minutes of sunrise and lasted approximately three hours, with the stations along each route always visited in the same order. Each observation recorded whether the first detection of an individual was audio or visual, and if the distance to that detection was less than or greater than 50 m.

Modelling species abundance

For analysis, we summarized data by tabulating yearly total numbers of each species of bird, as well as the total effort (number of 10-minute station-counts) each year. We use simple counts as an index of abundance, without adjusting for distance to bird, to avoid introducing additional uncertainty. For visualization and principal component analysis, we summarized abundance below using a matrix of "yearly sightings per unit of effort", i.e. abundance was the total number of birds detected, divided by the number of 10-minute station-counts performed that year (or, on that route, where appropriate).

These numbers, of course, include sampling noise, so we also fit a model to get more robust estimates of true abundances, along with measures of uncertainty. The main quantities that we were interested in estimating for each species were the abundance in year t, a_t, and the effect of rat removal, denoted A.

The model we used is a latent autoregressive model with hierarchical Bayesian priors, fit using Stan (Stan Development Team 2021). This approach effectively includes abundance as a latent variable (Thorson & Minto 2015; Ahrestani *et al.* 2017). For a recent summary of these methods see Korner-Nievergelt *et al.* (2015).

To understand how other factors (e.g. rat removal) affect abundance, the model includes additive effects of weather, year, and rat removal on log-transformed change in abundance. Weather data were obtained from the New Zealand National Climate Database (2020), and missing observations were interpolated at each station with a linear model of year, month, and adjacent observations. Other measures of temperature and rainfall (e.g. mean and minimum temperatures; other time periods) were highly correlated with these. Rat removal occurred in 1993, and a lag parameter was included for each species to allow for a delay in its effect.

In other words, the effect of rat control is shifted a period of time depending on the bird species and affects combined adult survival and fecundity. To account for variation in sampling date we also included an additive effect of day of the austral year on detectability.

To account for overdispersion (e.g. from species that are infrequently seen but in large flocks), we modelled the total observed counts for a given species in year t, as a negative binomial with mean equal to the (unobserved) abundance measure a_t multiplied by the total weighted effort that year, and a species-specific overdispersion parameter. Therefore, a_t is in units of birds per point count. Then, the model for abundance a_t in year t is:

$$a_t = \mu \, exp(Ar_{t-s})a_{t-1} + exp(Ar_{t-s} + B + \sum_j \gamma_j w_{j,t} + \epsilon_t),$$

where**:** $r_t = 0$ before rat (predator) removal, and $r_t = 1$ for t > 1993 (i.e. after rat control); s > 0 is the delay of the effect of rat control (in years); A is the effect of rat control (a positive value implies more birds after rat control); B is a species-specific term that could stand in for immigration or other population-size-independent effects (a mean increment, on a log scale); $w_{j,t}$ is the weather variable j in year t; γ_j is the effect of weather variable j on abundance; and ϵ_t is Gaussian noise with mean 0 and standard deviation σ. Weighted effort is the number of stations surveyed, weighted by detectability for that day and that species (so, the contribution to effort for species i at a station surveyed on day d relative to 1 January is $1 + \delta_i d$, where a negative value of δ_i indicates the species becomes less abundant or detectable as the season progresses).

The model is not appropriate for species that were reintroduced to the island more than a few years after the start of the study, so for these species, toutouwai and pōpokotea, the effect r is shifted in time in order to account for the effect of reintroduction, rather than rat removal. Note that the model is appropriate for those two species that self-introduced within a few years of rat removal (spur-winged plover and pūkeko) as well as for moho pererū, whose reintroduction was close enough to the year that pests were removed that no such shift was necessary.

All parameters are separate by species, but the effect of rats (A) and weather (γ) have a prior with a common mean. For remaining priors see our Stan implementation in Supplementary Material. The first term ($\mu \, exp(Ar_{t-s}) \, a_{t-1}$) might be interpreted as the number of surviving adults from the previous year; and the second term might be interpreted as the new offspring, although we likely do not have good power to distinguish survivorship, immigration, and production of new offspring. The parameter A can be interpreted as the log change in survival and fecundity after rat removal. For

instance, $A = 0.2$ implies that population growth (survival and fecundity per capita) is increased by $\exp(0.2) = 1.22$, and so is 22% higher after rat removal than before. A negative value would imply that population growth is lower after rat removal than before.

To visualize estimated species abundances through time, we plotted for each species the posterior mean of a_t against year (t), along with the 95% credible interval. Although in principle marginal posterior distributions may hide patterns in the full posterior distribution on abundance trajectories, visual inspection of full posterior samples found no such issues here.

RESULTS

Combining all counts for all years, we counted 45 species with more than 10 individuals in all years combined. Common myna and tūī were the two most common. The 33 species with more than a total of 70 individuals were included in our analysis (Table 1).

Are there more birds now than at the beginning?

The total abundance of individuals across all species increased about 50%, from an average of 14 birds per station in 1982, to an average of 21 birds per station at the end of the study (Fig. 2). This increase was largely due to two endemic species, tūī and pōpokotea. Roughly half the individuals in any year were from the most commonly detected five species; common myna, tūī, tauhou (silvereye, *Zosterops lateralis lateralis*), house sparrow (tiu, *Passer domesticus*), and Eurasian skylark (kairaka, *Alauda arvensis*).

There were more species and more individuals of most species at the end of the study than at

Figure 2. The abundance of all species on Moturoa Island (North Island, New Zealand) by origin of the species (Table 1): 18 non-natives (introduced by humans); 14 recent immigrants (with close relatives in Australia); tūī (*Prosthemadera novaeseelandiae*) (a very abundant endemic); and 13 New Zealand other endemic species.

the beginning. Part of this increase was the five species that were successfully reintroduced, i.e. pāteke, moho pererū, toutouwai, pōpokotea, kiwi-nui, and three species that self-introduced and bred prolifically, i.e. spur-winged plover, pūkeko, and pūtangitangi. Additionally, many species already present at the start increased in numbers of individuals. By the midpoint of the study (2005), of the 32 species then present, 24 were higher in abundance than they had been at the start, five were about the same, and five were lower. By the end of the study this had changed slightly, but still 16 were higher, 11 about the same, and six were lower in abundance.

What aspects of restoration drove population changes?

To explore general patterns of population trajectories, we used Principal Component Analyses (PCA) to visualize observed abundances by species and year. This method identifies patterns of temporal change that are shared by many species and allows us to visualise species trends on axes defined by these shared patterns. The common trends described by the first three PC axes (explaining 22.2%, 13.1%, and 7.5% of the variance, respectively) are shown in Figure 3, and the loadings of each species on these PCs (i.e., the amount that each species' trajectory resembles that trend) is shown in Figure 4. For instance, tūī has coordinates of -0.2, 0.08, and 0.13 on the first three PCs, and so we can obtain a good approximation for tūī abundance through time by summing PC1 (dark curve in Figure 3) multiplied by -0.2 with PC2 (grey dot-dash curve) multiplied by 0.08 and PC3 (grey dashed curve) multiplied by 0.13. Note that since PC1 is a decreasing curve, a negative PC1 coordinate implies a contribution to abundance that increases with time.

The shapes of PCs 1–3 over time suggested three periods of community change: (1) pre-control (1982–1995, two years after the 1993 rat control), a very stable 13-year period, with little changes in populations (the three PCs remained constant); (2) post-control period (1996–2005), when PC3 changed in a positive direction, a period when many populations increased, adjusting to the new predator-free norm, the expanding amount and complexity of vegetation, and the arrival of new species on the island; and (3) maturation period (2006–2020), when PC2 diverged from PC1, and PC3 changed direction, consistent for a period of 15 years, during which time the vegetation continued to mature and bird populations adjusted to the presence of more species and higher population counts in general. These temporal divisions are somewhat arbitrary but provide a useful framework in which to discuss changes over time.
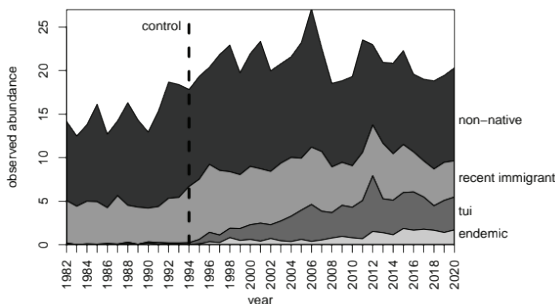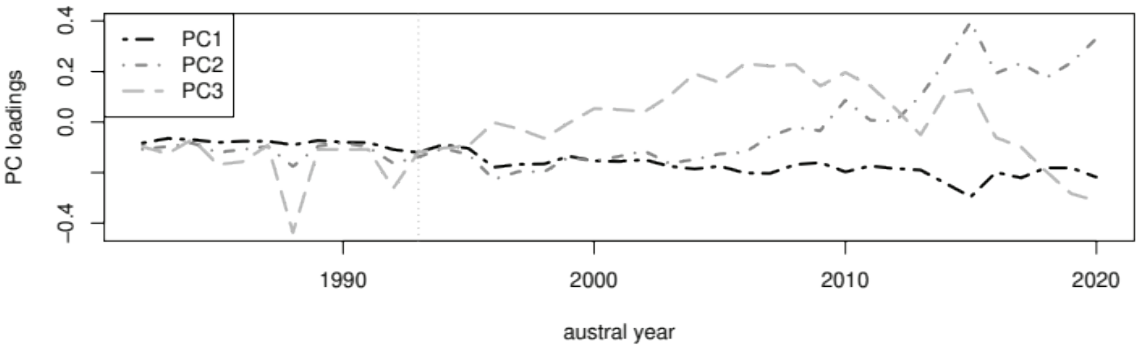
Figure 3. The first three principal components of raw observed species abundances over time, showing general trends in species composition. The vertical line indicates the first rat control (in 1993). As discussed in the text, this visualization suggests three time periods, divided roughly into pre-control, post-control (when PC3 is high), and a final period we refer to as "maturation" (when PC2 is high).
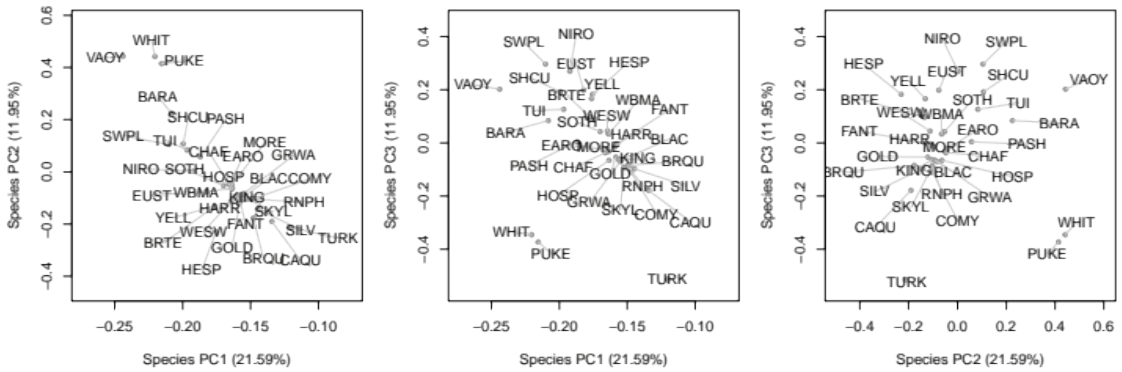

Figure 4. Loadings of each species' observed abundances on the first three principal components of Figure 3. The left figure is PC1 (x axis) vs. PC2 (y), the center is PC1 (x) vs PC3 (y), and the right is PC2 (x) vs. PC3 (y). The four-letter species codes are shown in Table 1. An interactive version of this is in Supplementary Material Figure A.

Model fit and the effects of weather

Before addressing more central questions that we obtained from our statistical model of population abundance, we first describe some minor details of model fit. The amount of overdispersion (the φ parameter) varied substantially between species (see Supplementary Materials Figure C), generally reflecting the expected degree of variance in sighting numbers, e.g. high for pīwakawaka (New Zealand fantail, *Rhipidura fuliginosa*), for which a single individual or entire flock might be detected; low for solitary and/or predictable species like song thrush (manu-kai-hua-rakau, *Turdus philomelos*) or pāteke (brown teal). We also found no statistically significant effects of weather, either in aggregate or for particular species (see Supplementary Materials Figure C).

How did rat control affect bird species?

In the first three years after control 15 of the 25 species present at the time of control appear to have increased: tūī, riroriro (grey warbler, *Gerygone igata*), pīwakawaka, European goldfinch (kōurarini, *Carduelis carduelis*), warou (welcome swallow, *Hirundo neoxena neoxena*), common starling (tāringi, *Sturnus vulgaris*), eastern rosella (kākā uhi whero, *Platycercus eximius*), California quail (tikaokao, *Callipepla californica*), yellowhammer (hurukōwhai, *Emberiza citrinella*), pūtangitangi, spur-winged plover, Australian brown quail (kuera, *Synoicus ypsilophorus australis*), kāhu (swamp harrier, *Circus approximans*), dunnock (*Prunella modularis*), and pāteke (Table 1 column "Increase timing", Figs. 5A–D).

Some of these apparent increases, however, may be due to demographic or sampling randomness, so we turned to our model for statistical analysis. For each species, the term *A* quantifies the increase (or decrease) in population growth rate that occurred after rat removal (Table 2). Seven species, moho pererū, toutouwai, pūkeko, pīpīwharauroa (shining cuckoo, *Chrysococcyx lucidus*), spur-winged plover, tūī, and pōpokotea, showed a statistically significant effect of rat removal, as indicated by estimated values of *A* with credible intervals that did not overlap zero. These species' values of *A*, that range from 0.173 to 0.288, indicate an approximate 15–25% increase in combined survivorship and production of young per capita per year (estimates are posterior means; 95% credible intervals span about 3% to 40%). In the case of toutouwai and pōpokotea, the significant positive values of *A* likely reflected the species' reintroductions, as well as rat removal.

Since statistical noisiness, due both to population fluctuations and observation, limited our power to identify unambiguously the effects of rat removal on any single species (reflected in the large credible intervals of Table 2), we also estimated the average effect of rat removal on a typical species, and found an estimated average effect of rat removal of 0.06 (with a 95% credible interval of 0.01–1.1), i.e. a mean increase in population growth rate of 6% per year. (Recall that the "typical" effect enters into our model through the mean of a hyper-prior on the species-specific *A* terms, interpreted as the average effect of rat removal on population growth of a typical species.)

The delay after rat removal after which the effect was seen (*s* in the model description above) was not precisely located, with the posterior distributions for all species closely resembling the prior (which was informative: half-Gaussian with mean 0 and standard deviation of four years).

Patterns of abundance changes

The arrangement of species in PC space (Fig. 4) suggested four groupings of species whose abundance dynamics were similar, identified as Groups A, B, C, and D (Fig. 5A–D). These were most readily distinguished in a 3-dimensional graph of PCs 1–3. An interactive version of this is in Supplementary Material Figure A (pca3dspecies_orig.htm). These groups are not well separated, but nonetheless the common population trends these diverse groups of species share may reflect a shared underlying cause. At the least, they provide us with a convenient framework to discuss many species. Grouping species accordingly, we display both raw (observed) and estimated abundance trends (with uncertainty) in Figure 5. Statements such as "...pūtangitangi steadily increased throughout the

Table 2. The effect of rat control (post-1993) on the mean population growth rate (positive or negative) of each species (the parameter *A* in the model), as shown by the posterior mean, 2.5%, and 97.5% credible intervals. The table is ordered by posterior mean effect, and those seven species with a marked effect of rat control are indicated by an asterisk (*). The parameter is on a log scale, so a value of 0.1 indicates an $e^{0.1}$ (roughly 10%) increase in population growth due to pest removal. Note that this effect is shifted for pōpokotea (whitehead, *Mohoua albicilla*) and toutouwai (North Island robin, *Petroica longipes*) to when they were reintroduced. See also Supplementary Figures B, C, D, E, and F for posterior distributions of other parameters.

Species	Mean	2.5%	97.5%
Pūkeko*	0.288	0.218	0.394
Whitehead*	0.277	0.141	0.427
Pīpīwharauroa*	0.248	0.096	0.407
Toutouwai*	0.188	0.039	0.348
Moho pererū*	0.176	0.030	0.331
Tūī*	0.173	0.041	0.332
Spur-winged plover*	0.165	0.006	0.340
Yellowhammer	0.147	-0.014	0.312
Common starling	0.115	-0.040	0.285
Tōrea pango	0.111	-0.133	0.343
Song thrush	0.090	-0.046	0.250
Eastern rosella	0.086	-0.020	0.205
Pūtangitangi	0.080	-0.071	0.246
Dunnock	0.072	-0.113	0.260
Pāteke	0.059	-0.102	0.237
Australian magpie	0.043	-0.103	0.200
Common pheasant	0.031	-0.082	0.164
Chaffinch	0.027	-0.068	0.165
Warou	0.027	-0.080	0.158
Eurasian blackbird	0.023	-0.070	0.131
House sparrow	0.023	-0.080	0.144
Kāhu	0.014	-0.124	0.170
Common myna	-0.004	-0.113	0.108
Ruru	-0.005	-0.165	0.169
Eurasian skylark	-0.006	-0.083	0.087
Brown quail	-0.008	-0.158	0.160
Riroriro	-0.012	-0.061	0.043
European goldfinch	-0.016	-0.135	0.129
Tauhou	-0.022	-0.119	0.085
Kōtare	-0.023	-0.125	0.094
Pīwakawaka	-0.034	-0.098	0.046
Wild turkey	-0.067	-0.229	0.097
California quail	-0.097	-0.210	0.014

Figure 5. Abundance curves for 33 species in four groups on Moturoa Island (North Island, New Zealand) 1982–2020. The y-axis gives abundances by year and on average across all routes, in units of birds per 10-minute station-count, with the raw observed value for each month (dotted line), the estimated values (posterior mean, dark solid line), and uncertainties (95% credible region in grey shadow). The date of rat control is a vertical line. Note that the y-axis is different for each species.
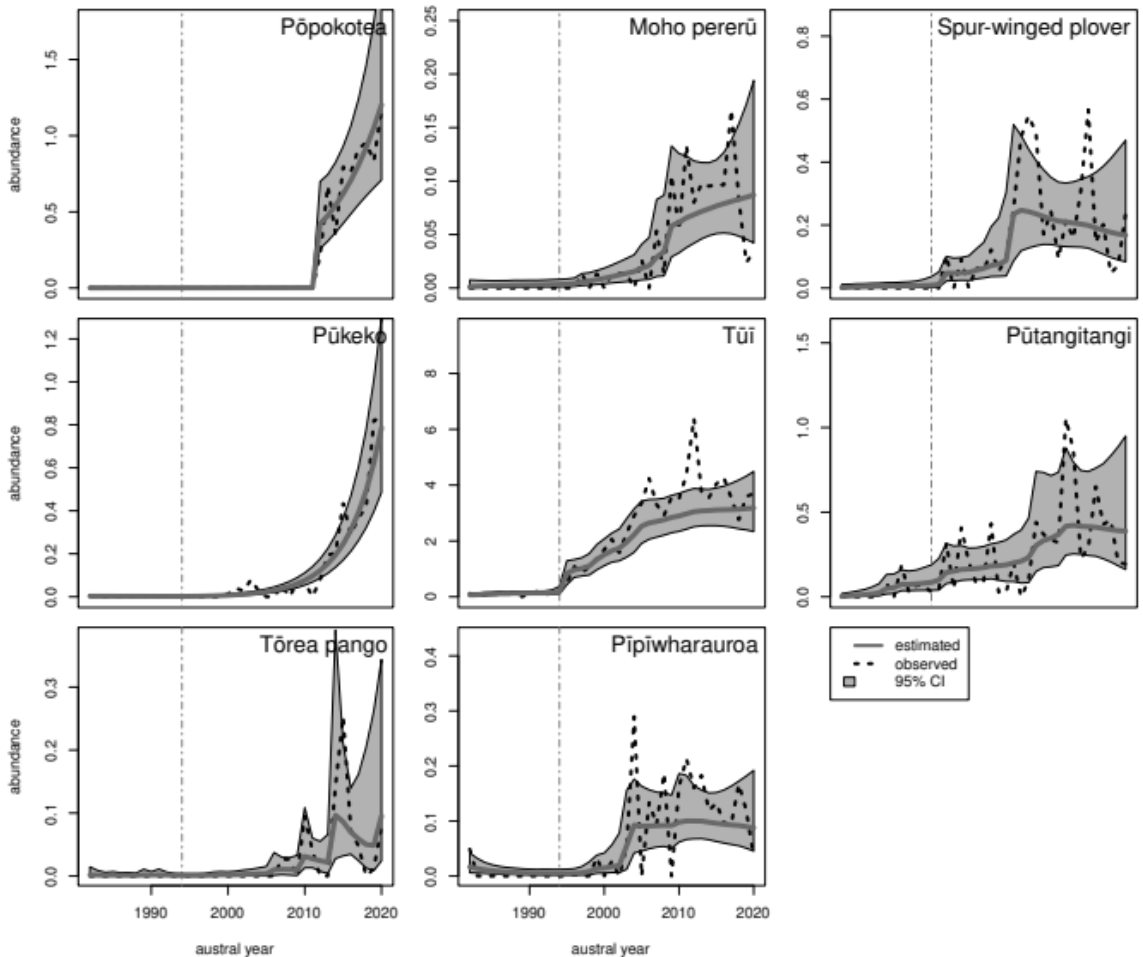

Figure 5A. Species Group A. Eight species that were uncommon or absent before rat control, increased dramatically after control, and continued increasing through the maturation period.

study," should be interpreted to mean that the set of species abundance curves for pūtangitangi that show a steady (but perhaps noisy) rise since their self-introduction has at least a 95% posterior probability. Below we mostly refer to the inferred population trajectories; for posterior distributions of the underlying parameters, see Supplementary Material Figures B, C, D, E, and F.

Birds in Group A were uncommon or absent before rat control, increased dramatically post

control, and continued increasing through the maturation period: tūī, pōpokotea, moho pererū (rail), pūkeko, pūtangitangi (shelduck), spur-winged plover, tōrea pango (variable oystercatcher, *Haematopus unicolor*), and pīpīwharauroa (cuckoo) (Fig. 5A). Six of the seven species whose populations were inferred to respond positively to the removal of rats (as shown by positive 95% credible intervals in Table 2), are in this group. The species in Group A are all native. Four of the six endemic species
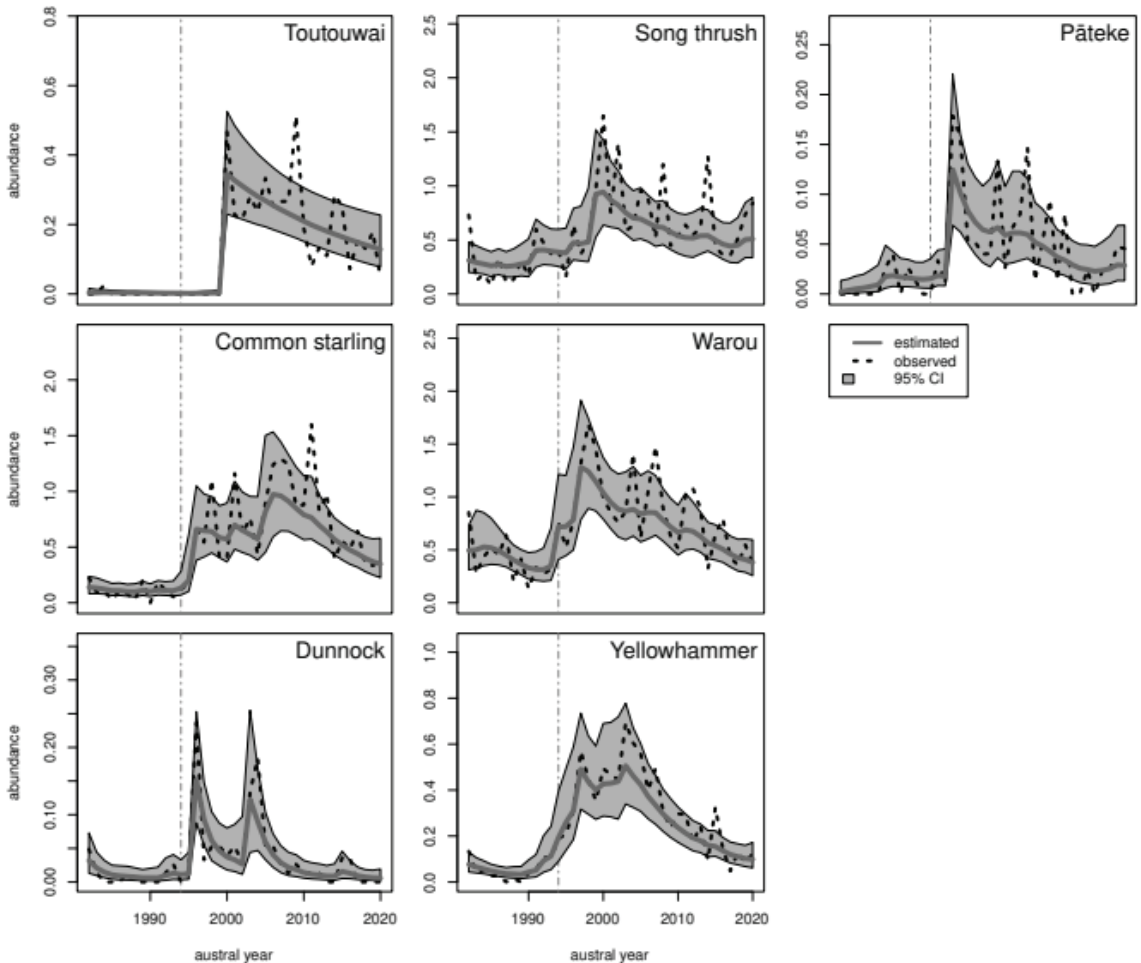
Figure 5B. Species Group B. Seven species that were uncommon or absent before rat control, increased markedly after control, and then declined through the maturation period.

that occur on the island are in this group (the other two are in Group B), as are four of the 11 recent immigrant species. Among the species in this group, the two reintroduced species, pōpokotea and moho pererū, both increased rapidly and are now found throughout the island. The self-introduced spur-winged plover, pūkeko, and tōrea pango increased dramatically even though they do not use directly the resources provided by vegetation restoration, and their increases were not obviously related to rat control. The pūkeko and the pūtangitangi were subjects of sporadic control efforts, pūkeko for its possible predation on pāteke chicks, and the pūtangitangi for fouling stock water troughs. Even the severe control of pūkeko in 2005 did not affect its numbers in our point counts. The tūī was very

rare pre-control. Then, through immigration, high fecundity, and/or survival, it increased markedly from about 0.2 birds per station before rat control to about five birds per station (depending upon the year) and appears to be stabilizing. The marked increase of pīpīwharauroa after rat control is curious because the abundance of its host, the riroriro, was slowly declining.

Group B included birds that were uncommon or absent before rat control, increased markedly after control, and then declined through the maturation period: toutouwai, common starling, dunnock, yellowhammer, pāteke (brown teal), song thrush, and warou (swallow) (Fig. 5B). Starling numbers were influenced by substantial daily movements to and from the mainland, probably involving a
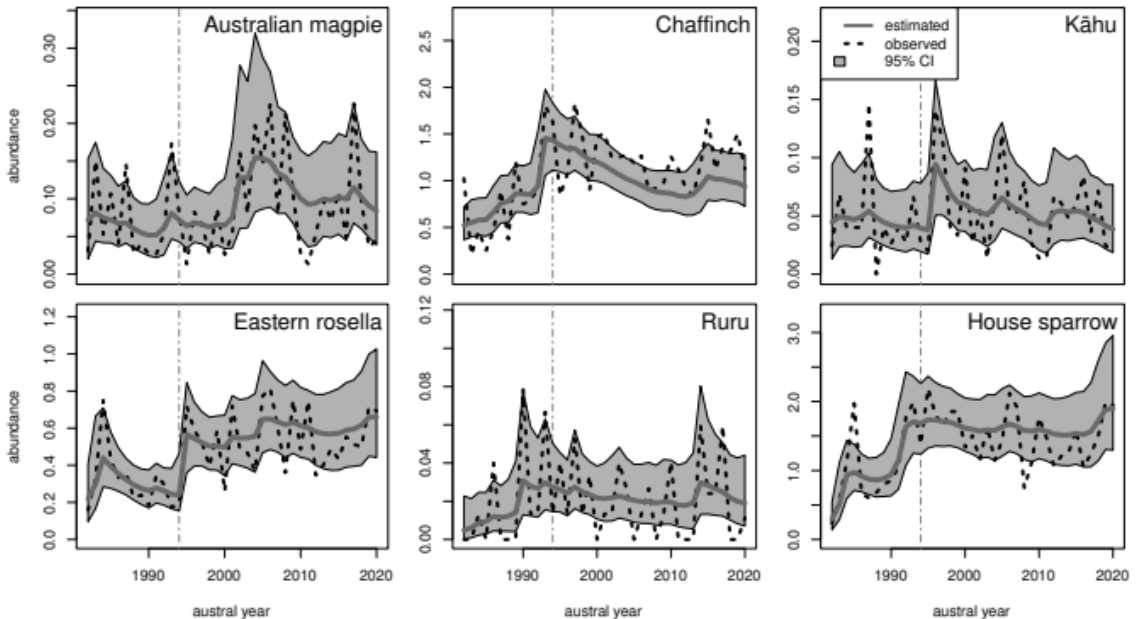
Figure 5C. Species Group C. Six species with fairly steady abundance throughout the study.

night roost on the island. Yellowhammer, song thrush, and warou declined steadily after a post-rat control increase. Two reintroduced birds were in this group, toutouwai and pāteke. Toutouwai were first reintroduced in 1983 but this was unsuccessful. A second reintroduction in 1999, after rat control, quickly became established. Despite successful breeding by these translocated birds, and a marked increase in numbers, the population has dwindled to just the residents of nine stable territories in damp forest patches on the south face of the island. Pāteke were first reintroduced in 1983. Most of these were seen only for about a year afterwards. Another introduction took place in 1985. The species has bred in some years, and has experienced a slow decline, despite the addition of ponds. Pāteke are strong fliers and readily disperse.

Birds in Group C were unchanging in abundance throughout the study: Australian magpie (*Gymnorhina tibicen*), kāhu (harrier), ruru (morepork, *Ninox novaeseelandiae*), rosella, chaffinch (pahirini, *Fringilla coelebs*), and house sparrow (Fig. 5C). These six species were in a fairly tight group in PC space. Their overall steady trends with no sustained increases or decreases suggest they adapt well to changing environments or are unresponsive to restoration on the island. Three of these species were generally sparse (Table 1). Ruru in particular, being nocturnal, was poorly sampled. Australian magpie was sporadically trapped out of concern for potential predation on native species (Innes *et al.*

2012) and is highly mobile.

Group D was made up of species that were common before rat control and then declined: pīwakawaka (fantail), tauhou (silvereye), riroriro (grey warbler), kōtare (New Zealand kingfisher, *Todiramphus sanctus vagans*), common myna, European goldfinch, Eurasian skylark, Eurasian blackbird (manu pango, *Turdus merula*), brown quail, California quail, common pheasant (*Phasianus colchicus*), and wild turkey (*Meleagris gallopavo*) (Fig. 5D). These 12 species included four of the 11 recent immigrants, notably the three common gleaners, pīwakawaka, tauhou, and riroriro, and eight of the 16 non-natives, including all four Galliformes. Wild turkey was subject to ongoing harvest, and in 1999 a severe reduction due to concerns that it was competing with sheep. Of special note in this group is the common myna, which was shown to cause mortality of small passerine birds on an island in the Seychelles (Feare *et al.* 2021). The low point in the estimated population (Fig. 5D) for common myna occurred during the 1995–6 myna control. During this time Tindall (1996) recorded decreased numbers of common mynas on the three forested census routes, compared to before control, while numbers in the two pasture counts remained the same. Tindall (1996) hypothesized that the pasture counts were influenced by a constant influx of birds from the mainland. No long-term effect on common myna abundance was seen from this control effort.
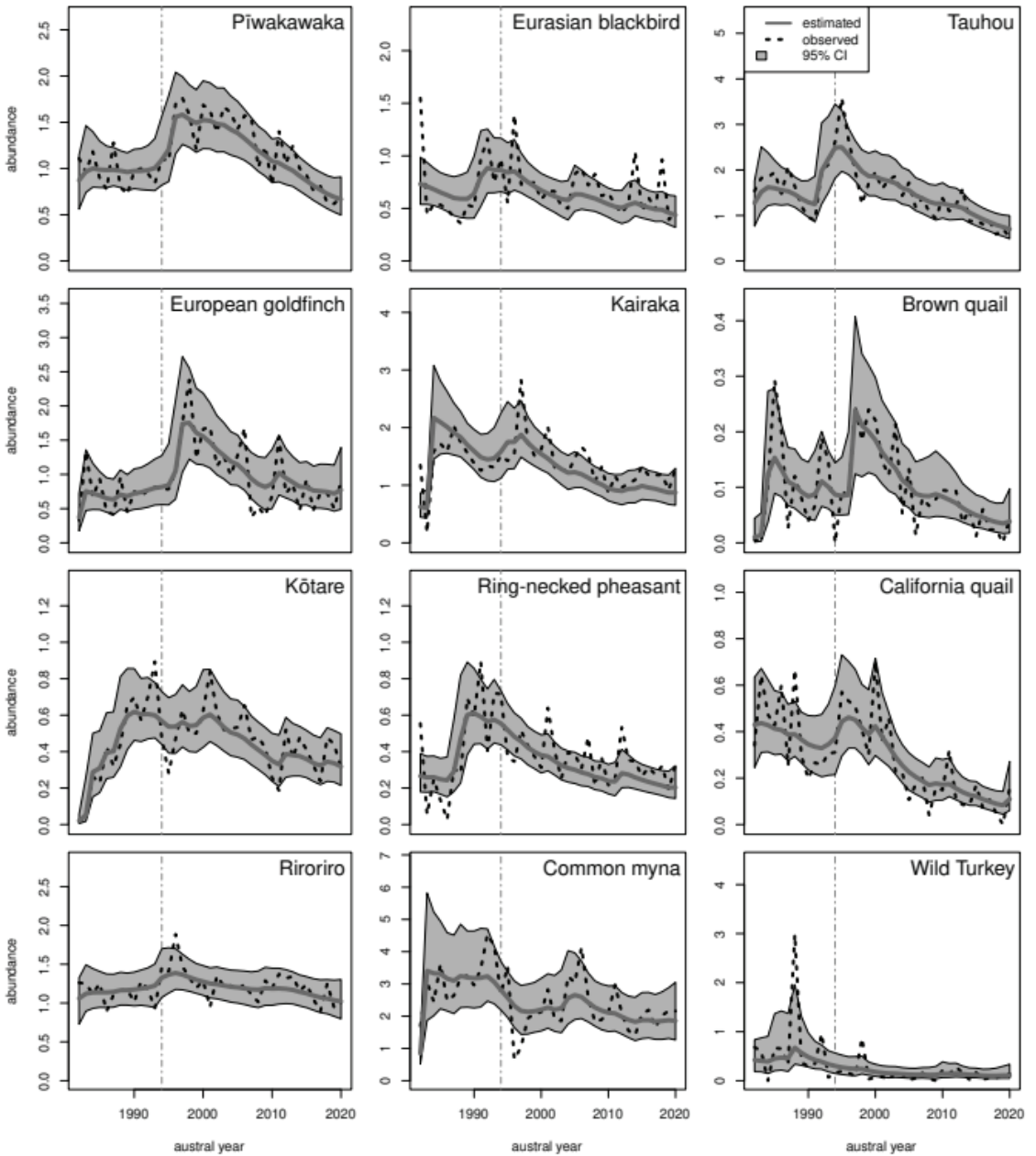
Figure 5D. Species Group D. Twelve species that were common before rat control, and then declined.

It was not hearing loss

When species' trends involve declines in numbers while the observers age significantly, the possibility of protocol drift or changes in hearing acuity is real. To test this possibility, we compared the proportion of observations that were audio or visual over the years (Fig. 6). The proportion of detections that were audio, though variable, was consistent (overall and separately by route). If observer acuity was changing, both audio and visual were shifting in tandem.
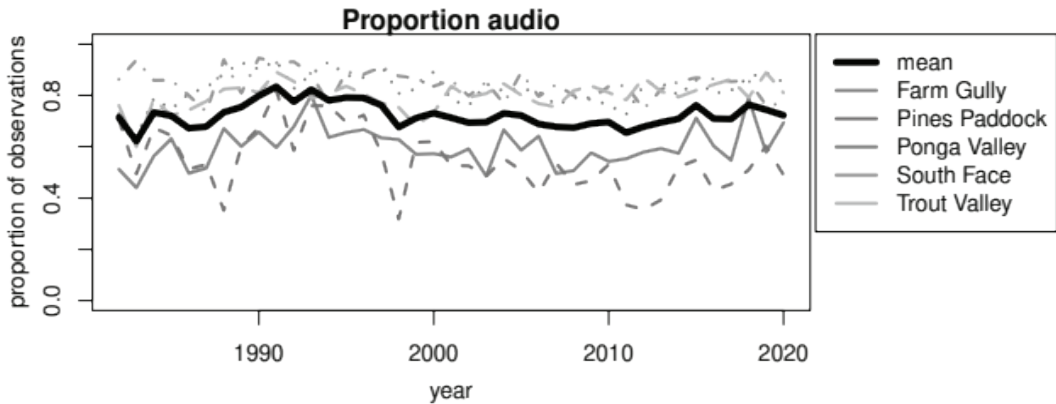
Figure 6. The proportion (%) of observations over time that were audio (first detected by hearing, rather than by sight) in each year in the five study routes, and the mean value (in black).

DISCUSSION

Our long-term record of bird abundances showed that after 38 years eight additional bird species became established (Table 1) and total bird abundance was 50% greater (Fig. 2). Our long, consistent, yearly record allowed statistical analysis and modelling to examine the causes of population changes.

Both reintroductions and self-introductions increased the total number of species. The five successful reintroductions, kiwi-nui, pāteke, pōpokotea, toutouwai, and moho pererū, credit the restoration efforts. The four unsuccessful reintroductions, korimako, tīeke, tētē-moroiti, and kākāriki, were part of the learning experience of reintroduction science. The self-introduction and breeding of six species – spur-winged plover, pūkeko, miromiro, Barbary dove, and rook (the last two were eliminated), are a credit to both their dispersal powers and the restoration efforts on the island.

As habitat changed on Moturoa, so did the bird community. This was shown through gradual shifts in many species' abundances and in Principal Component axis 1. This steady, gradual trajectory suggested it is the result of the change in the vegetation through restoration, a slow, steady process. Some species' abundances increased before predator control, as the first wave of planting and fencing was completed (Table 1, "Increase Timing" column). These species were likely responding to the vegetation restoration.

The effect on bird populations of controlling mammalian predators has been well documented in New Zealand, e.g. Miskelly 2018; Griffiths *et al.* 2019; Fea *et al.* 2020; Binny *et al.* 2020. Our study supports their conclusions with quantitative estimates. Our modelling showed that rat control:

(1) had a statistically robust effect for seven individual species; (2) likely caused a significant mean increase in abundance across all bird species combined; and (3) likely resulted in a typical increase in population growth of around 6% per year. These increases were likely due to increased reproduction and survival, although immigration could also have played a minor role.

Pest control on the nearby Ipipiri island group in the eastern Bay of Islands (about 8 km away) had a positive effect on bird abundances overall (Ralph *et al.* 2020). Despite the similar locations and overall results, all species did not respond the same in both places. Comparing the nine years after pest control in both the Ipipiri study and on Moturoa, of the 23 species in common, five increased in both studies, three declined in both, ten increased on Moturoa and decreased on the nearby islands, and trends in five were not significant. The fact that 10 out of 23 bird species responded differently to predator control, despite the similar climate, species lists, and general habitats, suggests other variables must be at play — one island vs. five, much active grazing vs. abandoned pastures, no tīeke vs. tīeke present, mice vs. no mice, etc.

The upward trajectories of many bird populations during the immediate post-control period on Moturoa gave way to different trends during the maturation period, signalled by the divergence of PC2 from PC1 about 2006 (Fig. 3). During these final years of the study, the only dramatic changes were large, ongoing increases in pōpokotea (reintroduced 2011) and pūkeko. Otherwise, most species' long-term declines or increases were continuing, although slowing. Nineteen species gradually declined, 11 of them in Group D (Table 1, "Later trend" column; Fig. 5). Other studies have found similar declines

after pest control, in a general context of overall increasing avian population. On Tiritiri Matangi, the abundance curves of Graham *et al.* (2013) often had inflection points, levelling off after increasing, at around eight years post control. Binny *et al.* (2020) found that many species abundance changes were stronger at and beyond seven years than at two years. Both these showed shifting trajectories on a time scale similar to our study.

These shifting trajectories and declining populations suggest a fourth cause of population changes, one that becomes visible in the maturation period; competition.

Competition

Competition has previously been suggested as a community organizing factor in some restoration studies. Specifically, at Zealandia, a predator-free, fenced sanctuary in Wellington, Miskelly (2018) found that the three most common and widespread natives (tauhou, riroriro, and pīwakawaka), as well as the non-natives, decreased when predators were removed. He suggested competition by restored endemics. In Fiordland, Miskelly *et al.* (2021) also found that kakaruai (South Island robin, *Petroica australis*) when reintroduced onto, or dispersed to, small, predator-free islands was a powerful competitor with other taxa.

On Moturoa the spectacular increases in abundance of tūī, pōpokotea, and pūkeko, while many other species largely declined, support the suggestion that these endemics can outcompete more recent arrivals. The obviously aggressive nature of tūī, its large size, and its numerical dominance on the island, cast it as a dominant competitor at any nectar source, and also it could deter other species foraging for insects. The prolific nature of pōpokotea, and their slightly larger size, position them as robust competitors with the other insectivorous native passerines: tauhou, riroriro, and pīwakawaka, especially when mammalian predators are removed or reduced. In recent years pōpokotea has become one of the most common species on the island, while other species have declined. Pūkeko is the largest common bird on the island and, while usually a grazer, can be a capable predator at times (Dey & Jamieson 2017). In principle, such competitive effects might be detected in our models; however, efforts to include between-species effects in our statistical model resulted in poor model convergence, likely due to a lack of power. The declining abundance of some species thus may be a sign that competition is a dominant force as the avian community develops. While the total number of individual birds at the end of this study was 50% higher than at the beginning (Fig. 2), that number stabilised, with more species fitting in, some species increasing, and some decreasing; suggesting a carrying capacity had been reached.

Endemicity of species

An interesting generalization about the winners and losers of competition after rat control is that populations of endemic species (with a long evolutionary history of being without mammalian predators) increased, while recent immigrants, and especially non-native species, remained unchanged or declined. Our study agrees on this subject with comprehensive meta-analyses by Binny *et al.* (2020) and Fea *et al*. (2020). Also, on Tiritiri Matangi Island, Graham *et al.* (2013) reported that 11 native species were reintroduced, and all increased. Non-natives and common, recent immigrants, such as pīwakawaka, riroriro, and tauhou, declined. Similarly, on islands in Fiordland, Miskelly (2021) found non-natives declined as endemics were introduced and rats and stoats controlled. In Zealandia, Miskelly (2018) showed strong positive population responses by endemic species to reduced pest populations. At the same time, non-native species and common recent immigrants declined after pest control. On the Ipipiri island group (Ralph *et al*. 2020), all six endemic species significantly increased (including three reintroduced species) after pest control, while 10 of 13 non-native species decreased. The eight species of recent immigrants had mixed trends, with six increasing and two decreasing.

On Moturoa the six endemic species increased after rat control (Table 2, Fig. 5). The three in Group A of Fig. 5, pōpokotea, tūī, and pūtangitangi, continued increasing, following the pattern of endemic species being strong competitors in restored habitat. The two endemic species in Group B, toutouwai and pāteke, increased and then declined. This is in contrast to the increase in the kakaruai (Miskelly 2021) in Fiordland, or toutouwai in Zealandia (Miskelly 2018). Similar to Moturoa, toutouwai on the Ipipiri group (Ralph *et al.* 2020), and on Tiritiri Matangi (Graham *et al.* 2013) decreased in a rat-free environment. These two latter studies are on islands off the east coast, in a drier climate than Wellington or Fiordland. As also found in other studies, on Moturoa the common recent immigrants pīwakawaka, riroriro, and tauhou, decreased, along with the non-native species, all in Group D of Fig. 5. Pūkeko expanded markedly, thriving in the pasture environment. The remaining four non-natives were in Group B, which also trended downward. Therefore, the development of the avian community on Moturoa generally supported the argument that endemic species out-compete non-natives in a restored environment especially when mammalian predators are removed.

Conclusions

On Moturoa our consistent, yearly, long-term bird counts produced data quantifying the success of our project. We demonstrate that both habitat improvement and mammalian predator control were effective, and that the effect of our predator control was a 6% mean increase in population growth rate. We can say with confidence that the shareholder efforts of fencing, planting, trapping, poisoning, weeding, and translocating have been rewarded with more species and more individuals of birds. Our data also suggested that important shifts in bird populations develop more than ten years after predator control starts. Consistent, ongoing bird counts like these could provide an important assessment of the nation-wide effort to rescue native wildlife in New Zealand via mammalian predator control, habitat improvement, and reintroductions.

SUPPLEMENTARY MATERIAL

Point count data and other supplementary material, including R code and the Stan model used to fit the data are available at https://doi.org/10.5061/dryad.4tmpg4fd6. Supplementary figures and tables are available at: https://doi.org/10.5281/zenodo.6896211.

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