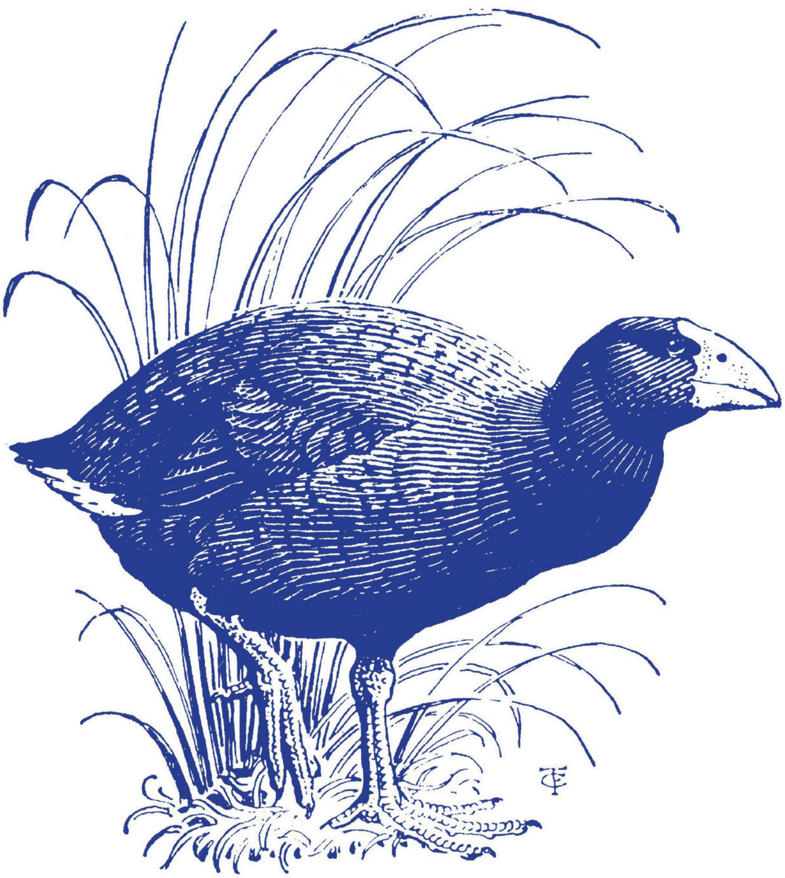
NOTORNIS

Ornithology of the Southern Pacific



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Short term effects of an aerial 1080 operation on mātātā (South Island fernbird, *Poodytes punctatus punctatus*) in a South Island wetland

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Abstract: New Zealand conservation managers use aerial 1080 (sodium fluoroacetate) to control invasive mammalian predators, often with the aim of protecting populations of threatened endemic birds. Matātā (South Island fernbird, *Poodytes punctatus punctatus*) are endemic to New Zealand wetlands and are vulnerable to mammalian depredation. Mātātā populations might benefit from aerial 1080 predator control, but they also can suffer non-target poisoning losses. This study measured the short-term effects of an aerial 1080 operation on mātātā adult survival (i.e. non target mortality) and nest survival (over one breeding season) on the West Coast of South Island. The study utilised two sites, with an October (mid-breeding-season) aerial 1080 operation at one of the sites. We found no evidence of a negative short-term effect of aerial 1080 – none of fourteen colour-banded adult mātātā exposed to 1080 baits died of 1080 poisoning. Conversely, we found evidence of a short-term positive effect – aerial 1080 improved mātātā nest survival over one breeding season. The presence of a positive effect, in the absence of a negative effect, suggests that the net effect of the 1080 operation for the mātātā population was positive, at the end of the breeding season.

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Keywords: mātātā, fernbird, *Bowdleria, Poodytes punctata punctata*, aerial 1080, pākihi, nest survival, predator, control, non-target

INTRODUCTION

Introduced mammalian predators are the primary reason for the decline of most New Zealand native avifauna (Innes *et al*. 2010; O'Donnell *et al*. 2015). Predator control, therefore, is a key activity for New Zealand conservation managers. However, tools and funding for predator control are limited and conservation interventions may not always deliver the desired outcomes. Designers of conservation programs require a sound knowledge base for deciding which control tools to use, and how to use them. Each tool must be tested in a systematic way to build confidence that the desired benefits will manifest.

Aerial 1080 (sodium fluoroacetate) baiting is commonly cited as a relatively cost-effective means by which invasive browsers and predators can be controlled in New Zealand landscapes. Indeed, aerial 1080 is the only invasive mammal control

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method deployed in many New Zealand ecosystems, including forests and wetlands. Field studies underpinning this action are more commonly from native forests than from wetlands, despite New Zealand's wetlands ranking highly in national and international conservation prioritisation systems and despite wetlands being inhabited by a suite of threatened birds and invasive mammals (O'Donnell *et al*. 2015).

One such bird, mātātā (fernbird, *Poodytes punctatus*), is endemic to New Zealand at the species level. A North Island subspecies (*P. p. vealeae*) and a South Island subspecies (*P. p. punctatus*) are both classified as At Risk/Declining (Robertson *et al*. 2021). Mātātā populations have declined through various agents, including habitat loss as wetlands have been converted to pasture (Miskelly 2013). Rates of wetland drainage have slowed to near zero in recent decades, but mātātā continue to be impacted by introduced mammalian predators such as stoats (*Mustela erminea*), ship rats (*Rattus rattus*), mice (*Mus musculus*), and feral cats (*Felis catus*) (see O'Donnell *et al.* 2015). For example, mustelids (Mustelidae) and mice were implicated as primary agents of nest failure in a North Island saltmarsh (Parker 2002).

Ground-based insectivory, with a component of omnivory, is the primary foraging mode for mātātā. This can potentially lead to both direct and indirect ingestion of poison intended for predators, and thus to the deaths of some individuals, as has been reported for similar-sized forest passerines with similar foraging ecology – robins and tomtits (*Petroica* spp.) (Powlesland *et al*. 1999; Powlesland *et al*. 2000; Bell *et al*. 2021). For mātātā, the single published study on non-target 1080 poison risk reports a mortality rate of 9.4% for South Island mātātā in South Westland (95% confidence interval 2.4–22.6%) (van Klink *et al*. 2013). Non-target poisoning rates of some bird species have varied significantly among aerial baiting operations (e.g. Veltman & Westbrooke 2011; Kemp *et al*. 2019). This suggests the need for measurements from several operations to enable sound conclusions about average risk levels.

The question of whether gains from aerial 1080 baiting, for mātātā, outweigh losses is not yet evaluated, largely due to absence of measurement. Here, we address this to some extent via a study of nest survival and non-target poisoning rates, conducted over a single mātātā breeding season. Our study utilises two wetlands, one of which was baited aerially with 1080 partway through the nesting season. We thereby contribute to the evidence base on the costs and benefits of aerial 1080 for wetland birds. We do not evaluate long term population outcomes, but in time our results may be useful for this.

METHODS

Study sites

Two wetlands, or 'pākihi', west of the Paparoa Range in the Buller district were utilised, one of which was subject to an aerial 1080 operation in the spring of 2017. Pākihi are open vegetated areas covered in tangle-fern (*Gleichenia dicarpa*), sedges (*Machaerina* spp.), and mānuka (*Leptospermum scoparium*), on infertile peaty soils. In the northwest of the South Island, pākihi are both natural and created by human disturbance (Williams *et al*. 1990). Both of our study pākihi were surrounded by beech forest and our treatment site, 'Tiropahi', was more than 1 km inside the boundary of the 1080 operation (Fig. 1).

Our non-treatment site, 'Costello Hill', was a readily accessible pākihi on the top of a rise at 70 m elevation. The sides of the rise were vegetated with beech, and surrounded by farmland, scrub, the

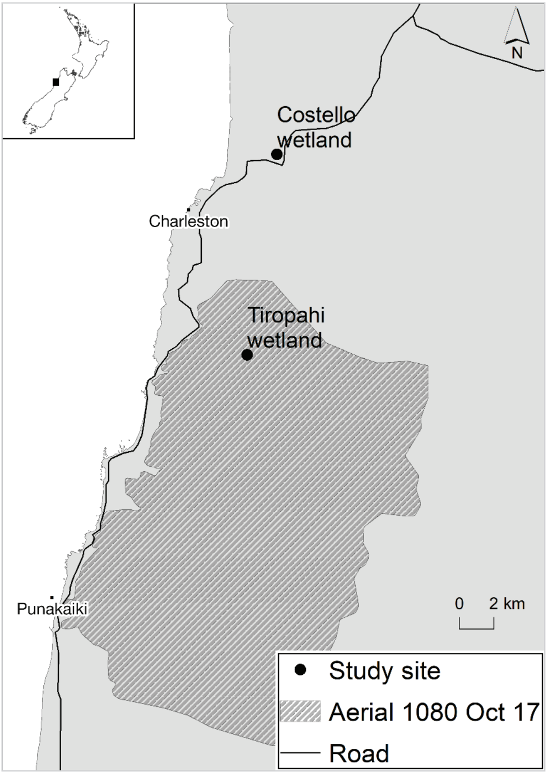

Figure 1. Locations, on the New Zealand West Coast of the South Island, of the two pākihi wetlands, 'Tiropahi' (aerial 1080 treated, 41′59″S, 171′28″E), and 'Costello' (untreated, 41′53″S, 171′29″E), used to measure short-term effects of aerial 1080 on mātātā (South Island fernbird, *Poodytes punctatus punctatus*) populations.

Little Totara River, and State Highway 1. Costello Hill had possum monitoring carried out annually, which included some kill-trapping (B. Waddell *pers. comm.*). The most recent organised pesticide used was ground-based poison baiting on farm edges about 1.2 km away, three to four years before this study (B. Waddell *pers. comm.*). The treatment site, Tiropahi pākihi, was at 180 m elevation. It had a cut-over pine (*Pinus radiata*) plantation on its northwest side, and beech-podocarp forest on the opposite side.

Study period

From September 2017 we visited both sites on an approximately weekly basis to capture adult mātātā (South Island fernbird) for marking with individually identifiable combinations of coloured leg bands, and to find and monitor mātātā nests. The Tiropahi site was treated with aerial 1080 on 28 October 2017, about a month after the first mātātā eggs were found, at which time we had already found 18 broods (nests containing eggs and/or young nestlings). We visitied the study sites until January 2018.

Predator monitoring

We monitored the abundance of mustelids and rats, using standard tracking tunnel transect methodology (Gillies & Williams 2013). We installed six tracking tunnels lines at each site, three on the pākihi and three in the surrounding forest. Lines were spaced at least 200 m apart. Overnight surveys for gauging rodent relative abundance were conducted on all installed lines. Peanut butter was smeared onto the ends of each tracking tunnel to attract rodents during overnight surveys. To gauge mustelid relative abundance, in addition to rodent abundance, further surveys lasting 8–9 nights were done, using three-four lines per site to maintain a spacing of >1 km between lines. Tunnels in these longer surveys were baited with salted rabbit meat to attract mustelids. Surveys were conducted simultaneously at the two sites. Both sites were surveyed twice for both rodents and mustelids – once prior to the aerial poison operation, and again afterward. We calculated the rat tracking as the mean proportion of tunnels per line that detected rats, and mustelid tracking as the proportion of lines that detected mustelids (Gillies & Williams 2013).

Colour banding of adult mātātā

We caught adults with mist nets and banded each with a unique combination of metal and colour bands. The resultant ability to identify individuals enabled measurement of non-target poisoning rate and assisted with nest finding and assessment of final nest outcomes, for measurement of nest survival.

Re-sighting surveys for non-target poisoning rate

On 26 October 2017, two days before the aerial 1080 operation, we surveyed for banded birds in their nesting territories (see below). We played pre-recorded mātātā vocalisations on portable speakers to attract birds, and allow colour-band combinations to be read with binoculars. Post-operation surveys were done on 31 October and again on 1 November, three and four days after baiting, respectively. Four consecutive days of heavy rain from 2 November to 5 November rendered the bait non-toxic, thus the 'risk period' of non-target poisoning was ended. Further re-sightings of banded individuals were recorded over the remainder of the nesting season.

Nest monitoring

Mātātā nests were found either by passive observation of adult birds, or by offering them feathers as nesting material and then following to the nest. Once located, nest fate was determined by weekly observer visits, and/or by trail cameras mounted on vegetation near the nest. Nest age was determined by comparing nestling appearance to a reference photo collection of known-age nestlings. Nests that failed at egg stage were assigned an age based on the median date of observer visits to that nest. Mātātā have a mean incubation period of 13 days and a nestling period of 17 days (Heather & Robertson 2005). For this study, we truncated observations at 28 days. Beyond this age we could not reliably distinguish nest failure from fledging (fledglings could not be consistently found to determine nest success).

Nest survival analysis

We constructed five alternative generalised linear models (GLMs) comprising various combinations of factors standing to affect nest survival. These models contained different combinations of Site and Time, within the Before-After-Control-Impact (BACI) experimental paradigm, plus all models included a quadratic effect for nest age, which allowed nest survival to vary across the nesting period, an effect which has been found in other New Zealand birds (Elliott 1996; Armstrong *et al*. 2002; Grant *et al*. 2005; van Heezik *et al*. 2020). This last model was important, as the interaction explicitly tests for the treatment effect of aerial 1080 treatment, whilst controlling for site and time effects. The time parameter was a binary covariate which codes whether a nest encounter date was before or after the 1080 operation date, regardless of site. It was therefore possible for a nest to experience both before and after time effects. We used GLMs with a binomial family to model daily survival rates (DSR) of nests (Rotella *et al*. 2004), with a complementary log-log (cloglog) link function (Bolker 2014). Exposure days were included as an offset in all models to account for variable-length nest monitoring histories (Rotella *et al*. 2004). Exposure was coded as one for each day a nest was active. If a nest failed, exposure was calculated as the number of days between the date the nest was last active and the date the nest was found failed.

Models were ranked by the Akaike Information Criterion corrected for small sample size (AICc). If the most parsimonious model was > 2 ΔAICc points above the next model, we took this as indicating strong support for that model (Burnham & Anderson 2002) and used this model to predict daily nest survival rates at each site before and after the operation. Nest success over 30 days, the average duration of a nest, was estimated by taking the product of DSR values from day 1 to day 30 (Dinsmore *et al*. 2002). Bootstrap 95% confidence intervals for nest success were estimated by running 500,000 bootstrap simulations (Cooch & White 2020). All analyses were run in program R (R Core Team 2021).

RESULTS

Predator abundance

Tracking tunnel surveys at the treatment site returned a small number of rodent prints before the operation and none after (Tables 1 & 2), while rodent tracking rates showed no clear pattern of increase or decline at the non-treatment site. Almost all mammal detections (i.e. footprints in tracking tunnels) at both sites were in forest adjacent to the pākihi. The only detections *on* the pākihi were of mice, at the non-treatment site.

Nest monitoring

A total of 45 nests were monitored, of which 22 were at the treatment site and 23 at the non-treatment site (Fig. 2). The timing of nesting was very similar at the two sites, with early clutches laid in early October in both sites (Fig. 2). About ten nests at each site were initiated prior to the aerial 1080 operation. There were 21 cases of nest failure, four at the treatment site prior to the aerial 1080, and 17 at the non-treatment site (Fig. 2).

Failed nests were usually found empty although they occasionally contained broken eggshells, suggesting predation had occurred. We had limited success identifying nest predators with trail cameras. However, five predators were recorded visiting failed nests: four stoat visits were recorded at the non-treatment site, and one western weka (*Gallirallus australis australis*) visit at the treatment site. Field sign at these failed nests ranged from no remains, to shell fragments, and nestling remains. The weka removed all eggs and disturbed the camera equipment. Of the other three failed nests at the treatment site, two were empty, whilst nestling pin-feathers were found at the third.

Nest survival

The "Site + Time + Site*Time + Nest age^2" model (i.e. the interaction model that explicitly tests the treatment effect) was the most parsimonious nest survival model, based on AICc. We present results based on this model, as the next best model, Site + Treatment + Nest age^2, was separated by >2 AICc points (Table 3). Overall, daily survival rates (DSR)

Table 1. Overnight survey tracking tunnel results at non-treatment and treatment sites before and after aerial 1080.

Site	Date	Rat (%)	Mouse (%)
Non-treatment before	17 October 2017	3	0
Non-treatment after	9 December 2017	5	2
Treatment before	17 October 2017	2	3
Treatment after	9 December 2017	0	0

Table 2. Extended survey tracking tunnel results at non-treatment and treatment sites before and after aerial 1080. The surveys occurred for eight and nine nights pre- and post-aerial 1080 respectively. Mustelid results calculated as proportion of transects with tracks.

Site	Date	Rat (%)	Mouse (%)	Mustelid (%)
Non-treatment before	18 October 2017	27	3	33
Non-treatment after	31 October 2017	33	0	33
Treatment before	18 October 2017	17	0	0
Treatment after	31 October 2017	0	0	0

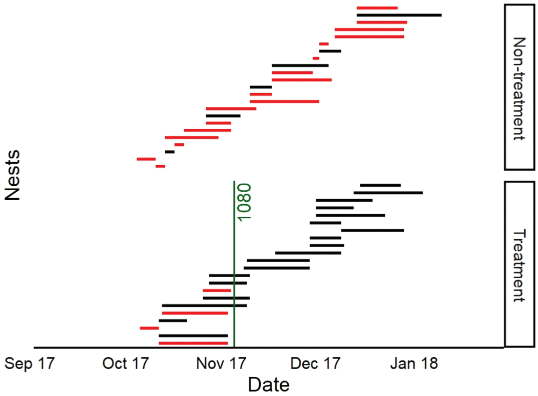

Figure 2. Summary of mātātā (South Island fernbird, *Poodytes punctatus punctatus*) nest survival observations. Treatment = Tiropahi wetland; non-treatment = Costello wetland. Each horizontal line represents an individual nesting attempt. Line length indicates the number of days each nest was under observation. Nests that failed are coloured red.

Table 3. Model results of mātātā nest survival analysis. k = number of parameters, weight = model weight.

Model	k	AICc	ΔAICc	weight
Site * Time + Nest age^2	6	131.822	0	0.84
Site + Time + Nest age^2	5	135.373	3.55	0.14
Site + Nest age^2	4	139.021	7.2	0.02
Time + Nest age^2	4	150.714	18.89	0
Nest age^2	3	152.222	20.4	0

derived from the top model, 1) declined with nest age, 2) were higher at the treatment site than the non-treatment site, and 3) were higher during the 'After' phase of the study (Fig. 3). That is, both Site and Time effects were evident. However, the high ranking of the interaction model indicates a disproportionate increase in DSR at the treated site in the 'After' phase. Here, nest success over 30 days, calculated using DSR estimates from the best model ([lower 95% confidence interval, upper 95% confidence interval]), improved from 39.9% [7.0, 69.3] to 100% (a confidence interval could not be estimated for the treatment site after the 1080 operation as there were no nest failures) with aerial 1080 treatment (Fig. 4). At the non-treatment site, nest success over 30 days was 5.2% [0.1, 24.9] during the 'Before' phase and 21.9% [5.1, 41.0] afterward (Fig. 4).

Survival of banded adults through 1080 baiting period

At the treatment site, 14 banded birds were confirmed as exposed to bait, via sighting within the treatment area just before and just after the operation. Significant rain occurred about a week after baiting, after which poison pellets were visibly disintegrated. All 14 exposed mātātā were resighted at least monthly until January 2018. That is, no mortality occurred among our sample birds during the period when toxic bait was present.

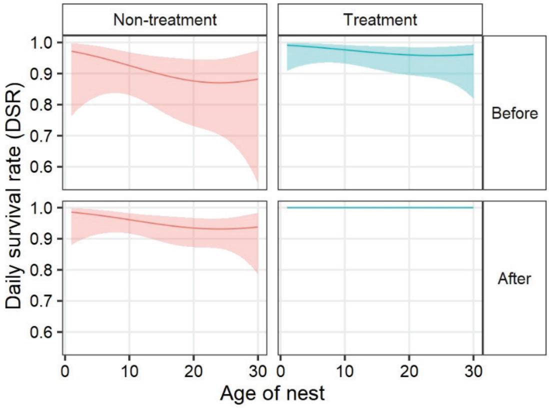

Figure 3. Mātātā (South Island fernbird, *Poodytes punctatus punctatus*) daily nest survival, by nest age, site (Treatment = Tiropahi wetland; non-treatment = Costello wetland) and time (Before and After aerial 1080 at Tiropahi wetland). Shading indicates 95% confidence bounds.

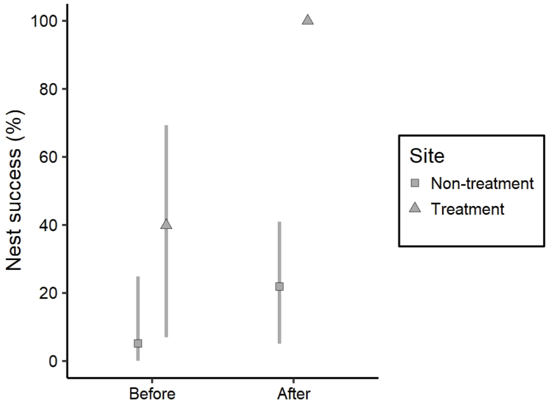

Figure 4. Mātātā (South Island fernbird, *Poodytes punctatus punctatus*) nest success results with bootstrap confidence intervals. Confidence intervals could not be calculated for the treatment site after aerial 1080 as no nests failed.

DISCUSSION

We found no evidence of any non-target poisoning losses to our study population of mātātā from aerial 1080 baiting. Conversely, we found evidence for a productivity benefit, manifest via improved nest survival. Therefore, our study supports the notion that the poison operation had a positive effect for the Tiropahi mātātā population, over the timeframe of our study (one breeding season).

Our finding of improved nest survival is consistent with previous research that has found aerial 1080 within a breeding season improved the nest survival of native birds, including birds of similar size with similar foraging ecology (albeit in forest rather than wetland) (Powlesland *et al*. 1999; Armstrong *et al*. 2002; Kemp *et al*. 2018; Bell *et al*. 2021).

Measurement of long-term population trends is required to check that a short term benefit, such as we found, translates to increased mātātā density and population security over longer time frames. Longer time frames include out-years, more distant from control operations, in which benefits can be undone by repopulating predator populations (Bell *et al*. 2021). We recommend long-term population trend measurement at multiple managed and unmanaged sites, rather than further studies of short-term costs and benefits.

The nest survival rates we report here for the no-predator-control context are like those reported in previous studies of mātātā, which were both in no-predator-control contexts. Parker (2002) found nest success to be 22% from 21 koroātito (North Island fernbird, *P. p. vealleae*) nests. Harris (1986) found 31% nest success (no confidence intervals reported) for 41 mātātā nests. We found nest success rates of 5% to 40% without predator control.

We were not able to clearly relate predator interactions with mātātā nests to site and treatment. While trail cameras at nests confirmed stoats and weka as predators of mātātā, it was not possible to determine the reason for failure of most failed nests. A reduction in weka density after 1080 seems an unlikely explanation for the improved nest survival at the treatment site, as Tinnemans *et al*. (2018) report a very low weka mortality rate of 1.8% from 1080 baiting. Control of mammalian predators is a more likely mechanism, based on consistency with other studies and on our predator survey results. While overnight rodent tracking rates were uninformative (Table 1), the extended predator surveys we ran over 8–9 nights indicate effective rodent control (Table 2). This is likely to have caused the deaths of mammalian carnivores (i.e. stoats) by secondary poisoning (Murphy *et al*. 1998). Therefore, we strongly suspect that rats and mustelids were at reduced density in the treatment site after the 1080 operation. (The zero-mustelid tracking rate at the treatment site before treatment could be an artefact of the small number of tracking tunnel transects). Alternative explanations for the disproportionate increase in nest survival at Tiropahi after aerial 1080 bait are difficult to surmise, given that the two study sites were comparatively similar in geography, aspect, vegetation, and climate. We note that mātātā habitat varies and the extent of water coverage at a site or proximity to other ecosystems such as coastal dunes, or farms, could affect predator assemblages at a site, but our two sites were intentionally selected as generally similar.

Our mammalian predator detections on tracking surveys were almost exclusively in the forest adjoining the pākihi wetlands. This emphasizes the importance of considering predators in areas surrounding mātātā habitat as a source of risk both to nests and nesting mātātā on the pākihi, and to juveniles and unmated individuals residing in adjacent ecosystems (see Parker 2002). Our study pākihi were adjacent to beech forests. Beeches are masting species, irregularly producing massive seedfalls that support large increases in mammalian predators including mice, ship rats, and stoats (King 1983; White & King 2006). Our nest survival results were from a post-mast year, when we expected low rat density but high stoat density in the adjacent forests, possibly spilling over onto the pākihi. Rat relative abundance was as we anticipated, but stoat relative abundance appeared lower than anticipated. While our study supports an effect of predator reduction on mātātā nesting success in this context, our result may have been different in other contexts.

In summary, our analysis suggests that aerial 1080 improved mātātā nest survival, probably via the control of mammalian predators, with no losses of adult mātātā from non-target poisoning. This builds on existing evidence which collectively indicates that aerial 1080 can be a constructive part of conservation programmes for threatened species in New Zealand.

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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.

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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).

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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

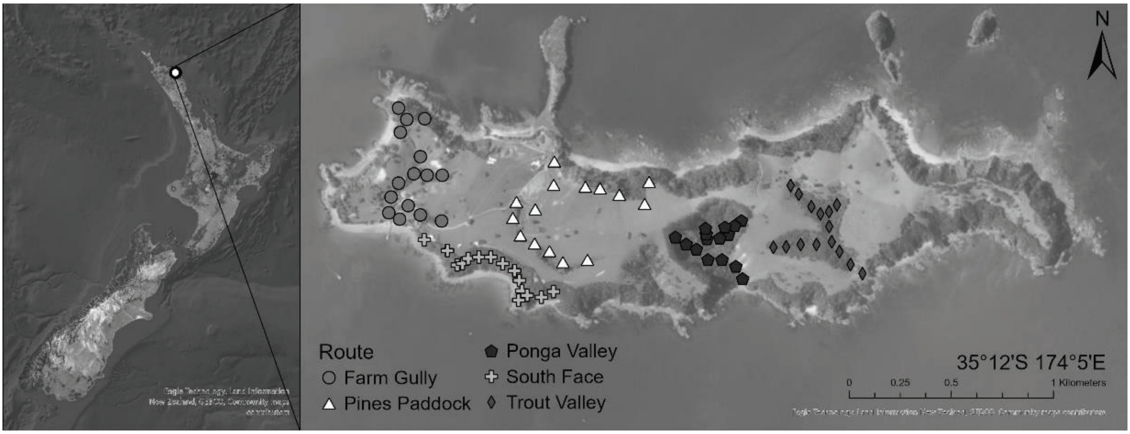

Figure 1. Moturoa Island (North Island, New Zealand) paddocks, bush, and bird counting routes, and stations.

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 rufusate*r) (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:

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

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 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.

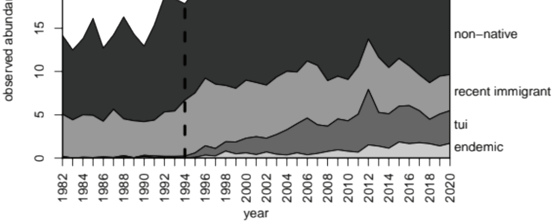

Figure 2. The abundance of all species on Moturoa Island (North Island, New Zealand) by origin of the species (Table 1): 18 non-natives (introduced by humans); 14 recent immigrants (with close relatives in Australia); tūī (*Prosthemadera novaeseelandiae*) (a very abundant endemic); and 13 New Zealand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

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.

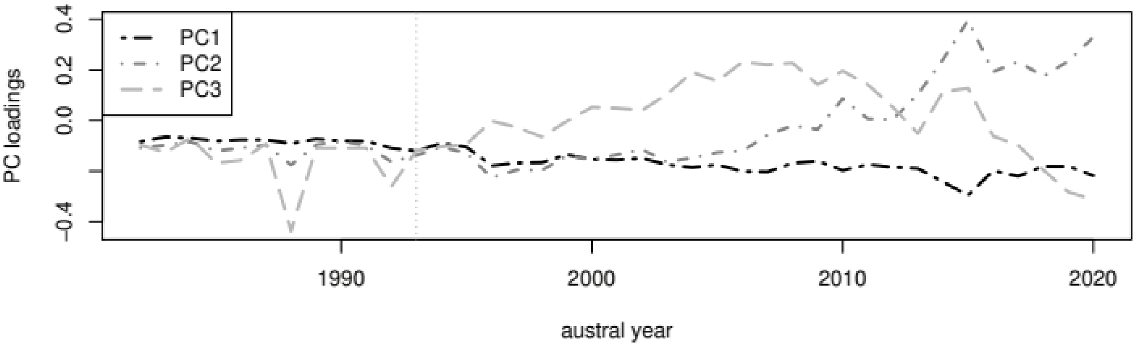

Figure 3. The first three principal components of raw observed species abundances over time, showing general trends in species composition. The vertical line indicates the first rat control (in 1993). As discussed in the text, this visualization suggests three time periods, divided roughly into pre-control, post-control (when PC3 is high), and a final period we refer to as "maturation" (when PC2 is high).

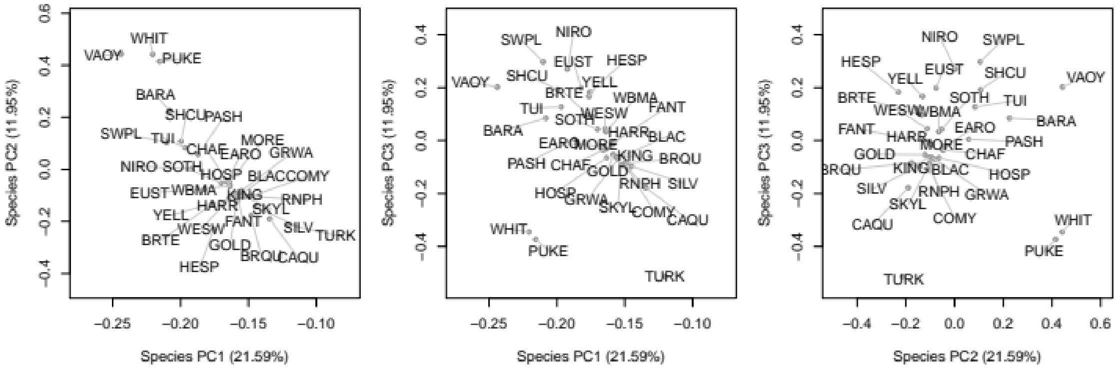

Figure 4. Loadings of each species' observed abundances on the first three principal components of Figure 3. The left figure is PC1 (x axis) vs. PC2 (y), the center is PC1 (x) vs PC3 (y), and the right is PC2 (x) vs. PC3 (y). The four-letter species codes are shown in Table 1. An interactive version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

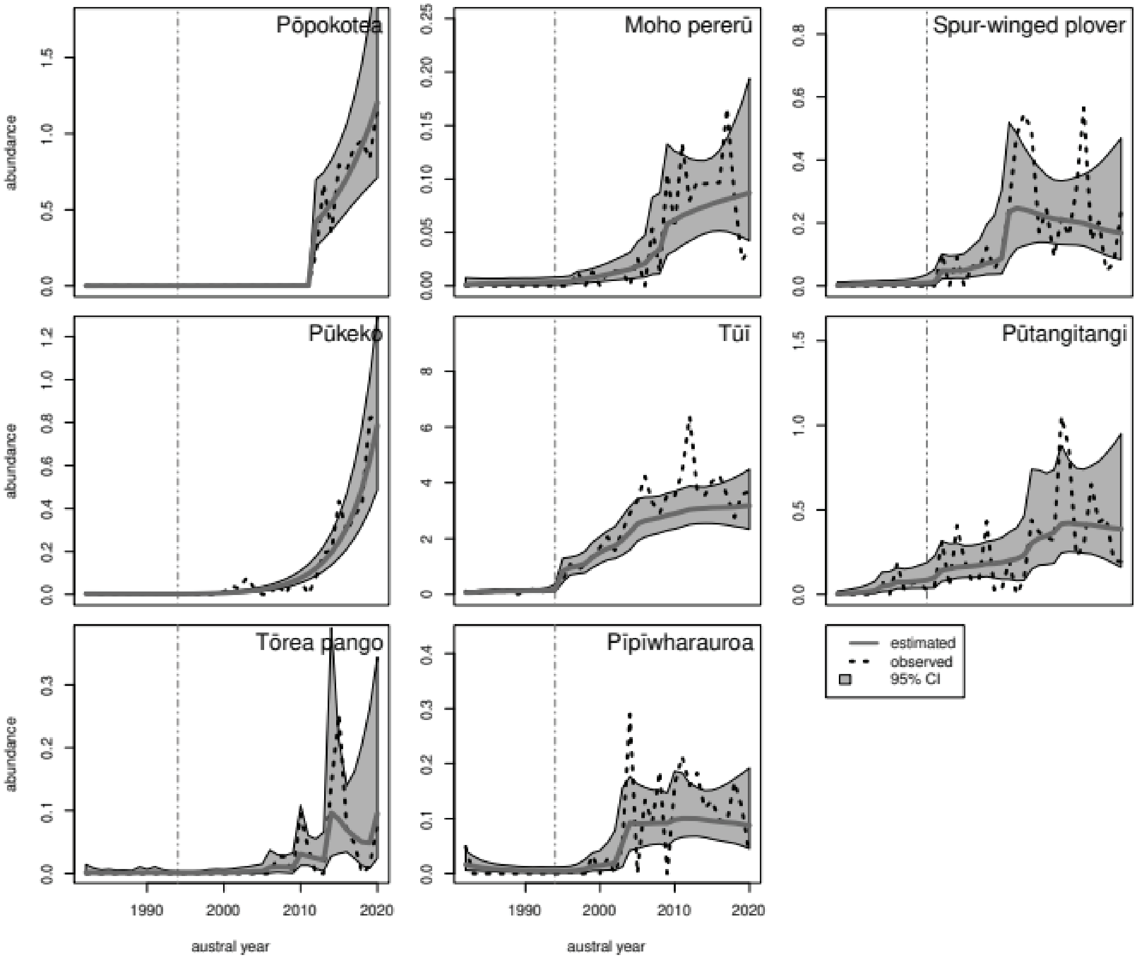

Figure 5A. Species Group A. Eight species that were uncommon or absent before rat control, increased dramatically after control, and continued increasing through the maturation period.

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

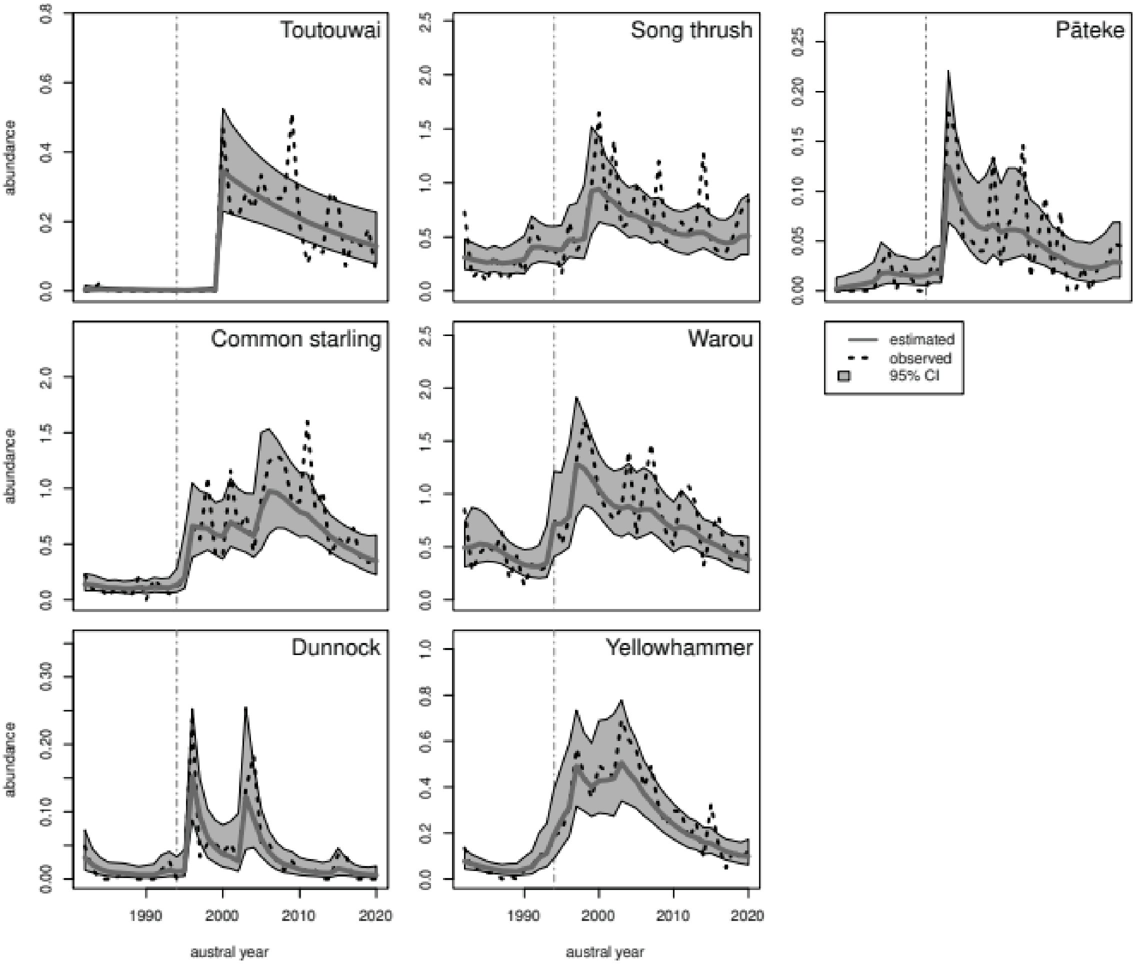

Figure 5B. Species Group B. Seven species that were uncommon or absent before rat control, increased markedly after control, and then declined through the maturation period.

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

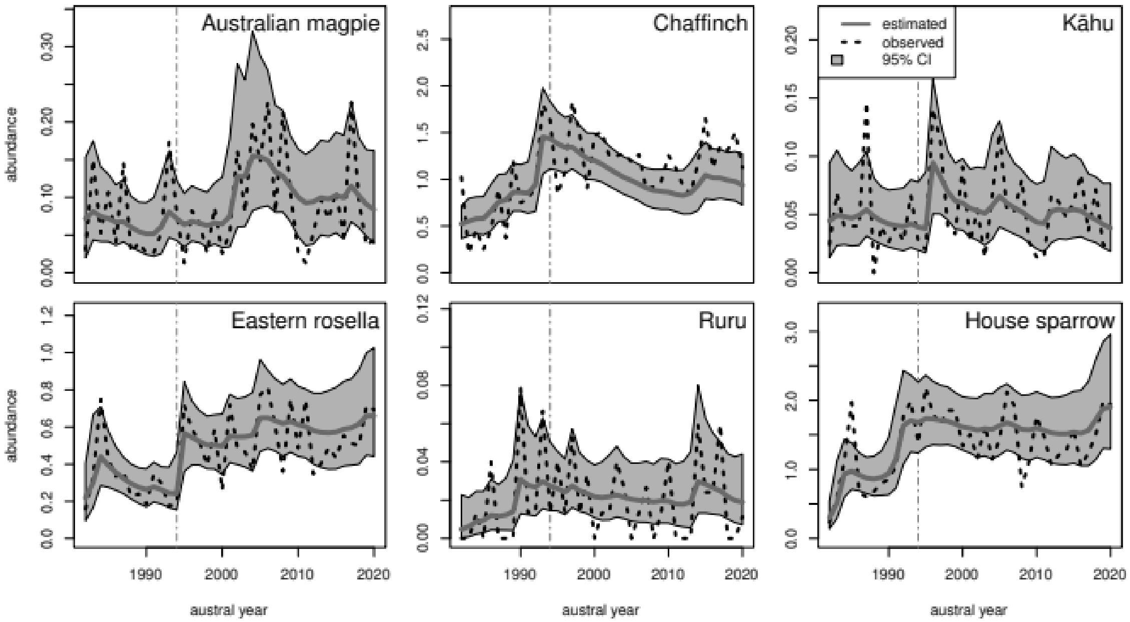

Figure 5C. Species Group C. Six species with fairly steady abundance throughout the study.

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.

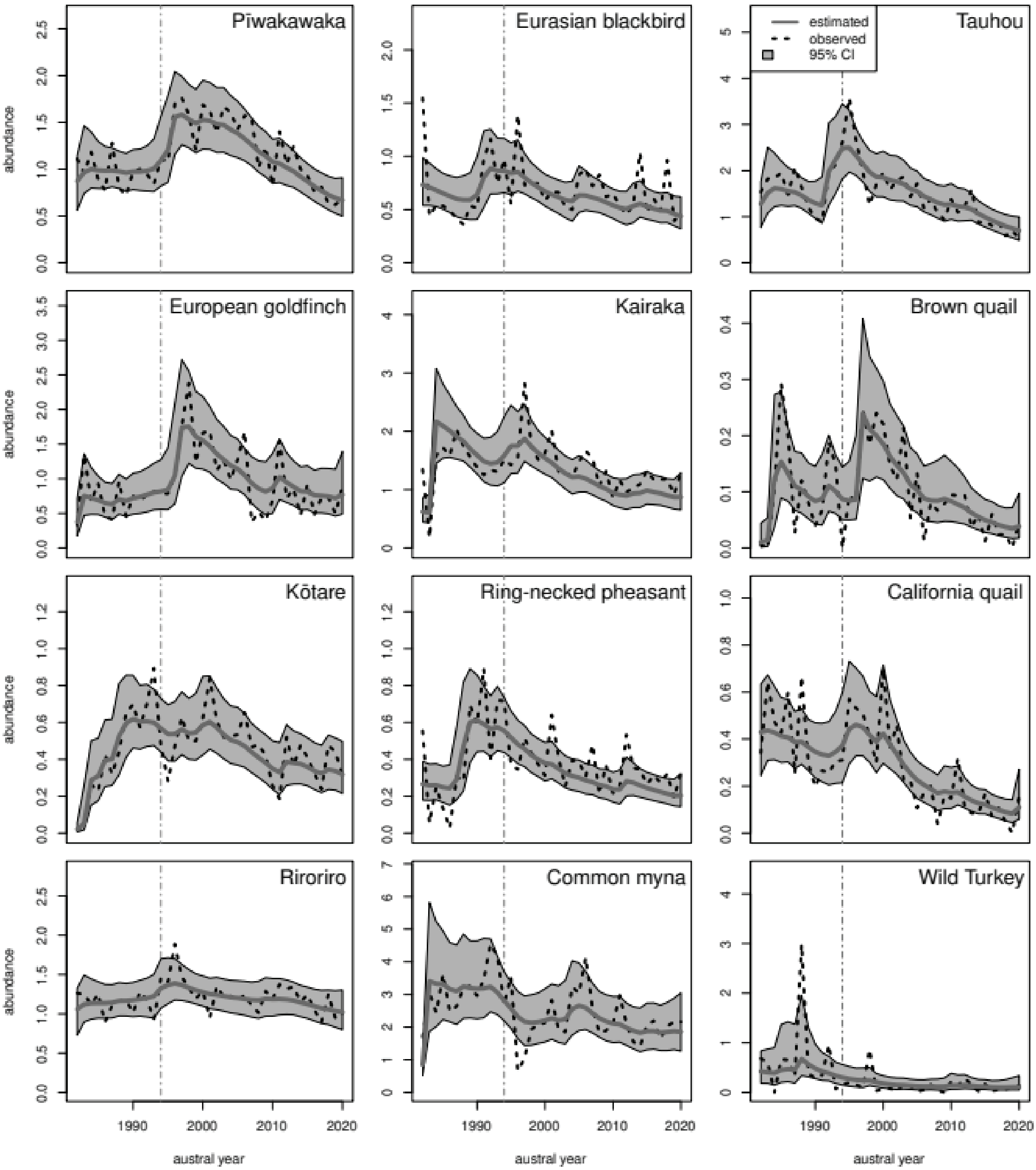

Figure 5D. Species Group D. Twelve species that were common before rat control, and then declined.

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.

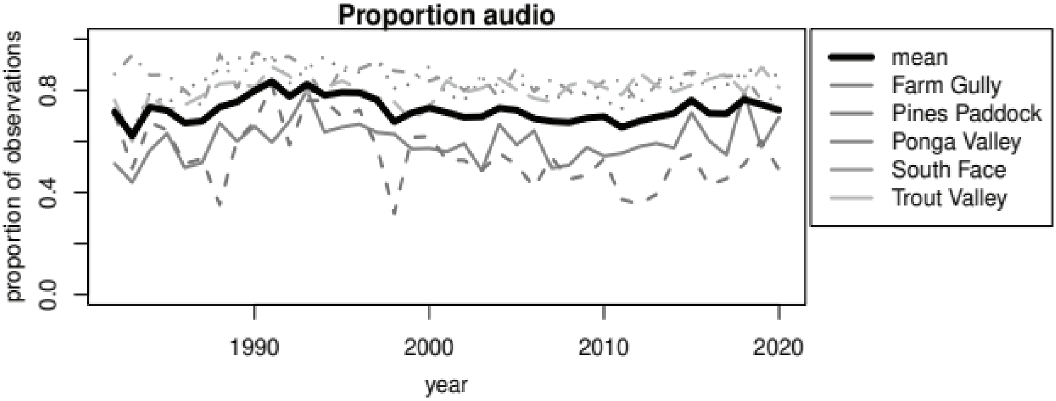

Figure 6. The proportion (%) of observations over time that were audio (first detected by hearing, rather than by sight) in each year in the five study routes, and the mean value (in black).

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.

ACKNOWLEDGEMENTS

We are grateful for the continued encouragement and support over the past decades of the shareholders and island managers of this special place with a special philosophy of a working farm coupled with a wildlife refuge. Logan Colmore-Williams first encouraged us to join in the effort and lay the foundation for its philosophy. Nelson and Mary Spiers, and Paul and Enid Asquith whose continued leadership of the wildlife committee and friendships have made many of the changes we document here feasible and timely. The tireless work of the farm managers, notably Vic and Margaret Goodin, Marion and Colin Cameron, and Stuart and Linda Crothers to control pests, both animal and plant, has made a great deal of difference. We have been joined in our efforts by many other shareholders, notably Eric and Barbara Spurr, all the Bunces, all the Wards, all the Jacksons, and Corry Tierney. We benefitted from much talented and thoughtful help in data analysis and thinking from Linda Long, Tami Matsumoto, Lisa Ollivier, Howard Stauffer, and Jared Wolfe**.** Tonnie Casey helped set up and count the routes in the first year. David Tindall was a cheerful and capable presence conducting censuses for 18 months, and the Spurrs contributed some non-breeding season counts. The paper benefitted greatly from thoughtful reviews of Paul Asquith, Rachelle Binny, Dianne Brunton, Neil Fitzgerald, Frank A. Fogarty, John Innes, Eric Spurr, Craig Symes, Jared Wolfe, and an anonymous reviewer. Sonja Lukaszewicz provided the map of the island. The Board of Moturoa enabled much of the work we outline, both in conservation and preservation. The shareholders of the island company all have participated directly and indirectly in the pest control operations and contributed observations of wildlife to the authors. We thank them for this and trust that this effort will continue for a long period.

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**.**

LITERATURE CITED

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Moa, climate, and eruptions: radiocarbon ages on habitat-specific moa show that their distributions were controlled by volcanic eruptions as well as climate

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Abstract: The species composition of moa assemblages reflected the local vegetation. These assemblages have been used as indicators of the geological age – glacial or Holocene – of the fauna. Within the assemblages, some species of moa have been associated with specific vegetation types, including *Anomalopteryx didiformis* with lowland rain forest, and *Euryapteryx curtus*, with dry shrubland. The sequence of radiocarbon ages for *A. didiformis* and *E. curtus* in the Waitomo karst, in the west central North Island, New Zealand, records changes in the distributions of their habitats over the past 28,000 years. The presence of *A. didiformis* shows that, contrary to current reconstructions, there was lowland rain forest in the karst during the Last Glacial Maximum. An abrupt change to *E. curtus* and hence of its shrubland habitat coincided with the Oruanui super eruption of Taupo volcano 25,400 years ago. *Anomalopteryx didiformis* and its rain forest habitat did not return to the karst until *c.* 13,000 years ago. *E. curtus* disappeared from the karst some time before that, during the gradual post-glacial warming, but remained elsewhere on the Volcanic Plateau, probably in the seral vegetation that followed the continual eruptions. Moa distributions were not always altered just by climate change. Major eruptions such as the Oruanui could change their habitat and hence their distribution over much of both main islands.

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Keywords: habitat, rain forest, shrubland, moa, *Anomalopteryx didiformis*, *Euryapteryx curtus*, Dinornithiformes, Oruanui eruption, glacial-interglacial transition, New Zealand, North Island

INTRODUCTION

Changes in the distribution of moa (Aves: Dinornithiformes) and the composition of their species assemblages as the New Zealand vegetation responded to a warming climate at the end of the most recent (Otiran-Weichselian) glaciation have been reported for both the North (Worthy 1984, 1987, 2000; Holdaway & Worthy 1993; Worthy & Holdaway 2000, 2002; Worthy & Swabey 2002) and South islands (Worthy & Mildenhall 1989; Worthy & Holdaway 1993, 1994, 1995, 1996, 2002; Worthy 1997, 1998a, 1998b). Some moa were associated with particular vegetation types (Worthy 1990, 2000; Worthy & Holdaway 1993, 1994, 1995, 1996, 2002; Worthy & Swabey 2002) and have been used

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as "broad brush" indicators of climate in terms of "glacial" and "Holocene" faunas. However, changes in moa species dated by radiocarbon can also record rapid environmental change (Holdaway 2021), although the method requires a sufficiently complete series of radiocarbon ages for the taxa in the area of interest.

To date, radiocarbon ages have been measured on only a small proportion of the well preserved moa material available in museum collections. However, there are still enough radiocarbon ages on moa, from many sites with wide geographic coverage, to demonstrate that they are a largely unexploited but potentially extremely useful resource for following changes in vegetation – and hence climate and other phenomena – through space and time. The geographic coverage is wider, and sampling sites more abundant, than for pollen and other lake and bog deposit proxies. In addition, ages on individual moa provide chronological precision for the type of vegetation beyond that of even the most intensively dated stratigraphic profile, for which age-depth models are required. The moa were witness to the vegetation where they lived, during a period defined by the radiocarbon age for their death.

Five moa taxa – *Anomalopteryx didiformis*; *Euryapteryx curtus* sensu lato; *Pachyornis australis*; *P. elephantopus*; *P. geranoides* – all members of the family Emeidae, were sufficiently closely associated with particular vegetation types, such as lowland rain forest, shrublands, or dry forests, to be useful proxies for vegetation. Comparison of their dated presence with reconstructions of the surrounding vegetation during the Holocene shows that *A. didiformis* was always associated with lowland rain forest (Worthy 1990; Worthy & Holdaway 2002). Similarly, pollen-based reconstructions of contemporary vegetation contemporary with their fossil remains show that *E. curtus* was found in dry forest such as that in the eastern South Island during the Holocene (Worthy & Holdaway 1996; Holdaway & Worthy 1997; Worthy 1997, 1998b) and, during glacial periods, shrublands and dry forests elsewhere (Worthy 1994; Worthy & Holdaway 1994; Worthy 1997, 1998b, 2000). On the same basis, it is accepted that *P. elephantopus* in the South Island and *P. geranoides* (formerly *P. mappini*) in the North Island similarly required dry forest and shrubland (Worthy 1987, 1990, 1997, 1998b; Worthy & Holdaway 1993, 1994, 1996; Rawlence *et al.* 2012). Lastly, *P. australis* was confined to low productivity, cool climate vegetation in the mountains west of the South Island's Main Divide (Rawlence *et al.* 2012; Holdaway & Rowe 2020).

Of the habitat-specific species, remains of *A. didiformis*, a small – *c.* 40–50 kg (Worthy & Holdaway 2002) – moa are nearly ubiquitous in deposits of Holocene age in the North Island south of the Auckland isthmus and in the northwest, west, and south of the South Island (Millener 1981; Worthy 1990, 1993, 1997, 1998a, 1998b; Worthy & Holdaway 1993, 1994, 2002). However, perhaps because the species has been taken to be an indicator of Holocene vegetation, fewer radiocarbon ages have been measured: the remains have instead been assumed to be of Holocene age (10,000 years ago to present).

Only two radiocarbon dates of Otiran-Weichselian Last Glacial Maximum age on *A. didiformis* are available, both from the North Island. Both are from the Waitomo karst (*c.* 38°15'S; Fig. 2), for which environmental reconstructions (McGlone *et al.* 2010; Newnham *et al.* 2013) suggest a glacial vegetation of "shrubland-grassland with some beech forest and rare patches of conifers" during the Last Glacial Maximum. These authors also map a sliver of lowland rain forest extending south along the coast to the west of the karst. Apart from this sliver, the model shows no rain forest south of the Kaipara Harbour at 36°40'S, 125 km north of Waitomo Caves. Lees *et al.* (1998) reported cold, wet conditions in bogs near the coast northwest of Waitomo between 25,000 and 20,000 years ago, with at least two species of beech in the surrounding hills. Neither analysis provides evidence for the contemporary vegetation in the Waitomo karst.

Because of a wider interest in the systematics of the genus, more radiocarbon ages have been measured on *E. curtus* than on *A. didiformis*. Of the 11 North Island ages, six are from the Waitomo karst. The species' presence there indicates a period or periods when the area vegetation was indeed as mapped by Newnham *et al.* (2013). However, throughout the Holocene, until present, the natural vegetation of the karst has been lowland rain forest. As the radiocarbon ages were measured on individuals from the same sites, it is unlikely that they record the presence of individuals from significantly different habitats.

A complicating factor in reconstructions of the vegetation of the central North Island is the prevalence there of volcanism in the Taupo Volcanic Zone. Ash falls and ignimbrite/pyroclastic flows can damage or destroy vegetation over significant areas (Clarkson *et al.* 1988; Wilmshurst & McGlone 1996; Segschneider *et al.* 2002; Manville *et al.* 2009). Prevailing westerly winds and the moderate size of most eruptions mean that most damage has been on the Volcanic Plateau itself and to its east. Extremely large eruptions have spread deep ash to the west and indeed across much of both the North and South Islands. Although many — perhaps most — people are aware of the most recent (First Millennium) eruption of Taupo Volcano, its effects were much less widely felt than those of the Oruanui super eruption of *c.* 25,000 years ago (Vandergoes *et al.* 2013).

The Oruanui eruption was the largest from the Taupo Volcanic Zone since the even larger

Figure 1. The effects on the rain forest at Tikitapu, near Blue Lake, Rotorua, of 3 cm of airfall volcanic tephra from the 1886 eruption of Mt Tarawera (Pullar & Birrell 1973). Top left, before the eruption. Valentine, George Dobson, 1852–1890. In the Tiki Tapu bush – Photograph taken by George Dobson Valentine. Mair, Gilbert Henry, 1875–1966: Photographs. Ref: PA7-54-24. Top right, same place, after the eruption. Valentine, George Dobson, 1852–1890: Scenic photographs of New Zealand. Ref: PA7-54-03. Bottom, same area, post eruption, in a wider view. Images: Tiki-Tapu bush, after eruption. Coxhead, Frank Arnold, 1851–1908. Tikitapu Bush destroyed by the 1886 Tarawera eruption – Photograph taken by Frank Arnold Coxhead. Christie, Hettie Florence, 1902–1988: Photographs and album of New Zealand scenes. Ref: PA7-41-15. All images, Courtesy of Alexander Turnbull Library, Wellington, New Zealand.

Rangitawa-Whakamaru eruption *c.* 340,000 years ago. Manville & Wilson (2004) pointed out that the thick ash and ignimbrite would have been enough "…to have wholly destroyed or buried vegetation over virtually all of the central North Island". They note that even in the present climate, vegetation would have developed on the new tephra very slowly. Under the glacial climate of that time, regeneration would have probably taken millennia. This is supported by the aeolian sediments widespread in the central North Island. Dunes formed from the volcanic sands are widespread in the North Island, including along the Whanganui and Rangitikei rivers (Manville & Wilson 2004). They noted that the presence of the Oruanui ash in the lower half of the Ohakea loess, the youngest North Island loess layer, indicates that the eruption occurred before the peak of the Last Glacial Maximum. Even 2 cm of ash can defoliate a forest for a year (Fig. 1) (Oppenheimer 2011), eliminating the local avifauna so damage from the Oruanui eruption was far more widespread than presently acknowledged by, for example Manville & Wilson (2004).

To resolve the apparent contradiction of the presence of *A. didiformis* in the Waitomo karst during the depths of the Otiran-Weichselian glaciation, reconstructions of karst vegetation at that time, and the likely effects of the Oruanui eruption, I analysed patterns in the radiocarbon age sequences for that species and for *E. curtus* from the karst's cave systems in relation to the modelled vegetation pattern and dates for major, potentially landscape-changing, eruptions from the Taupo Volcanic Zone. *Anomalopteryx didiformis* and *E. curtus* were approximately the same size (Worthy & Holdaway 2002) so resident populations of both species presumably had the same probability of being trapped in cave systems.

MATERIALS AND METHODS

Radiocarbon ages

A total of 27 radiocarbon ages (Table 1) are presently available for *A. didiformis*, 14 from the North Island (10 from the Waitomo karst) – collated from Millener (1981), Worthy & Swabey (2002), and Bunce *et al.* (2009) – and 13 from the South, collated from Worthy & Holdaway (1993, 1994), Worthy (1998a), Worthy & Roscoe (2003), and Bunce *et al.* (2009). There are fewer ages for this taxon than for others in the fauna because research interest has been focused on the two giant moa (*Dinornis* spp.) and the species of *Euryapteryx* and *Pachyornis*.

For *E. curtus*, 11 ages are available for the North Island, including six from the Waitomo karst (Table 2) (Worthy & Swabey 2002), and five from other areas (Worthy 2000) and Holdaway (previously unpublished data). Of the 57 ages available for South Island birds, most (40) are from a few sites in North Canterbury. Ages for South Island birds were collated from McCulloch & Trotter (1979), Ritchie (1982), Anderson (1989), Worthy & Holdaway (1993, 1994, 1996), Worthy (1998a, 1998b), Worthy & Roscoe (2003), and Allentoft *et al.* (2014).

Statistics

The conventional radiocarbon ages were calibrated to calendar time via the OxCal4.4 (Bronk Ramsey 2009) software, invoking the SHCal20 calibration

Table 1. Radiocarbon ages (years BP) on individual *Anomalopteryx didiformis* from North and South Islands, New Zealand, from literature records. Shaded, ages used in analysis of faunal replacement around Waitomo. CRA, conventional radiocarbon age; SD, measurement 1σ; δ^{13}C, measurement carbon stable isotope ratio; SHCal20, mean calibrated date in relation to SHCal20 calibration curve; SD, 1σ date range for calibrated dates; median, median calibrated date; -, data not available; AU, Geology Department, University of Auckland collection; WO, Caves Museum, Waitomo; AIM, Auckland Institute and Museum; MNZ, Museum of New Zealand Te Papa Tongarewa.

Age ref.	CRA	SD	δ^{13}C	SHCal20	SD	Median	Locality	Sample and Reference	Island
NZ4838	24,100	450	-	28,323	456	28,299	Moa Cave, Stubbs Farm, Waitomo	AU4973; Millener (1981)	N
NZ4843	21,200	350	-	25,429	381	25,452	Dawson's Moa Cave, Piopio	AU5801; Millener (1981)	N
NZ4840	10,600	200	-	12,390	291	12,429	Dinornis Cave, Waitomo	AU4081; Millener (1981)	N
NZ4844	10,150	150	-	11,728	300	11,707	Zweiholen, below Entrance	AU4966; Millener (1981)	N
NZA11612	9,510	60	-22.7	10,780	154	10,737	F1c Cave, Rockfall deposit	Worthy & Swabey (2002)	N
NZ3088	7,300	150	-	8,092	150	8,091	Auckland City	Nelson & Grant-Mackie (1980)	N
NZ4841	6,150	100	-	6,994	134	6,992	Dinornis Cave, Waitomo	AU4081; Millener (1981)	N
NZA10054	5,876	60	-22.5	6,645	84	6,649	Zweiholen, ZW5, spit 1, L1	WO473; Worthy & Swabey (2002)	N
NZ4842	3,200	60	-	3,367	77	3,376	Rorison's Quarry, Piopio	AU4975; Millener (1981)	N
NZ4867	2,790	80	-	2,881	94	2,868	Waikiekie Quarry, Northland	AU5800; Millener (1981)	N
NZA7185	2,749	68	-22.3	2,836	74	2,828	Hukanui Pool rockshelter	Holdaway & Beavan (1999)	N
NZ5035	1,860	70	-	1,744	88	1,746	Peryer's Anomalopteryx Cave	AU7108; Millener (1981)	N
NZ4871	1,340	64	-	1,201	69	1,210	Clevedon	AIM 1.160; Millener (1981)	N
OxA12726	1,041	24	-21.9	890	47	910	Hangitiki, Waitomo	AM4943; Bunce *et al.* (2009)	N
OxA12728	11,575	45	-21.4	13,406	52	13,407	Takaka Fossil Cave	MNZ S38943; Worthy & Roscoe (2003)	S
NZA11614	11,354	60	-22	13,223	55	13,221	Takaka Fossil Cave	50 cm depth; Worthy & Roscoe (2003)	S
NZA3288	8,274	72	-22.66	9,217	114	9,213	Kairuru Extension Cave	Worthy & Holdaway (1994)	S
NZA3258	6,656	141	-21.01	7,500	127	7,503	Hawke's Cave	Worthy & Holdaway (1994)	S
NZA2506	5,447	87	-22.5	6,178	108	6,195	Madonna Cave site 10	Worthy & Holdaway (1993)	S
NZA8071	4,951	69	-23.5	5,667	93	5,656	Hamilton's Swamp, Winton	inner pt	S
NZA8072	4,735	72	-23.1	5,429	95	5,429	Hamilton's Swamp, Winton	outer pt	S
NZA3289	4,072	59	-21.67	4,544	117	4,524	Kairuru Extension Cave	Worthy & Holdaway (1994)	S
NZA2443	2,197	86	-23	2,153	114	2,141	Madonna Cave, site 8	Worthy & Holdaway (1993)	S
NZA13547	1,576	60	-22	1,429	65	1,425	Takaka Fossil Cave	Worthy & Roscoe (2003)	S
NZA2521	1,076	83	-22.9	936	97	936	Madonna Cave site 12	Worthy & Holdaway (1993)	S
NZA3048	670	59	-22.5	604	39	604	Irvine's Cave	MNZ S30183; Worthy & Holdaway (1994)	S
OxA12729	623	28	-21.2	588	33	603	Echo Valley Cave, Southland	Southland Museum; Bunce *et al.* (2009)	S

Table 2. Radiocarbon ages (years BP) for the taxon known presently as *Euryapteryx curtus*. Shaded rows, individuals from the Waitomo karst. Abbreviations as in Table 1.

Age no.	CRA	SD	$\delta^{13}C$	SHCal20	SD	Median	Locality, Sample, and Reference	Island
NZA9985	20,920	180	-24.1	25,191	255	25,188	Zweiholen, ZW5, BL3; WO612; Worthy & Swabey (2002)	N
NZA9277	20,150	130	-22.6	24,143	180	24,126	Zweiholen, ZW2; WO442; Worthy & Swabey (2002)	N
NZA9950	20,120	180	-24.2	24,149	227	24,120	Zweiholen, ZW5, BL2A; small moa; WO590; Worthy & Swabey (2002)	N
NZA9342	19,170	150	-24.3	23,123	230	23,084	Zweiholen, ZW1; WO440; Worthy & Swabey (2002)	N
NZA10055	18,040	140	-23.2	21,870	218	21,900	Zweiholen, ZW5, spit 3, L2; WO542; Worthy & Swabey (2002)	N
NZA11613	13,144	70	-25.1	15,719	118	15,718	F1c Cave, Rockfall; ; Worthy & Swabey (2002)	N
NZA9513	11,551	85	-21.8	13,389	83	13,389	Te Aute Swamp; MNZ S121; Worthy (2000)	N
NZA 34021	2,026	35	-20	1,940	44	1,943	Taupo Bypass Highway pitfall; Holdaway, this paper	N
NZA 34019	1,617	35	-21.5	1,464	45	1,465	Taupo Bypass Highway pitfall; Holdaway, this paper	N
NZA 34022	1,354	35	-24.3	1,227	41	1,228	Taupo Bypass Highway pitfall; Holdaway, this paper	N
NZA 34020	1,343	35	-23	1,222	43	1,225	Taupo Bypass Highway pitfall; Holdaway, this paper	N
NZA7553	37,080	950	-22.6	41,683	597	41,715	Kauana Swamp; MNZ S34502; Worthy (1988a)	S
NZA7749	32,000	370	-22.5	36,348	411	36,334	Kauana Swamp; MNZ S34501; Worthy (1988a)	S
NZA2445	23,780	210	-21.8	27,964	249	27,924	Madonna Cave, site 16; Worthy & Holdaway (1993)	S
NZA3050	14,080	100	-22.6	17,096	154	17,093	Irvine's Cave; Worthy & Holdaway (1994)	S
NZA3051	13,889	95	-21.7	16,805	153	16,813	Irvine's Cave; Worthy & Holdaway (1994)	S
NZA1567	13,400	130	-23.4	16,083	196	16,082	Kairuru Cave; MNZ S27794; Worthy & Holdaway (1994)	S
NZA13267	12,450	65	-23.24	14,563	206	14,547	Takaka Fossil Cave; Rock fall slope; Worthy & Roscoe (2003)	S
NZA13266	12,361	65	-22.16	14,407	223	14,349	Takaka Fossil Cave; Base of excavation; Worthy & Roscoe (2003)	S
NZA2779	11,090	100	-22.6	12,971	101	12,977	Madonna Cave, site 13; Worthy & Holdaway (1993)	S
NZ1728	9,490	200	-	10,756	279	10,747	Pukemata; Anderson (1989)	S
NZ7924	6,359	100	-23.4	7,225	123	7,235	Madonna Cave, site 13; redone NZA2779; Worthy & Holdaway (1993)	S
NZA 29908	4,736	25	-23	5,417	70	5,399	Rosslea Swamp; Allentoft *et al*. (2014)	S
NZA 31038	3,649	25	-23.8	3,927	57	3,922	Pyramid Valley; Allentoft *et al*. (2014)	S
NZ623	3,450	71	-	3,667	103	3,662	Pyramid Valley; gizzard, Anderson (1989);	S
NZA 30225	3,077	25	-22.8	3,249	60	3,246	Pyramid Valley; Allentoft *et al*. (2014)	S
NZA 29240	2,828	35	-23.8	2,892	59	2,893	Pyramid Valley; Allentoft *et al*. (2014)	S
NZA 30691	2,680	55	-23.8	2,762	78	2,766	Pyramid Valley; Allentoft *et al*. (2014)	S
NZA 34181	2,572	25	-24	2,616	81	2,614	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA 30099	2,570	25	-23.8	2,614	80	2,610	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA 30274	2,544	20	?	2,595	77	2,585	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA 34195	2,503	25	-24.6	2,555	98	2,561	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA6747	2,438	64	-23.3	2,486	128	2,467	Hamilton Swamp, Otago; OM Av4754; Worthy (1988b)	S

Table 2. *continued*

Age no.	**CRA**	**SD**	**δ^{13}C**	**SHCal20**	**SD**	**Median**	**Locality, Sample, and Reference**	Island
NZA 31011	2,378	35	-23	2,339	105	2,348	Pyramid Valley; Allentoft *et al.* (2014)	S
D-AMS 1219-099	2,336	29	-13.2	2,250	70	2,225	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA 34193	2,319	25	-24.7	2,240	64	2,220	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
D-AMS 1219-091	2,302	30	-15.6	2,236	61	2,223	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA 30113	2,267	30	-24	2,232	59	2,234	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA 31040	2,238	25	-24.4	2,227	64	2,246	Pyramid Valley; Allentoft *et al.* (2014)	S
NZA 34250	2,205	25	-23.9	2,187	80	2,142	Pyramid Valley; Allentoft *et al.* (2014)	S
NZA4615	2,176	76	-24.4	2,131	109	2,114	Earnscleugh Cave; Ritchie (1982)	S
D-AMS 1219-083	2,075	27	-17.8	1,984	43	1,986	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZ1727	2,020	70	-	1,931	87	1,931	Enfield; Anderson (1989); McCulloch & Trotter (1979)	S
D-AMS 1219-085	1,951	27	-19.8	1,850	44	1,854	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
D-AMS 1219-088	1,797	30	-9.4	1,657	41	1,653	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
D-AMS 1219-090	1,771	32	-8.9	1,641	42	1,644	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA 31044	1,734	25	-23.5	1,605	47	1,594	Pyramid Valley; Allentoft *et al.* (2014)	S
D-AMS 1219-089	1,718	30	-23.9	1,586	47	1,577	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA 34253	1,679	25	-24.2	1,532	40	1,539	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZ4874	1,670	75	-	1,524	91	1,521	Awamoa; Anderson (1989)	S
NZA 30519	1,540	270	-23	1,440	292	1,429	Rosslea Swamp; Allentoft *et al.* (2014)	S
NZ918	1,525	60	-	1,384	62	1,374	Timpendean rockshelter; Worthy & Holdaway (1996)	S
NZA 29127	1,492	35	-23.5	1,341	29	1,338	Pyramid Valley; Allentoft *et al.* (2014)	S
NZ4900	1,445	50	-	1,305	51	1,308	North Dean, North Canterbury; Anderson (1989)	S
NZA 34194	1,410	25	-22.5	1,274	37	1,288	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA30223	1,293	30	-24.4	1,174	61	1,167	Pyramid Valley; Allentoft *et al.* (2014)	S
D-AMS 1219-084	1,249	30	-25.2	1,122	50	1,119	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA 31042	1,172	25	-23.5	1,016	38	1,014	Pyramid Valley; Allentoft *et al.* (2014)	S
NZA 31054	1,168	25	-23.9	1,014	36	1,014	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA 31041	1,116	25	-23.9	981	40	969	Pyramid Valley; Allentoft *et al.* (2014)	S
NZA 31037	1,102	25	-23.9	963	36	951	Pyramid Valley; Allentoft *et al.* (2014)	S
NZ5321	1,070	60	-	923	75	930	Firewood Creek, Cromwell; Anderson (1989); Ritchie (1982)	S
NZA 28039	1,027	30	-23.9	872	45	862	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZ1724	1,025	60	-	874	63	869	Castle Hill; Anderson (1989);	S
D-AMS 1219-086	930	27	-25.2	799	51	784	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
D-AMS 1219-081	655	25	-20.2	601	28	606	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
D-AMS 1219-098	655	26	-15.9	601	28	606	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
D-AMS 1219-094	619	28	-	585	34	600	Bell Hill Vineyard; Allentoft *et al.* (2014)	S

curve (Hogg *et al.* 2020). Mean, with 1σ error, and median calibrated dates are given in Tables 1&2. Calibrated dates are given as "before present", BP, conventionally 1950 CE.

The temporal patterns in the numbers of dated North and South Island individuals of both *A. didiformis* and *E. curtus* were summarised by box-whisker plots, with outliers, using the PAST® statistical software (Hammer *et al.* 2001).

Calibrated date probability distributions were generated using the OxCal4.4 software and the SHCal20 curve. For the two moa taxa from sites in the Waitomo karst, Bayesian probability distributions for the end of the initial presence of *A. didiformis* and first presence of *E. curtus* were generated using the Sequence option in OxCal4.4. Similarly, the probabilities for the last occurrence of *E. curtus* and renewed presence of *A. didiformis* were generated and plotted. It was assumed *a priori*, because their habitat requirements were mutually exclusive, and the date series were also mutually exclusive between the change events, that the first and last occurrences of each taxon marked faunal turnover events.

Eruption dates and volumes

A revised date of 25,360 ± 160 calendar years before present for the Oruanui eruption and its resulting Kawakawa/Oruanui tephra was presented by Vandergoes *et al.* (2013). In their title, the authors maintain that the tephra "is a key stratigraphic marker for the Last Glacial Maximum in New Zealand". Dates for other major eruptions are from the list in Lowe *et al.* (2013). Eruptive volumes are from Froggatt & Lowe (1990) and Vandergoes *et al.* (2013).

RESULTS

General

Of the 27 *A. didiformis* which have been radiocarbon dated so far, only two have ages greater than 13,500 calendar years before present (Table 1). Both of these are from caves in the Waitomo karst (Fig. 2). These two ages are extreme outliers in the available series (Fig. 3). The two coeval outliers in the South Island series (Fig. 3) are from Takaka Hill, where the species made a brief pre-Holocene appearance before being replaced by *P. australis* during the period of the Younger Dryas (Holdaway 2021). No older *A. didiformis* is known from the South Island, or indeed from the North Island south of Waitomo. Indeed, apart from the Waitomo birds, nothing is known of the distribution of *A. didiformis* before the Holocene (Fig. 2).

The oldest radiocarbon ages for *E. curtus* in the North Island are all from the Waitomo karst (Table 2). The cluster in the glacial and late glacial of the Waitomo karst has no parallel in the South Island (Fig. 3). The next oldest North Island individual was from the glacial-interglacial transition site of Te Aute in southern Hawke's Bay (Table 2). All others are from the Holocene. In contrast, radiocarbon ages for *E. curtus* (taken in the broad sense of the taxon) in the South Island include ten older than 10,000 years BP (Table 2), from sites at both ends of the island. The many North Canterbury records are all of mid- to late-Holocene age (Table 2).

The Waitomo karst

Neither *A. didiformis* nor *E. curtus* was present continuously in the fossil record from the Waitomo karst (Fig. 4). *A. didiformis* was present before 25,400 calendar years BP, *E. curtus* between 25,400 calendar years BP and *c.* 15,000 years BP. *Anomalopteryx didiformis* reappeared in the caves *c.* 12,500 years BP and was present then until moa extinction

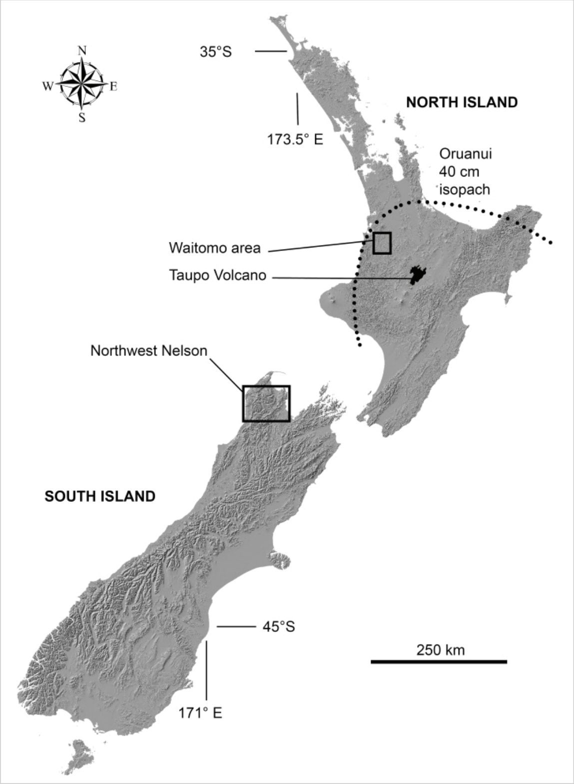

Figure 2. Location of Waitomo study site in relation to Taupo Volcano (site of the Oruanui super eruption) and Northwest Nelson (site of evidence for Younger Dryas cold period in New Zealand, Holdaway [2021]). Oruanui 40 cm isopach from Vandergoes *et al*. (2013).

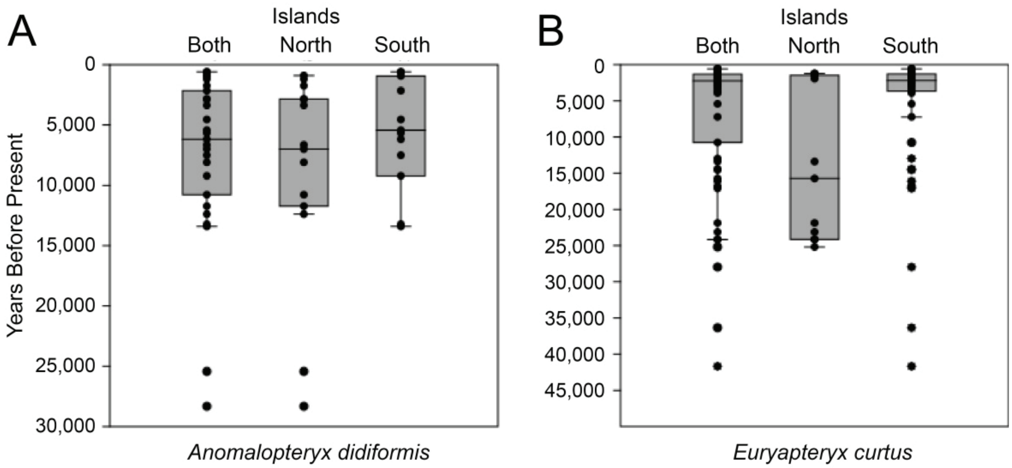

Figure 3. Box-whisker plots (quartile rounding, with outliers) of mean calibrated radiocarbon ages for (**A**) *Anomalopteryx didiformis* (the two outliers at >25,000 BP are both from the Waitomo karst), and (**B**) *Euryapteryx curtus*.

after 1000 CE (Fig. 4). *Anomalopteryx didiformis* reappeared in the Waitomo karst contemporary with the moa-signalled cooling event in Northwest Nelson (Holdaway 2021).

The change from *A. didiformis* to *E. curtus* coincided with the date of the Oruanui super eruption from Taupo Volcano (Figs 4&5). There is a gap in the available date sequence for *E. curtus* between *c.* 22,000 and *c.* 15,500 years BP and another between the final record of *E. curtus* at *c.* 15,500 BP and the first *A. didiformis* at *c.* 12,500 years BP. Several major eruptions affected the central North Island between the Oruanui and Taupo First Millennium eruptions but they each involved *c.* 2 orders of magnitude less ash than the Oruanui (Fig. 4A).

Glacial-Interglacial Transition

There was a gap in the date series for the two taxa from 22,000 to 15,500 years ago, before the final record of the (continued?) presence of *E. curtus* in the karst (Fig. 4). At 12,500 BP, *A. didiformis* replaced *E. curtus*, with its radiocarbon-dated presence attested until moa extinction (Fig. 4).

DISCUSSION

Climate is taken conventionally to be the major control on the distribution of vegetation types including grassland, shrubland, dry forest, and lowland rain forest (McGlone 1985; Newnham *et al.* 2013) and therefore of bird habitat, including that of moa (Worthy 1990, 2000; Worthy & Holdaway 1993, 1994, 1996; Worthy & Swabey 2002), in New Zealand. Volcanism has been seen as affecting vegetation only in the central North Island, around the volcanoes of the Taupo Volcanic Zone (McGlone 1985; Wilmshurst & McGlone 1996). As long ago as the 1950s, however, volcanism was seen as having a wider role in controlling the distribution of fauna, at least of soil fauna (Lee 1953, 1959).

A few of the largest eruptions, such as the Rangitawa/Whakamaru (*c.* 340 ka) and Oruanui/Taupo (25.4 ka), have deposited ash over significant areas of both main islands (Pillans *et al.* 1996; Vandergoes *et al.* 2013). The area covered by the Kawakawa-Oruanui tephra ejected during the Oruanui super eruption included the Cook Strait land bridge and the other land areas exposed by glacial low sea levels (Vandergoes *et al.* 2013). The mapped isopachs (ash depths) for the Oruanui eruption (Vandergoes *et al.* 2013) are consistent with widespread destruction of vegetation (Oppenheimer 2011), and hence of its associated avifauna, including moa.

Super eruptions, at least, must be seen as major factors determining the distribution and composition of vegetation between the Auckland isthmus and the Waitaki River, the limits of the 2 cm isopach mapped by Vandergoes *et al.* (2013). Many, if not most, New Zealand pollen records post-date the Oruanui eruption. The question therefore arises as to whether the vegetation (and faunal) patterns ascribed to glacial climate were not actually the result of the damage caused by the Oruanui eruption, exacerbated by the cold climate in which it took place, and not driven just by the climate itself. Indeed, contrary to the current model, the presence of *A. didiformis* indicates the presence of lowland rain forest in the Waitomo karst more

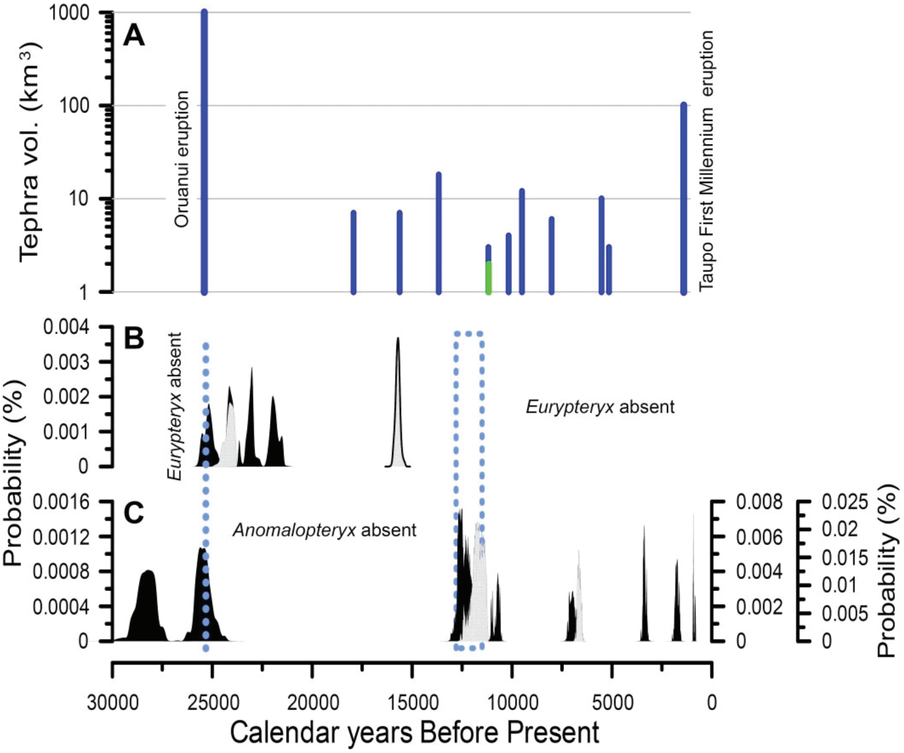

Figure 4. Calibrated calendar date probability distributions for radiocarbon ages showing alternation of the presence of two moa taxa, *Anomalopteryx didiformis* (rain forest) and *Euryapteryx curtus* (shrubland and dry forest), in the Waitomo area, western central North Island, New Zealand in relation to major volcanic eruptions. **A**, Tephra volumes for eruptions ($\log_{10}$ scale). **B**, *E. curtus* ages. **C**, *A. didiformis* ages. Dotted line, date for the Oruanui super eruption of Taupo Volcano (*c.* 1,000 km³ tephra); dotted rectangle, timing and duration of Younger Dryas post-glacial cold period. Two distributions have grey fill to differentiate them from nearly synchronous individuals. Two almost coeval eruptions (Poronui; Karapiti) are shown with different colours for clarity. Multiple y-axes for probabilities allow better comparison of date distributions. See Table 1 for details of radiocarbon ages.

than 25,400 years ago, during the extended Last Glacial Maximum (eLGM) (Newnham *et al.* 2007). Although Newnham *et al.* (2007) suggested that pollen records from Auckland, 145 km north of Waitomo, show that the Oruanui eruption fell "within a period of climate amelioration" that lasted for *c.* 2,000 years (26,000 to 24,000 BP) within their 29,000 to 19,000 year-long BP eLGM. To what extent that "amelioration" would have allowed lowland rain forest to spread south again is unknown, but the *A. didiformis* that died in Moa Cave nearly 29,000 years ago (Table 1) shows that rain forest was in the karst at the start of their period of warmer climate.

Previous environmental reconstructions for the Waitomo karst

There are no significant pollen records from the Waitomo karst so reconstructions of the vegetation have depended on records from surrounding areas, especially from the Waikato Basin to the north (Worthy 1984; Worthy & Swabey 2002). Worthy & Swabey (2002) noted that Newnham *et al.* (1989) suggested that that landscape was "largely unforested" from 18,000 to 14,000 ^{14}C years ago, a period corresponding to a calendar date range from 21,900 to 17,000 years BP. The presence of the shrubland moa *E. curtus* in the karst during this period is consistent with the pollen-based interpretation of the vegetation.

The most intensively dated fossil deposits within the karst are those near the Zweiholen entrances in Gardners Gut Cave, just west of Waitomo Caves, *c.* 30 km east of the present coastline, and F1c cave, 9.5 km to the south (Worthy & Swabey 2002). All of the dated *E. curtus* and three of the *A. didiformis* individuals were from these two cave systems. Both species were living, for protracted but non-overlapping – at least in terms of the present sample – periods around the entrances to these caves. The change in their recorded presence is therefore unlikely to have resulted from a local spatial difference in their distributions, for example if one or other lived in riparian vegetation while the other was on the intervening hills.

The two ages were measured early in the application of radiocarbon in moa research when any age measurement was important. That these are still the only two pre-Holocene radiocarbon ages for *A. didiformis* is, as noted above, partly because most programmes have focused on other taxa and dating is expensive. It may also be in part because there are fewer or even, as in the Marlborough Sounds no, fossil deposits in possible ice age rain forest refugia. Indeed, where South Island *A. didiformis* survived until the Holocene is still a mystery. The two pre-Holocene *A. didiformis* may indicate that one of the elusive refugia was near Waitomo, until Oruanui.

The nine radiocarbon ages from the Zweiholen system include one on *A. didiformis* (Table 1) and five on *E. curtus* (Table 2). The oldest dated *E. curtus* was in the ZW5 deposit. It died 25,191 ± 255 years ago (NZA9985), just after the Oruanui eruption. Its remains were within Layer 4, "a fluvial layer of sand and gravel (< 10 mm)… bones in these sediments were water-worn, indicating that they had been transported some distance" (Worthy & Swabey 2002). The thin Layer 4 lay on "the original clay infill of the passage transported to the site from a considerable distance away by the last presence of the stream that formed this high level of the Zweiholen passages … The surface of Layer 5 in the excavation reveals the extent to which these clays were excavated before sedimentation recommenced." (Worthy & Swabey 2002). Based on the NZA9985 date on the moa, the interface of Layers 4 and 5 is contemporary with the Oruanui eruption.

The ZW5 deposit represented mostly the fauna in the 3,500 years following the Oruanui eruption. Throughout this period, the presence of *E. curtus* records a local shrubland environment. One *E. curtus*, about 20 cm above the oldest, and in Layer 3, lived 24,149 ± 227 years ago (NZA9950), about 1,000 years after the Layer 4 bird and the eruption. Deposition in that site continued for at least another 2,500 years, with a third *E. curtus* 20 cm above the Layer 3 bird dated at 21,870 ± 218 BP (NZA10055). Sometime after that, a long hiatus in the dated fauna began that lasted until the early Holocene. The only dated moa from their Layer 1 was an *A. didiformis*: it lived in the Holocene lowland rain forest there 6,645 ± 84 years ago (NZA10054). The next oldest dated *E. curtus* from the cave system was from ZW2; this individual was, at 24,143 ± 180 years ago (NZA9277), contemporary with the oldest bird in ZW5, just after the Oruanui eruption.

Other than the two *A. didiformis*, the only dated evidence from the avifauna for the vegetation preceding the Oruanui eruption is the presence of a North Island goose (*Cnemiornis gracilis*). The goose's radiocarbon date of 26,879 ± 226 years BP (NZA9071) places it over 1,000 years before both the eruption and the final presence of *A. didiformis* at 25,452 ± 381 BP (NZ4843), but c. 1,500 years after the earlier *A. didiformis* (28,323 ± 456 BP, NZ4838). The two *A. didiformis* show that rain forest was present in the karst up to the Oruanui eruption. The presence there of the goose at that time might be seen therefore as anomalous. Based on its distant relationship to the Cape Barren goose (*Cereopsis novaehollandiae*) of Australia (Rogers 1990; Worthy *et al.* 1997), its habitat has traditionally been thought to have been grassland. Worthy & Swabey (2002) suggested that the goose and the waterfowl preserved in the Holocene deposits when the local vegetation was certainly rain forest reflected the presence of water bodies within the forest: "the presence of both *E. finschi* [= *Chenonetta finschi*] and *A[ptornis] otidiformis* in F1c may be related to the surroundings of the cave, which was probably a small glade with a tarn in an otherwise forested habitat (Worthy 1984b)". However, Finsch's duck (*Chenonetta finschi*) was a forest species whose presence is not an indicator of standing or running water (Worthy & Holdaway 1994). Neither the North Island goose nor the South Island goose (*C. calcitrans*) may have been confined to grassland (Johnston *et al.* 2022).

Comparison of moa-derived and pollen evidence for eLGM forest near Waitomo

Lees *et al.* (1998) described the composition of the coastal forest from pollen in a bog ("Airstrip bog") presently at 135 m a.s.l., 90 km NNW of Waitomo (Fig. 5). That pollen record began somewhat earlier than the 24,000 years BP proposed by the authors, based on the lower of the two radiocarbon ages measured on dried, untreated peat samples. The calibrated mean date for radiocarbon age Wk-1139A (23,400 ± 340 ^{14}C years BP) from 7.0–7.20 m depth using the SHCal20 curve (Hogg *et al.* 2020) gave a revised calendar date of 27,619 ± 321 years BP. Between the sample and 7.0 m depth, the pollen record ceased: the next counts were not until 6.60 m (fig. 4 in Lees *et al.* [1998]). No sample was collected from 6.80–7.0 m because of "a possible water pocket". The gap, which is near the base of Lees *et al.*'s (1998) Zone 1A, is not discussed by those authors, but the stratigraphic record (their Table 1) describes the sediment at 7.10 m as being "Black coarse sand, pollen very scarce, large amount of organic matter", and that the pollen grains were severely clumped, as might be expected in a forest soil developed in tephra. That tephra could have been the Oruanui.

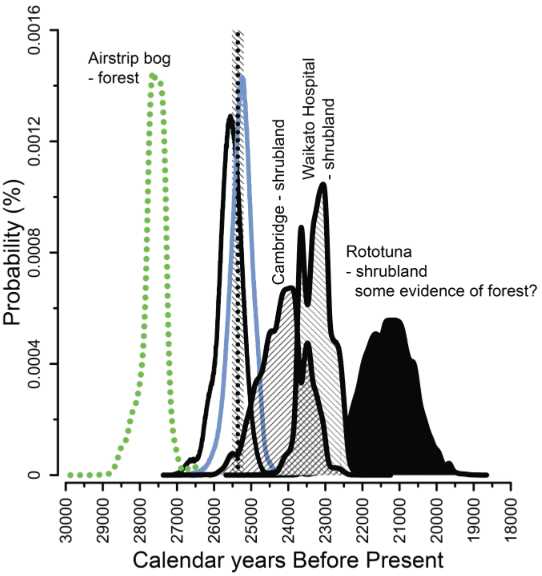

Figure 5. Date distributions for coastal rain forest (green dotted line) (Lees *et al.* 1998), and shrubland (dashed and solid fill) in the lower Waikato (McGlone *et al.* 1978) around the eLGM, in relation to the date of the Oruanui eruption and of the change from *Anomalopteryx didiformis* to *Euryapteryx curtus* in the Waitomo karst, as shown Figure 4&6.

The authors calculated dates for changes in the pollen spectrum assuming a constant accumulation rate of 0.75 mm year^{-1} (an interval of 7,350 years for the 5.5 m between 1.6 m and the bottom of the core). However, the radiocarbon age for the 1.58–1.62 m sample (Wk-1137A 16,050 ± 180 ^{14}C years) yielded a calibrated date of 19,330 ± 216 years BP. The new calibration means that a period of 8,290 years was encompassed by the 5.5 m between the samples, giving a lower accumulation rate of 0.664 mm year^{-1}. The 4.10 m level would then have an approximate calendar date of 23,100 years BP rather than the 20,400 years BP suggested by Lees *et al.* (1998).

The new calibrated dates suggest that Lees *et al.*'s (1998) Zone 1A (7.55 to 4.10 m) lasted from c. 27,600 years BP to 23,100 years BP. This range encompasses the revised date of 25,400 BP for the Oruanui eruption (Vandergoes *et al.* 2013), which, if the accumulation rate was indeed constant, corresponds to a depth of 5.70 m in the core. *Leptospermum* and *Coprosma* peaked just above this level in their figure 3, *Dacrydium* started a decline, and *Metrosideros* dropped out. However, if the rate was not constant, the eruption may have occurred in the interval corresponding to the "water pocket" and the rise in *Leptospermum* and other shrubs after 7.0 m may reflect ash damage to the rain forest in the area.

Assuming, as the authors did, a constant accumulation rate within the revised chronology, Lees *et al.*'s (1998) Zone 1B dated from 23,100 to 22,200 BP, Zone 2 from 22,200 to 19,500 BP, Zone 3 from 19,500 to 18,600 BP, and Zone 4 from 18,600 BP to present. Consequences for these changed dates for the patterns of vegetation change at the site are not explored here, but should be taken into account in future modelling of vegetation in the area.

Inland, in the Waikato River basin, McGlone *et al.* (1978) described the pollen records in three peat lenses exposed in the alluvium of the Hinuera Formation near Hamilton (Waikato Hospital, 0.5 m thick; Rototuna, 0.1 m thick) and Cambridge (0.3 m thick), respectively 55 km NNE and 50 km NE of Waitomo. Only one radiocarbon age was obtained for each peat layer. For the Waikato Hospital site, the Wk-23 ^{14}C age of 19,804 ± 340 years BP (new T$_{1/2}$) gives a conventional Libby T$_{1/2}$ age of 19,243 ± 340 years BP; calibration using the SHCal20 curve gives a calendar date of 23,214 ± 387 years BP. For the Rototuna site, the reported age (Wk-59, 18,100 ± 550 ^{14}C years BP [new T$_{1/2}$] [17,587 ± 550 ^{14}C, Libby T$_{1/2}$]), the calibrated date is 21,312 ± 676 years BP. Similarly, the Cambridge peat (NZ330, 20,600 ± 500 ^{14}C years BP [new T$_{1/2}$] [20,016 ± 500 ^{14}C, Libby T$_{1/2}$]), yields a calendar date of 24,130 ± 615 years BP (95.4% confidence interval of 25,321 to 22,961 years BP) (Fig. 5).

These dates show that all the pollen records post-date the Oruanui eruption: none provides evidence of the vegetation before the eruption. The Cambridge peat immediately follows the eruption, the Waikato Hospital peat was laid down 2,000 years, and the Rototuna peat 4,000 years, after the eruption. All three pollen profiles suggest that the post-eruption vegetation was "dominated by scrub, grassland and swamp", with perhaps more forest several thousand years after the eruption.

Glacial-Interglacial Transition

The discussion of F1c in Worthy (1984) was revisited by Worthy & Swabey (2002), who also added more radiocarbon ages. An *E. curtus* preserved in the F1c rockfall deposit was, at 15,719 ± 118 BP (NZA11613, Table 2), the geologically youngest of that species known from the karst, shows that shrubland was present near Piopio, 25 km south of Waitomo, at that time. The date of 10,780 ± 154 BP for the *A. didiformis* in F1c (NZA11612) shows that the species, and its rain forest habitat, had reached the karst 5,000 years later. It is unfortunate that the sample dated for NZ4844 was "Mixed *D.*[*inornis*] *struthoides* and *A. didiformis*" (Worthy & Swabey 2002). As

"*Dinornis struthoides* is now recognised as being the smaller male of, in the North Island, the giant moa *D. novaezealandiae*, whose habitats included rain forest as well as shrubland, the species presence does not contradict that of *A. didiformis* and lowland rain forest at, perhaps, 11,728 ± 300 years BP. The date is uncertain because radiocarbon dating of a mixed sample that includes not only more than one individual but more than one taxon must yield a geometric mean age. There was no evidence that the sampled birds were contemporary. Fortunately, accelerator mass spectrometric radiocarbon dating requires such small samples that mixed samples are no longer necessary.

None of the eruptions between the Oruanui and Taupo First Millennium was as large as the Oruanui (Fig. 4). The few ages on Waitomo karst moa from the period between 21,000 and 15,000 BP limit the temporal resolution of the moa record of environmental change. A denser coverage begins with two ages (NZ4840, NZ4844) on *A. didiformis* and these are the more interesting because they confirm a change to lowland rain forest around Waitomo at the same time as a change from *A. didiformis* to *Pachyornis australis* on Takaka Hill (at 41°S) signalled a return to glacial climate contemporary with the Northern Hemisphere Younger Dryas event (Holdaway 2021). As reported there (Holdaway), there is less evidence for a cold period in tree rings in the northern North Island. The disjunction in moa-derived records in the two areas, three degrees of latitude apart, suggests that a possible northward movement of the Subtropical Convergence Zone, or the appearance of a jet of subantarctic water from south of the zone (Nelson *et al.* 2000), may have affected the climate of the northern South Island but not farther north, where the landmass would still have been surrounded by the subtropical water mass.

Conclusions

Half to one degree of latitude south of the pollen sites, the Waitomo karst was, until the 19th century, clothed in lowland rain forest. The presence of *A. didiformis* in the fauna >25,400 years ago shows that the vegetation then was also lowland rain forest (Worthy 1990; Worthy & Holdaway 1993, 1994, 2002), despite its being within the period of the eLGM. Then, precisely at the time of the Oruanui eruption (Fig. 4A), the rain forest moa was replaced rapidly by the shrubland species *E. curtus* (Worthy 1990, 2000; Worthy & Holdaway 2002).

Changes in the distribution of habitat-specific taxa such as these imply changes in the distribution of their habitats. The 40 cm isopach for the

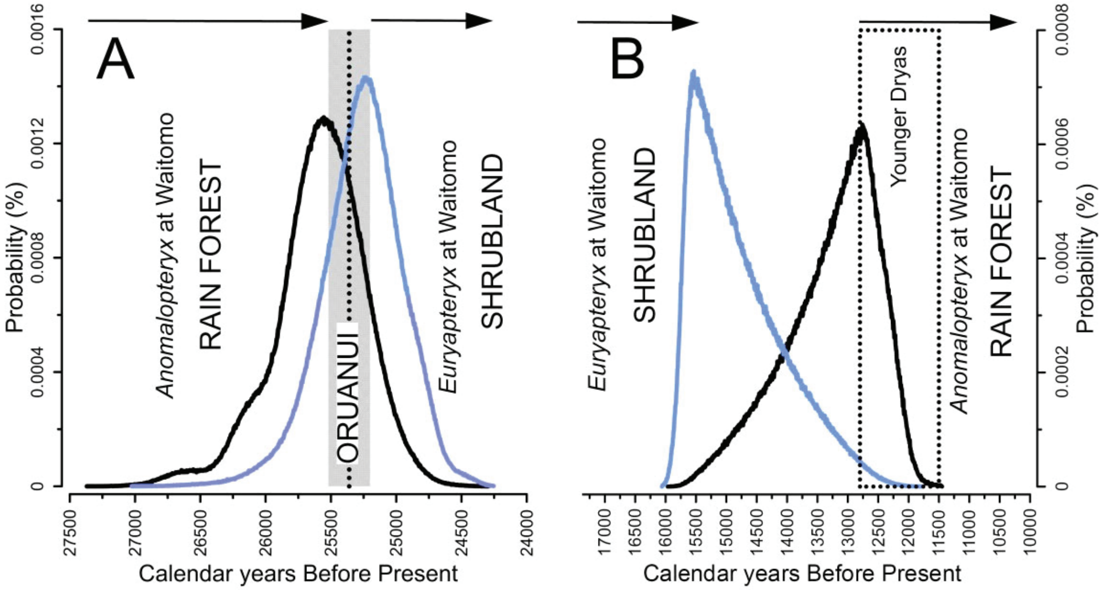

Figure 6. Bayesian estimated date distributions for (**A**) end of presence of *Anomalopteryx didiformis* (black) and arrival of *Euryapteryx curtus* (blue) in the Waitomo area, indicating a change of vegetation at time of the Oruanui eruption. **B**, end of presence of *E. curtus* (blue) and return of *A. didiformis* (black) during the transition between the Weichselian-Otiran glaciation and the Holocene interglacial, and the indicated change in vegetation. Oruanui eruption date: dotted line, mean; shaded rectangle, 95.4% confidence interval, from Vandergoes *et al.* (2013). Younger Dryas, dotted rectangle indicates duration of Younger Dryas post-glacial cold period.

Kawakawa-Oruanui tephra (Vandergoes *et al.* 2013) extends across the Waitomo karst (Fig. 2). Volcanic ash that deep will not only kill the vegetation but sterilise the soil (Oppenheimer 2011). The extent of the ashfall suggests that it would have taken some time (some centuries perhaps) for propagules from surviving vegetation to arrive from refugia that may have been hundreds of kilometres away. From an unknown refugium of its own, *E. curtus* colonised the developing shrubland.

The presence of rain forest in the karst until the eruption suggests that the present reconstruction of the LGM vegetation for that area is not correct. In addition, the abrupt change from forest to shrubland at, so far as it is possible to tell, the time of the Oruanui eruption suggests that the shrubland in the Waitomo karst and indeed farther north in the Waikato Basin during the eLGM was volcanogenic. It was probably not the normal vegetation in the area under a glacial climate.

Abruptness of faunal change at 25,400 years BP, contemporary with the Oruanui eruption in a period of glacial climate, is consistent with the eruption having been the driver of the vegetation (and faunal) change. In contrast, the apparently protracted change to lowland rain forest from shrubland is consistent with a (slower) climatic driver. As the global climate has been “glacial” for most of the past million years (Ehlers & Gibbard 2007), the recent post-glacial southward spread of rain forest through the main islands can be seen as a brief anomaly rather than – as usually done – a “recovery”. The normal southern boundary of rain forest and its avifauna during glacial periods was probably south of its presently accepted position, which is itself probably an artefact of the effects of the super eruption. In that respect, the southward spread of *A. didiformis* into the Waitomo karst was, for that species at least, a recovery of its pre-eruption distribution. *Euryapteryx curtus* remained in the central North Island avifauna at the behest of the ongoing lesser eruptions, as its presence after the Taupo First Millennium eruption attests. The species may there have been a “volcanic nomad”, its distribution ebbing and flowing with the changing patterns of post-eruption shrublands.

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Changes in the Mana Island, New Zealand, bird community following mouse (*Mus musculus*) eradication

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Abstract: House mice (*Mus musculus*) have proven to be the most difficult introduced mammal to eradicate from (and keep out of) New Zealand reserves and sanctuaries. Partly as a consequence of this, little is known about how bird communities respond to mouse eradication. Mice were successfully eradicated from 217 ha Mana Island Scientific Reserve, near Wellington, in 1989–90. Five-minute bird count surveys undertaken in spring and autumn before and after mouse eradication revealed that 13 of 22 species were recorded significantly more often after mouse eradication, and just two species were recorded significantly less often following the eradication (and each of these in one only of the two seasons that were compared). Four species had no significant change, and three species showed mixed responses between the two seasons. While the overall pattern was of increased relative bird abundance after mouse eradication, there is limited information on why individual bird species increased during the study period, and whether this was a consequence of mouse eradication. Bird count data revealed that insectivorous passerines may have benefited the most from mouse eradication on Mana Island, suggesting that competition for invertebrate prey was the main impact that mice had on the birds of the island. The use of anticoagulant rodenticides to eradicate mice from Mana Island had little detectable impact on populations of the island's birds.

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Keywords: anticoagulant, bird, brodifacoum, conservation management, ecological restoration, flocoumafen, Mana Island, mouse eradication

INTRODUCTION

The house mouse (*Mus musculus*) is one of the most widespread invasive mammals in the world, including throughout New Zealand (Moors & Atkinson 1984; Angel *et al*. 2009; Murphy & Nathan 2021). Due to their small size, ubiquity, and reluctance to consume baits, mice have proven difficult to eradicate from mainland sites, and to prevent from reinvading (Burns *et al*. 2012; Innes *et al*. 2012; Norbury *et al*. 2014; Lynch 2019; Watts *et al*. 2022). Although mice have been eradicated from at least 22 New Zealand islands, most of the larger islands had multiple rodent species eradicated simultaneously (Broome *et al*. 2019), and there have been few opportunities to investigate how bird communities respond to mouse eradication alone (Horn *et al*. 2019; Russell *et al*. 2020).

Mice are omnivorous, and can affect food webs at multiple levels, both directly and indirectly (Thoresen *et al*. 2017; Murphy & Nathan 2021; Watts *et al*. 2022). Invertebrates are an important part of mouse diet (Le Roux *et al*. 2002; Jones & Toft 2006; Russell *et al*. 2020; Murphy & Nathan 2021), and so when mice are at high densities they may limit the food supply of both insectivorous and granivorous birds (Goldwater *et al*. 2012; Watts *et al*. 2022). Conversely, a dense mouse population may benefit predatory birds that prey on mice (Hayward &

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MacFarlane 1971; Davey & Fullagar 1986; Twigg & Kay 1994).

In the absence of other mammalian predators, mice can reach very high densities, and may change their behaviour, potentially increasing their impacts on other wildlife (Newman 1994; Angel *et al*. 2009). On at least three widely-separated islands (Gough and Marion Islands, and Midway Atoll), mice have become predators of albatrosses and burrowing-nesting petrels, attacking both chicks and adults, and driving some species towards extinction (Cuthbert *et al*. 2004; Jones & Ryan 2009; Wanless *et al*. 2012; Davies *et al*. 2015; Dilley *et al*. 2016, 2018; Jones *et al*. 2019; Work *et al*. 2021).

Mice occurred at extremely high densities on Mana Island, near Wellington, in the late 1980s, with a total population estimate of up to 5–15 million animals (Anonymous 1989; Hutton 1990). As the island is only 217 ha, these estimates equate to a phenomenal 2.3–6.9 mice per m^2 over the entire island. Even if these estimates were excessive, it is likely that mice were adversely impacting many of the bird species present, and were drivers of ecosystem change. However, the only direct impacts of mice on birds recorded on Mana Island were anecdotal observations of mouse predation of eggs and chicks of New Zealand fantail (*Rhipidura fuliginosa*) and European goldfinch (*Carduelis carduelis*) (Phil Todd *pers. comm.* to CMM).

The main driver for the mouse eradication on Mana Island was to safeguard populations of two threatened lizard species (McGregor's skink *Oligosoma macgregori* and goldstripe gecko *Woodworthia chrysosiretica*) and Cook Strait giant weta (*Deinacrida rugosa*) that had survived naturally on the island (Hutton 1990; Hook & Todd 1992; Newman 1994). Fortuitously, Wellington branch of the Ornithological Society of New Zealand had initiated bird counts on Mana Island two years before the mouse eradication project commenced. These counts were continued for four years after the last mouse was caught on Mana Island, providing an opportunity to investigate changes in the bird community during and following mouse eradication.

We present analyses of 5-minute bird counts undertaken on Mana Island before, during, and after mouse eradication (which was achieved through application of rodenticide baits), to investigate changes in bird conspicuousness following mouse eradication. We also investigate population-level changes following aerial application of anticoagulant rodenticide baits.

METHODS

Study site and mouse eradication

Mana Island (41°05'S, 174°47'E) is a 217 ha scientific reserve that lies 2.5 km off the Wellington west coast, 5 km west of the entrance to Porirua Harbour (Fig. 1). Administered by the Department of Conservation since 1987, Mana Island was managed as a farm for more than 150 years until the last farm stock (cattle *Bos taurus*) were removed in April 1986 (Miskelly 1999; Maysmor 2009). The island has a gently sloping summit plateau (from 121 m a.s.l. in the north to 95 m a.s.l. in the south), and several steep-sided valley systems that flow to the east coast (Fig. 1). Little forest remained on the island before a major revegetation programme was initiated in 1987 (Timmins, Atkinson *et al*. 1987; Miskelly 1999, 2010, 2022). The bird counts reported here were undertaken during 1987–93, while the island was still predominantly covered in rank grass (dominated by cocksfoot *Dactylis glomerata*, perennial ryegrass *Lolium perenne*, and prairie grass *Bromus willdenowii*; Timmins, Ogle *et al*. 1987). One count station was under tall kānuka (*Kunzea robusta*) in Forest Valley, a few count stations were near patches of tauhinu (*Ozothamnus leptophyllus*) scrub in Weta Valley, and a line of stations along the eastern and northern shoreline was along the foot of steep slopes predominantly covered with *Coprosma propinqua*, tauhinu, and boxthorn (*Lycium ferocissimum*) (Timmins, Ogle *et al*. 1987). The only

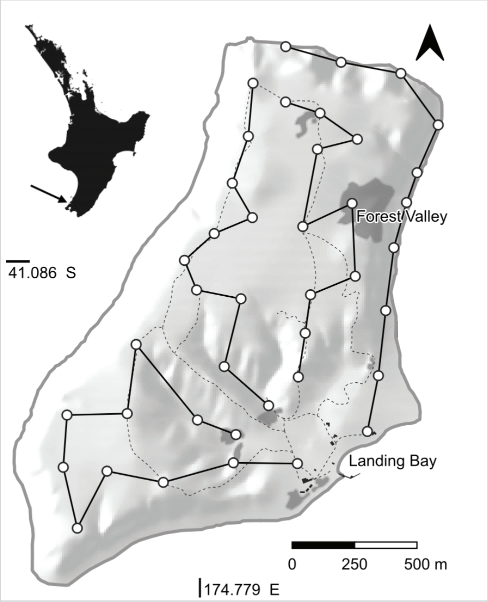

Figure 1. Bird count station locations on Mana Island (Wellington, New Zealand) during 1987–93. Black = buildings; dark grey = trees (macrocarpa *Cupressus macrocarpa* stands, apart from Forest Valley, which was predominantly kānuka *Kunzea robusta*). Dashed lines are farm tracks based on a 1987 aerial photograph. Straight lines link consecutive count stations, and do not represent the routes walked.

bird translocations undertaken to Mana Island during this period were a few South Island takahe (*Porphyrio hochstetteri*) released from 1987 (Miskelly & Powlesland 2013; Miskelly 2022), and which were temporarily moved to Kapiti Island or confined to pens when rodenticide pellets were used during mouse eradication (1989–92).

The 5-minute bird counts reported here were initiated around the same time that the replanting programme began (Timmins, Atkinson *et al*. 1987; Miskelly 1999). The removal of cattle in 1986 resulted in the pasture grasses growing rank, and a proliferation of grass seed. House mice were the only introduced mammals left on the island, and their numbers exploded in response to the abundant grass seed, increased shelter, and absence of predation (Hutton 1990; Newman 1994). Mice were eradicated by a combination of two methods: aerial distribution of anticoagulant rodenticide baits, and similar baits placed in a 25 m grid of bait stations (Hook & Todd 1992). The first air drop of baits (4 g wax pellets containing 0.005% flocoumafen) was undertaken on coastal slopes on 24 July 1989. Two days later, 5,500 bait stations across the entire island were each baited with ten x 16 g wax blocks containing the same concentration of flocoumafen. These were replenished on 8–10 August. Bait consumption had dropped to low levels by 4 September, when 2 tonnes of pellets containing 0.0002% brodifacoum were air-dropped over the whole island. Consumption of bait in bait stations by mice effectively ceased after this date. A second brand of wax block bait (containing 0.0005% brodifacoum) was added to the bait stations from the end of October 1989 (details from Hook & Todd 1992, Newman 1994, and Phil Todd *pers. comm.* to CMM). Rodenticide baits were maintained in the bait stations until the stations were removed in February and March 1992. The last known mouse on Mana Island was caught on 5 February 1990, about 5 months after the previous last evidence of mouse presence (Newman 1994). The eradication was declared a success in November 1991 (Hook & Todd 1992).

Seven swamp harriers (*Circus approximans*), three mallards (*Anas platyrhynchos*) and a sacred kingfisher (*Todiramphus sanctus*) were found dead on Mana Island during August and September 1989 (Phil Todd *pers. comm.* to CMM). None was assayed for the presence of flocoumafen or brodifacoum, but it is likely that some of the harriers at least succumbed to secondary poisoning after eating dead or dying mice. Over the following 19 months, a song thrush (*Turdus philomelos*) and a house sparrow (*Passer domesticus*) were found dead inside bait stations, and two European greenfinches (*Chloris chloris*) and a song thrush were killed in snap traps used to monitor for the presence of mice (Phil Todd *ibid*.).

Study design, data collection and analysis

Forty-one count stations along four lines were established on Mana Island by AJB and Russell Thomas in 1987 (Fig. 1). Count stations were spaced at least 200 m apart on 4 lines, with observers typically counting two count station lines (i.e. 20 or 21 count stations) on each survey day.

The 5-minute count methodology used was based on Dawson & Bull (1975). Observers recorded all birds of all species seen or heard during 5 minutes while stationery at each count station (unbounded counts, *sensu* Dawson & Bull 1975; Hartley & Greene 2012). Any birds that were both seen and heard were recorded as seen only, with totals for seen + heard combined in analyses. Any birds recorded while walking between count stations were excluded from analyses. Each station was counted up to four times by four different observers per count session (i.e. the same month in a given year), with no more than two counts at any station on the same day. Counts were postponed till later in the month if there was forecast persistent rain or strong winds.

Counts were undertaken in three blocks: before mice were eradicated (July 1987 to May 1989), during eradication (October 1989), and after eradication (January 1990 to September 1993). Each 5-minute count was initiated between 0630 and 1756 hours, with a similar spread of count start times for each line and station across survey years. All 2,304 counts ('checklists') have been entered in eBird; only data from the 1,503 spring and autumn counts are presented here (Table 1), as these were the only seasons that were counted sufficiently often after mouse eradication for statistical and graphical comparison.

The analyses were based on 909 'Spring' 5-minute bird counts and 593 'Autumn' counts, with 519 counts before mouse eradication, 150 during eradication, and 833 after eradication. The mean count for each species was calculated for each of the 41 stations for each count session, to minimise pseudo-replication and to compensate for variance in observer ability. Counts undertaken in the same calendar month were pooled for each count block, to provide up to 123 independent estimates per species per 'month' (i.e. 41 count stations x 3 years).

The main comparisons presented are combined pre-eradication counts compared to combined post-eradication counts for each of the 22 most frequently recorded species for each season (i.e. spring 1987–88 vs spring 1991–93, and autumn 1988–89 vs autumn 1991–93). Counts undertaken 33–34 days after the second aerial spread of rodenticide ('Spring 1989') are presented graphically, but were excluded from the 'before and after' statistical comparisons that are presented in Figures 2–5. The spring 1989 counts were compared with spring 1987 & 1988 counts, to determine whether any

Table 1. Bird count effort on Mana Island during 1987–93; 'days' refers to how many days 5-minute bird counts were undertaken, and 'replicates' refers to how many counts were undertaken at each of the 41 count stations. Counts undertaken soon after rodenticide was spread over the island are shown in bold.

Count block (number of days, replicates, total counts)	**Summarised herein as**
July 1987 (2, 2–4, 117)	–
October–November 1987 (4, 2–4, 160)	Spring 1987
February 1988 (2, 3, 120)	–
April 1988 (2, 1–3, 90)	Autumn 1988
July 1988 (2, 2, 80)	–
November 1988 (3, 3–4, 138)	Spring 1988
February 1989 (3, 2–3, 108)	–
May 1989 (2, 1–4, 131)	Autumn 1989
October 1989 (2, 3–4, 150)	**Spring 1989**
January 1990 (2, 2–4, 139)	–
July 1990 (1, 2, 80)	–
April 1991 (1, 2, 82)	Autumn 1991
July 1991 (2, 2–4, 157)	–
October 1991 (2, 3–4, 148)	Spring 1991
March 1992 (2, 4, 160)	Autumn 1992
October 1992 (2, 3–4, 152)	Spring 1992
March 1993 (2, 3–4, 130)	Autumn 1993
September 1993 (2, 4, 161)	Spring 1993

species had declined (or increased) following the aerial spread of rodenticide baits, with significant results presented in the text.

Count means for each species-station-month were transformed (square root (x+1)) to reduce skew in order to meet requirements for least squares parametric comparisons. Transformed count means between count blocks for each month were compared with 2-way analyses of variance (ANOVA).

Limitations of study design

The Mana Island bird survey was an Ornithological Society of New Zealand project undertaken by a large team of volunteers, each with varying ability to detect and recognise the full range of bird calls, and it was run over 7 years, with changing personnel. This necessitated some compromises in study methods and design. The first was to use the 5-minute bird count technique (Dawson & Bull 1975), rather than a distance-sampling methodology that may have allowed calculation of absolute density estimates for a smaller subset of focal species (Broekema & Overdyck 2013; Greene & Pryde 2013). Five-minute bird counts do not provide a measure of absolute or relative abundance, but do provide an index of abundance and conspicuousness (or 'encounter rate') suited for comparisons within the same species at the same site over time (Dawson & Bull 1975; Verner 1985; Koskimies & Väisänen 1991; Ralph *et al*. 1995). In order to reduce the effects of varying observer ability (Bibby *et al*. 2000; Hartley 2012), each station was counted 2–4 times by different observers each count session, and the mean count for each station was used in analyses, rather than single-observer counts.

There was no suitable control site that could be used to generate data on changes in bird numbers or encounter rates over time that may have been independent of mouse eradication, e.g. population responses to severe weather events. This was the main reason for undertaking counts in multi-year blocks, and pooling session counts for each count-month, in order to smooth out inter-annual variations that may have obscured bird population responses to mouse eradication. Pooling several years of counts plus undertaking counts on 2–4 different days per session also compensated for variation in count start times, and variation in weather conditions on count days affecting bird behaviour and detectability (Simons *et al.* 2007; Hartley 2012).

Scientific names of bird species recorded during the counts are presented in Appendix 1 (and follow Checklist Committee 2022). Scientific names for any additional species mentioned are provided in the main text.

RESULTS

Mana Island bird community during 1987–93

The bird community recorded during 5-minute counts undertaken on Mana Island between 1987 and 1993 was dominated by gulls and introduced passerines (Table 2, Appendix 1). The most frequently recorded native land bird species were silvereye (ranked 6th), New Zealand fantail (8th), and swamp harrier (11th).

Table 2. The twelve species with the highest counts during spring and autumn 5-minute bird counts on Mana Island during 1987–93. The figures presented are the mean number of birds recorded per 5 minutes (all years combined).

Species	**Spring**	**Autumn**
Southern black-backed gull *Larus dominicanus*	30.538	0.636
Common starling *Sturnus vulgaris*	3.655	1.905
Red-billed gull *Chroicocephalus novaehollandiae*	3.099	0.030
European goldfinch *Carduelis carduelis*	1.727	1.169
Eurasian skylark *Alauda arvensis*	1.567	0.507
Silvereye *Zosterops lateralis*	0.568	1.160
European greenfinch *Chloris chloris*	0.578	0.360
New Zealand fantail *Rhipidura fuliginosa*	0.299	0.471
White-fronted tern *Sterna striata*	0.527	0.046
Yellowhammer *Emberiza citrinella*	0.249	0.254
Swamp harrier *Circus approximans*	0.071	0.343
House sparrow *Passer domesticus*	0.164	0.244

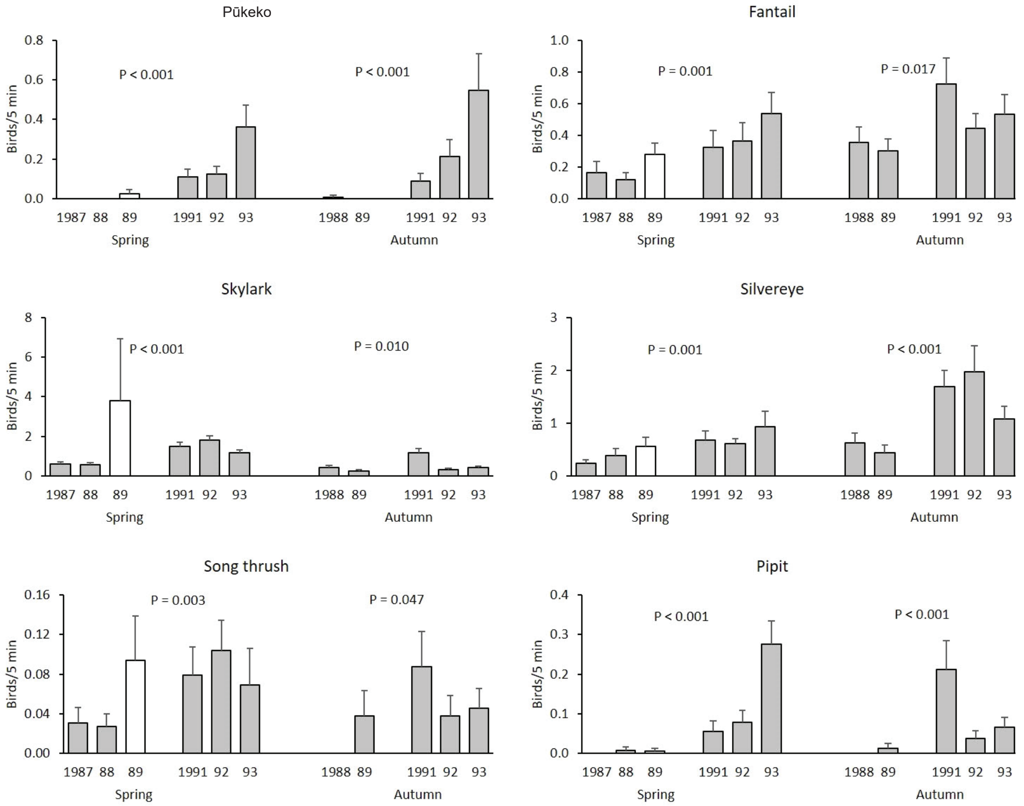

Figure 2. Bird species that had higher counts in both spring and autumn after mice were eradicated from Mana Island. Spring 1989 counts (when rodenticide was present, shown as a white bar) were excluded from the statistical analyses presented in this Figure. The data presented are birds per 5-minute bird count (mean plus standard error). P values show significant differences in mean counts between count blocks (where $P<0.05$).

Species that were recorded more frequently after mouse eradication

Six bird species had significantly higher counts in both seasons after mice were eradicated from Mana Island: pūkeko, New Zealand fantail, Eurasian skylark, silvereye, song thrush, and New Zealand pipit (Fig. 2). Both pūkeko and pipit were rarely recorded before mouse eradication, and pūkeko increased rapidly over the final years of the survey (Fig. 2).

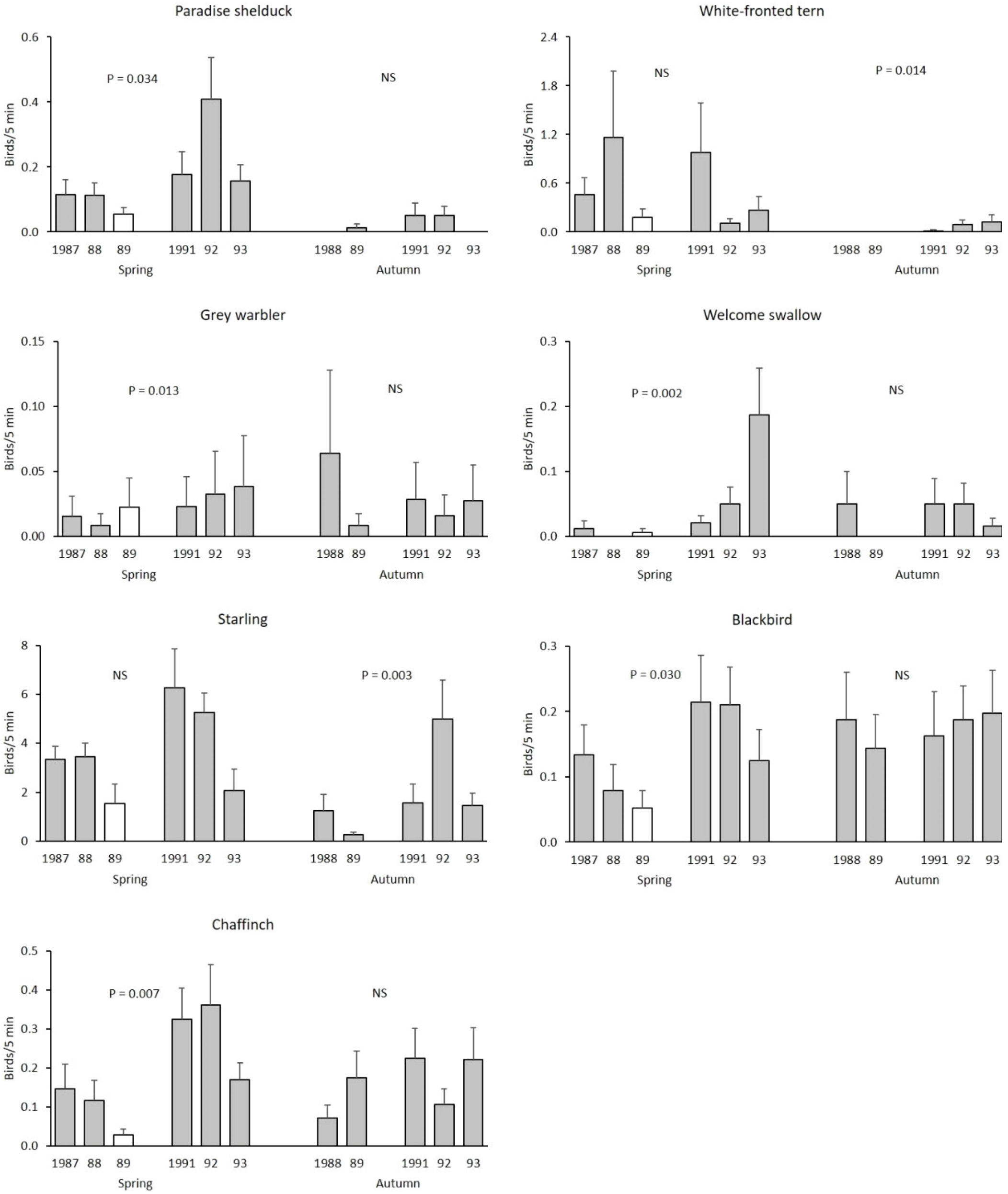

Figure 3. Bird species with significantly higher counts in one of two seasons after mice were eradicated from Mana Island. Spring 1989 counts (when rodenticide was present, shown as a white bar) were excluded from the statistical analyses presented in this Figure. The data presented are birds per 5-minute bird count (mean plus standard error). P values show significant differences in mean counts between count blocks (where P<0.05). NS = not significant.

A further seven species had significantly higher counts in one of the two seasons after mice were eradicated (with no significant difference in the other season). Paradise shelduck, grey warbler, welcome swallow, Eurasian blackbird, and chaffinch had significantly higher counts in spring, and white-fronted tern and common starling had significantly higher counts in autumn (Fig. 3).

Species that were recorded at the same rate before and after mouse eradication

Four bird species had no significant difference in both their spring and autumn counts after mice were eradicated from Mana Island: rock pigeon, southern black-backed gull, dunnock, and yellowhammer (Fig. 4). Black-backed gulls were an abundant breeding species on the island's plateau and coastal slopes in spring, but were recorded much less frequently in autumn (Fig. 4).

Species that were recorded less often in one season after mouse eradication

No bird species had significantly lower counts in both seasons after mice were eradicated from Mana Island. Three species had significantly higher counts in one season, and significantly lower counts in the other. Harriers were more abundant in autumn than in spring throughout the study; however, they were recorded significantly more often in spring, and less often in autumn, following mouse eradication (Fig. 5). In contrast, European goldfinches and European greenfinches were recorded significantly more often in autumn, and less often in spring, following mouse eradication (Fig. 5). Red-billed gulls and house sparrows were recorded significantly less often in spring, with no significant change in their autumn counts (Fig. 5).

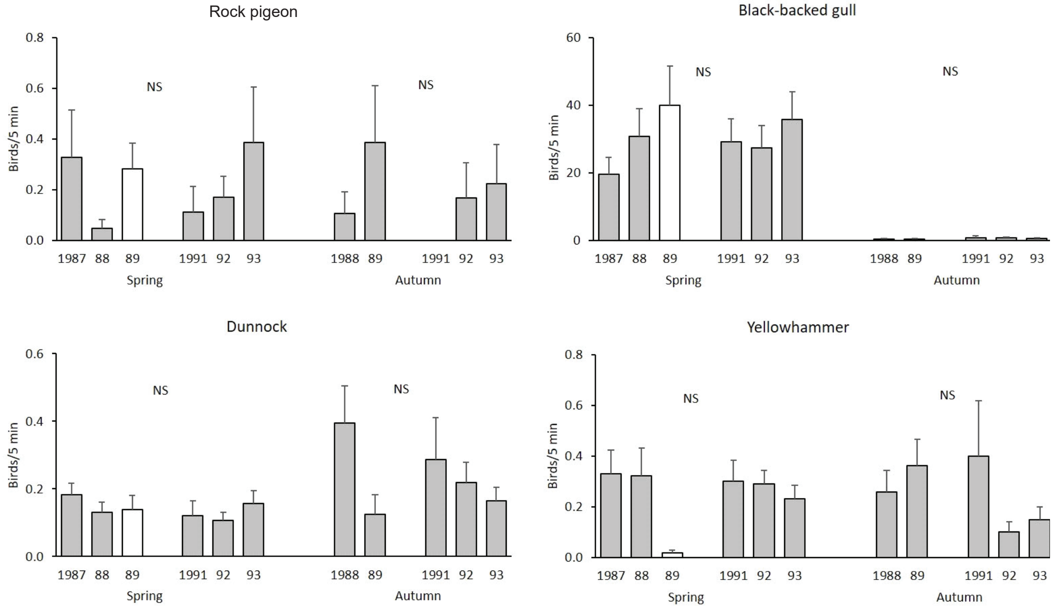

Figure 4. Bird species that had no significant difference in both spring and autumn counts after mice were eradicated from Mana Island. Spring 1989 counts (when rodenticide was present, shown as a white bar) were excluded from the statistical analyses presented in this Figure. The data presented are birds per 5-minute bird count (mean plus standard error). NS = not significant.

Species that were recorded more or less often while rodenticide was being used on the island

Two of the 22 species were recorded significantly less frequently in spring 1989 compared to the previous two years: common starling and yellowhammer (Figs 3 & 4; starling p = 0.002, yellowhammer p = 0.005; note that starlings were recorded at about ten times the frequency of yellowhammers in most years). In contrast, New Zealand fantails were recorded significantly more often in spring 1989 compared to the spring 1987 & 1988 counts (Fig. 2, p = 0.029). There were no significant differences between spring 1989 counts and previous spring counts for the other 19 species.

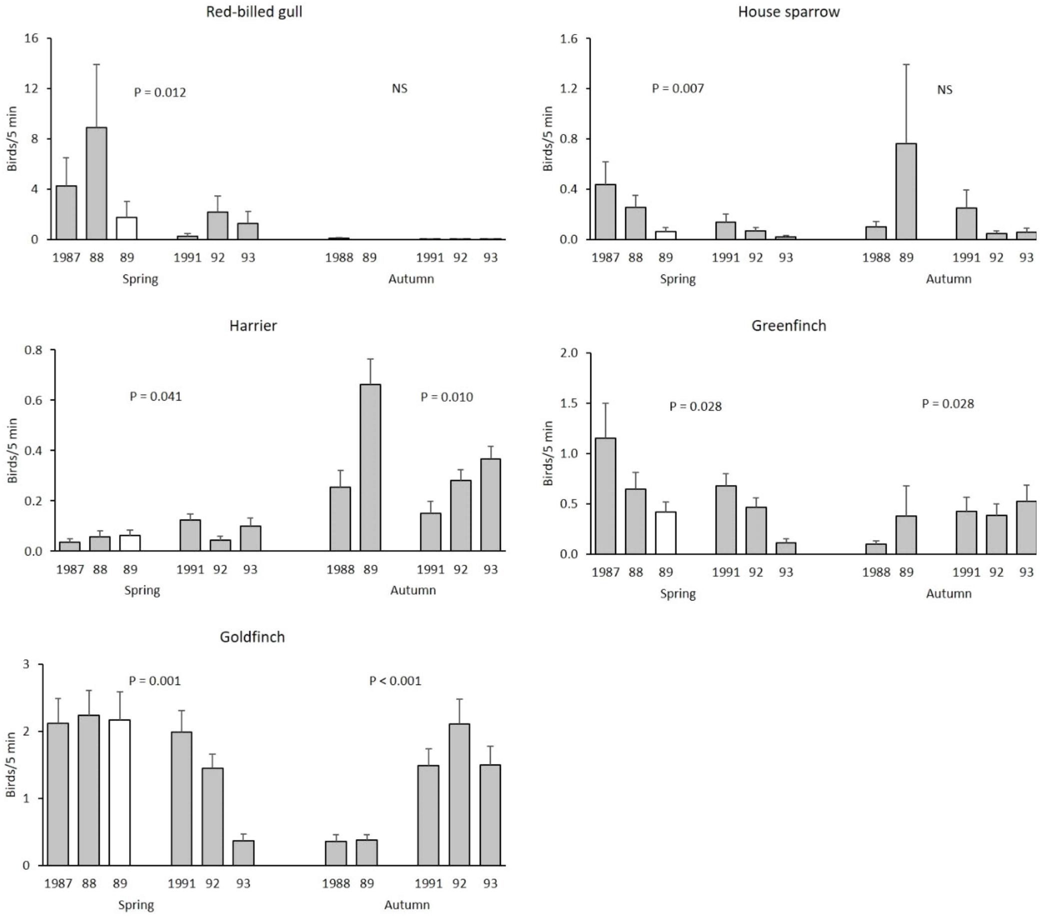

Figure 5. Bird species that had significantly lower counts in one of two seasons after mice were eradicated from Mana Island. Spring 1989 counts (when rodenticide was present, shown as a white bar) were excluded from the statistical analyses presented in this Figure. The data presented are birds per 5-minute bird count (mean plus standard error). Swamp harriers were counted more often in spring after mouse eradication, and less often in autumn, while the two finch species were counted more often in autumn, and less often in spring. P values show significant differences in mean counts between count blocks (where P<0.05). NS = not significant.

DISCUSSION

Changes in the Mana Island bird community between 1944 and 1993

Mana Island was predominantly covered in rank grass during 1987–93, and the bird fauna apparently changed rapidly after grazing ceased in April 1986. Information on the Mana Island bird community during the farming era is based on two days of surveys in January 1944 (Wodzicki & Oliver 1944) and three days in each of June 1972 and April 1975 (Appendix 1 *in* Department of Lands & Survey 1981); both sets of earlier data are here included with a summary of 1987–93 data in Appendix 1.

Wodzicki & Oliver (1944) did not report any native land bird species, whereas the Ecology Division DSIR survey teams in 1972 & 1975 reported fantail and pipit as abundant, 'many' kingfishers and silvereyes, and the presence of fewer than five harriers and grey warblers. Among the introduced bird species, Wodzicki & Oliver (1944) reported only a single finch species (chaffinch, ranked second in abundance after common starling), whereas in 1972 & 1975, greenfinch was abundant, and 'many' goldfinches and common redpolls were reported. Eurasian skylark and yellowhammer were both reported in 1944, but not in 1972 & 1975.

Among the more notable changes between 1975 and 1987–93, were the detection of skylarks, yellowhammers, welcome swallows, pūkeko, and paradise shelducks in the latter period, with skylark and yellowhammer both ranked among the ten most frequently recorded species (Table 2, Appendix 1). Swamp harriers were apparently more abundant during autumn 1987–93 compared to April 1975, when they were listed as 'present' (fewer than five individuals) across both the 1972 & 1975 surveys.

Pūkeko began breeding on the island in 1989, and were common by the end of the 1987–93 surveys. By then they were causing problems with the revegetation programme (by pulling out new plantings), and also interfering with supplementary feeding stations used for takahē (Miskelly 1999).

Impacts of use of rodenticide baits on Mana Island birds

Despite seven harriers being found dead over the first two months of the mouse eradication, we did not detect any decrease in their numbers in spring 1989 compared to previous years (Fig. 5). However, there was a spike in the harrier counts a few months before mouse eradication (Fig. 5). There were also very high counts of 14 and 16 harriers visible simultaneously around the time of the autumn 1989 counts (on 15 & 21 May respectively; Phil Todd and Olga Vincent, *pers. comm.* to AJB), indicating that harriers were more abundant than usual on Mana Island at the time that anticoagulant baits were applied. The large number of harriers present on Mana Island in 1989 complicated our ability to detect unusual mortality rates when comparing counts of live birds with previous years.

Many harriers from the South Island migrate across Cook Strait in autumn (Seaton *et al*. 2022). As harriers readily catch and consume mice (Redhead 1969; Baker-Gabb 1981), including on Mana Island before mice were eradicated (Efford *et al*. 1988), it is likely that some of the migrating birds stayed on Mana Island due to the super-abundance of mice in autumn 1989.

The two bird species that were recorded in significantly reduced numbers in spring 1989 (common starling and yellowhammer) soon returned to their 'pre-mouse-eradication' levels, with starlings becoming significantly more abundant in autumn after mice were eradicated (Fig. 3). As no corpses of either species were recorded during the intensive field work during the mouse eradication programme, the low numbers of starlings and yellowhammers on Mana Island in spring 1989 may have been unrelated to rodenticide use. It is possible that the island had become less suitable for them due to consumption of invertebrates and seeds by the plague numbers of mice, although some insectivorous bird species were more abundant than usual in spring 1989 (Fig. 2; this was significant for fantail only).

As with Kapiti Island 22 km to the north, the conservation benefits of anticoagulant use on Mana Island greatly exceeded the impacts of its use (Empson & Miskelly 1999, and next section).

Changes in the Mana Island bird community following mouse eradication

The significantly increased count rates for 13 of 22 bird species monitored on Mana Island following mouse eradication indicates that mice were likely impacting on the bird community on the island. However, in the absence of detailed ecological studies, it is difficult to separate direct impacts (e.g. predation) from indirect impacts (e.g. competition for food), or even to separate bird population increases that were independent of mouse eradication (e.g. immigration or colonisation) from those that were a consequence of it.

Many of the bird species that increased following mouse eradication were small passerines with diets that likely overlap those of mice, and/or that produce eggs and chicks small enough to be vulnerable to mouse predation (New Zealand fantail, Eurasian skylark, silvereye, song thrush, New Zealand pipit, grey warbler, welcome swallow, common starling, Eurasian blackbird, and chaffinch; Figs 2 & 3). While it is tempting to attribute population increases for some or all of these ten species to mouse eradication, we note that five other passerine species did not increase after mice were eradicated (dunnock, yellowhammer, house sparrow, European greenfinch, and European goldfinch; Figs 4 & 5). It is noteworthy that the passerine species that increased following mouse eradication were predominantly insectivorous, while the second group (with the exception of dunnock) were predominantly seed-eaters.

Invertebrates comprised 57.9% by volume of mouse diet on Mana Island during 1981–82, while the island was being grazed by cattle (Pickard 1984). By May 1989 this had dropped to 6.6 ± 20.3% invertebrates by volume (Fitzgerald & Cong 1989), implying a relatively greater availability of plant material (likely grass seed) in the rank pasture then present. There are few data on the availability of either invertebrates or seeds for birds on Mana Island when mice were at plague densities. However, Newman (1994) reported significant increases in catch rates of Cook Strait giant weta and garden snails (*Cornu aspersum*) in pitfall traps on Mana Island after mice were eradicated, indicating that some invertebrate populations were suppressed by the mice. Indirect evidence from the bird population responses reported here suggest that invertebrates may have been a limiting resource when mice were at high densities on Mana Island (as reported for Antipodes Island; Horn *et al*. 2019, Russell *et al*. 2020), while sufficient seeds likely remained available throughout for granivores, i.e. sparrows, finches, and buntings.

We suggest that the colonisation of Mana Island by pūkeko in the late 1980s was likely a consequence of the cessation of grazing providing more cover for the birds. However, pūkeko increased on Tiritiri Matangi Island after eradication of kiore / Pacific rats (*Rattus exulans*) (Graham *et al.* 2013), so it is possible that mouse eradication allowed pūkeko to increase more rapidly on Mana Island than would have occurred in the presence of mice.

The autumn decline in harriers on Mana Island following mouse eradication was most likely a functional response to the removal of a major food supply (i.e. mice). Swamp harriers were among the species that were recorded more frequently during mouse plagues in Australia, and were not as evident once the plagues subsided (Hayward & MacFarlane 1971; Twigg & Kay 1994). Harriers continued to be commonly recorded on Mana Island after mice were eradicated, likely switching their main diet from mice to diurnal skinks (*Oligosoma* spp.; authors *pers. obs.*).

While mouse eradication on Mana Island apparently benefited many introduced bird species and a few common native species, the major conservation benefit of the eradication was that it helped prepare the island for the successful reintroductions of numerous more vulnerable bird, reptile and insect species (Miskelly 1999, 2010, 2022). Further to the six successful bird translocations to Mana Island reported by Miskelly & Powlesland (2013), rowi (*Apteryx rowi*), fairy prion (*Pachyptila turtur*), fluttering shearwater (*Puffinus gavia*), bellbird (*Anthornis melanura*), and fernbird (*Poodytes punctatus*) are now well-established on the island, contributing to Mana Island as one of the most comprehensive and successful ecological restoration sites in New Zealand.

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*Deceased.

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APPENDIX 1. Mean counts of 40 bird species recorded during 2,463 5-minute bird counts on Mana Island between 1987 and 1993. Species are listed in decreasing frequency of encounters. The two columns at the right show data from 1–2 January 1944 (Wodzicki & Oliver 1944) and 28–30 June 1972 and 1–3 April 1975 (data collected by M.J. Daniel, M.J. Meads & A.H. Whitaker, Ecology Division, DSIR, and published as Appendix 1 *in* Department of Lands & Survey 1981). Three additional species were recorded in 1944, and one in 1972 & 75. The superscripts in the 1944 column show nine introduced bird species in "numerical sequence", with common starling the most abundant.

Species	Birds per 5 minutes	1944	1972 & 75
Southern black-backed gull *Larus dominicanus*	14.8159	Breeding	Abundant, breeding
Common starling *Sturnus vulgaris*	2.2273	Present[1]	Abundant
European goldfinch *Carduelis carduelis*	1.5795	–	Many
Red-billed gull *Chroicocephalus novaehollandiae*	1.2487	Breeding	Abundant
Silvereye *Zosterops lateralis*	0.9747	–	Many
Eurasian skylark *Alauda arvensis*	0.7661	Present[6]	–
European greenfinch *Chloris chloris*	0.4058	–	Abundant
New Zealand fantail *Rhipidura fuliginosa*	0.3099	–	Abundant
White-fronted tern *Sterna striata*	0.2964	Breeding	Abundant
Yellowhammer *Emberiza citrinella*	0.2751	Present[8]	–
House sparrow *Passer domesticus*	0.2487	Present[3]	Abundant
Rock pigeon *Columba livea*	0.2137	–	Many
Swamp harrier *Circus approximans*	0.1569	–	Present
Fluttering shearwater *Puffinus gavia*	0.1534	–	–
Chaffinch *Fringilla coelebs*	0.1488	Present[2]	Many
Dunnock *Prunella modularis*	0.1369	Present[9]	Many
Eurasian blackbird *Turdus merula*	0.1303	Present[4]	Abundant
Mallard *Anas platyrhynchos*	0.0947	–	Present
Pūkeko *Porphyrio melanotus*	0.0946	–	–
Paradise shelduck *Tadorna variegata*	0.0859	–	–
New Zealand pipit *Anthus novaeseelandiae*	0.0439	–	Abundant
Grey warbler *Gerygone igata*	0.0423	–	Present
Song thrush *Turdus philomelos*	0.0413	Present[7]	Abundant
Variable oystercatcher *Haematopus unicolor*	0.0280	–	Present
South Island takahe *Porphyrio hochstetteri*	0.0232	–	–
Welcome swallow *Hirundo neoxena*	0.0231	–	–
Common redpoll *Acanthis flammea*	0.0197	–	Many
Australian magpie *Gymnorhina tibicen*	0.0191	Present[5]	Many
Little shag *Microcarbo melanoleucos*	0.0189	–	Present
Black shag *Phalacrocorax carbo*	0.0175	Offshore	Present
Sacred kingfisher *Todiramphus sanctus*	0.0160	–	Many
Reef heron *Egretta sacra*	0.0147	Breeding	Present
Little black shag *Phalacrocorax sulcirostris*	0.0074	–	–
Australasian gannet *Morus serrator*	0.0068	Offshore	Present offshore
Little penguin *Eudyptula minor*	0.0026	Breeding	Abundant, breeding
Spur-winged plover *Vanellus miles*	0.0012	–	–
White-faced heron *Egretta novaehollandiae*	0.0012	–	–
Shining cuckoo *Chrysococcyx lucidus*	0.0007	–	–
South Island pied oystercatcher *Haematopus finschi*	0.0004	–	–
Caspian tern *Hydroprogne caspia*	0.0003	–	Present offshore
Arctic skua *Stercorarius parasiticus*	–	Offshore	–
Sooty shearwater *Ardenna grisea*	–	Breeding	Present, breeding
Ruru *Ninox novaeseelandiae*	–	1 dead	Present
Common diving petrel *Pelecanoides urinatrix*	–	–	Present offshore

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Sexing of the endangered Floreana mockingbird (*Mimus trifasciatus*) using morphometric measurements

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Abstract: Male and female adult Floreana mockingbird (*Mimus trifasciatus*) have monomorphic plumage features that make them impossible to sex in the field. In this study, we use discriminant function analysis (DFA), a widely used technique, to assess the best measures to determine sex. We measured six morphological characteristics (mass, beak depth, beak width, tarsus length, wing length, and head-beak length) for birds of known sex (determined by molecular techniques) from the two extant populations of *M. trifasciatus* on Champion and Gardner islets, within the Galápagos archipelago. Using a coefficient of sexual dimorphism, we found that males are significantly larger than females in three of the variables. Discriminant functions using wing length and a combination of wing length + mass, and wing length + tarsus length could classify birds with a 98% level of accuracy. Furthermore, we were able to estimate a robust cut-off point to determine the sex of individuals in the field through a decision tree, using only wing length as morphological variable. Fast and accurate sexing of the bird based on one variable will reduce handling times and minimise stress for captured birds.

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Key words: sex identification, morphometry, discriminant function analysis, Floreana mockingbird, management, Galápagos Islands.

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INTRODUCTION

Identifying the sex of individuals is important in ecological research and conservation biology because knowing the sex of birds can tell us about possible biases in population sex ratios and improve our knowledge of the population dynamics of endangered species. For example, in many populations, one sex may have higher mortality rates than the other causing a bias in the operational sex ratio of a population and potentially lowering population growth rates (Brekke *et al*. 2010). An efficient method for sexing monomorphic species can also improve protocols and methodologies for translocations and captive breeding programmes. In addition, the correct interpretation of behavioural and ecological data often relies on knowing the sex of the study individuals. Many avian species can be sexed using visually distinct phenotypes such as size and colour dimorphism; features usually correlated with social mating systems (Owens & Hartley 1998; Dunn *et al*. 2001) or by observing sex-specific behaviours (Lewis *et al*. 2002; Joo *et al*. 2018). However, for monomorphic species or juvenile birds, differences are less obvious and considerable overlap in male and female characteristics can cause uncertainty. When sex-specific behaviours are used for assigning sex, observers may need long periods of observations that are time-consuming and logistically expensive, especially in areas of difficult access.

For sexing monomorphic species, with an absence of sexually dimorphic external factors, a variety of techniques have been proposed. These techniques include both invasive and non-invasive methods such as cloacal inspection, molecular analysis, vocalisations, statistical methods based on morphometrical measurements, and combinations of these (Lessells & Mateman 1998; Bourgeois *et al*. 2007; Volodin *et al*. 2009; Ellrich, *et al*. 2010; Bazzano *et al*. 2012; Morinha *et al*. 2012). Of these methods, one of the most reliable in sexing birds has been the use of discriminant function analysis (DFA) for morphometric measurements. This technique has been used widely in different birds taxa from Procellariforms (Mischler *et al*. 2015) to passerines including species of Mimidae (Martínez-Gómez & Curry 1998; Fuchs & Montalti 2016), even in juvenile birds (Martín *et al*. 2000; Thorogood *et al*. 2009). This method identifies individuals of known sex by creating a linear function of measurements that best discriminates between males and females (Phillips & Furness 1997) and the coefficient outputs can be used to generate an equation to classify the sex of further sampled individuals (Queen *et al*. 2002). However, despite the wide use of the method, there are some caveats in the robustness of discriminant equations when using small sample sizes (Dechaume-Moncharmont *et al*. 2011). Moreover, although easy to understand by experts, the equations may be problematic for use by those involved in citizen science or community conservation without an academic background.

The Floreana mockingbird (*Mimus trifasciatus*) is the rarest and most range-restricted mockingbird species in the Galápagos archipelago and is classified as "endangered" by the IUCN (Fig. 1). Historically, *M. trifasciatus* occurred in the lowlands of Floreana Island and its surrounding islets. *Mimus trifasciatus* disappeared in the early 1900s from Floreana Island due to a combination of factors, in particular, the effects of introduced species (Curry 1986; Hoeck *et al*. 2010). Currently, *M. trifasciatus* is restricted to two islets representing less than 1% of its former range. Because of its rarity (<350 individuals) and the inaccessibility of these islets, the ecology of the *M. trifasciatus* is poorly understood, which has prevented the development of management plans directed towards increasing the number of individuals and populations, in particular via reintroduction of birds to the lowlands of Floreana Island. Despite its relevant role in the history of biology (Hoeck *et al*. 2010) and its conservation importance (Ortiz-Catedral 2018), basic aspects of the natural history of this species are still missing. Although there are existing criteria using the wing length for sexing Mimids in the Galápagos, most of these criteria have been developed based in the morphometric characters of a different species, the Galápagos mockingbird (*Mimus parvulus*) (Kinnaird & Grant 1982; Curry 1988; 1989; Curry & Grant; 1989). To date, sex determination for *M. trifasciatus* has been

Figure 1. Adult Floreana mockingbird (*Mimus trifasciatus*) perched on an *Opuntia* cactus. Champion Islet. Photo: Enzo M. R. Reyes.

mentioned in Grant *et al*. (2000) and in Deem *et al*. (2011) but neither of these publications report specific criteria to determine sex of this species using morphometric measurements. Our goal was to determine whether morphological differences could be used to distinguish between the sexes of *M. trifasciatus* using discriminant function analysis. We then used a decision tree analysis to identify the trait(s) that provided the greatest discriminatory power and estimated cut-off points of morphological measurements that could be easily interpreted in the field.

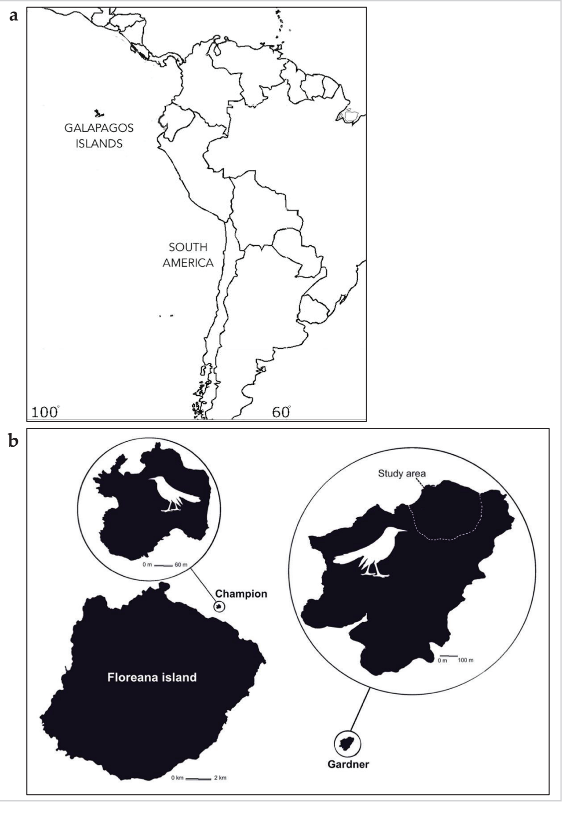

Figure 2. a) Location of the Galapagos Islands in South America. B) Floreana mockingbird (*Mimus trifasciatus*) populations. For the Champion population (90°23′100′′W, 01°14′240′′S), the study area corresponds to the whole islet. For the Gardner population (90°17′700′′W, 01°19′969′′S) the dotted area indicates the 12 ha study which is the only area accessible on the island.

MATERIALS & METHODS

Study site

This study was conducted on Champion (90°23′100′′W, 01°14′240′′S) and Gardner-by-Floreana (90°17′700′′W, 01°19′969′′S) islets in the northern part of Floreana Island (Fig. 2). Champion is a 9.4 ha circular islet (~400 m diameter). It is a crater emerged from the seafloor whose maximum elevation is 46 meters above sea level and is located less than one kilometre from the coastline of Floreana Island (Grant *et al*. 2000). The Gardner-by-Floreana islet (76.5 ha) is located 8 km off the coast of Floreana Island. It is a partially sunk volcanic cone, creating an islet covered by cliffs of 50–100 m high and reaching an elevation of 210 meters a.s.l. The islet has a 100 m high plateau of approximately 12 ha located in the eastern part of the islet (Jiménez-Uzcátegui *et al*. 2011) that is the only place accessible and safe for humans.

Morphometry and molecular sexing

Birds were captured as part of an annual long-term monitoring study carried out since 2006. During November 2015, a total of 41 birds (24 males, 17 females) were caught using a wire cage trap with a lure; these birds were then banded measured, and released. We took six morphological body measurements (Fig. 3) following a standardised measurements protocol for the species: (1) mass; (2) beak depth, in vertical plane in the middle of the nares; (3) beak width, in the upper mandible in a horizontal plane in the anterior edge of the nares; (4) tarsus length, from the intertarsal joint to the foot joint; (5) wing length, with the wing in a natural arc and at 90° angle with the radius/ulna; (6) head-beak length, from the upper beak tip to the nape. All measurements were taken to the nearest 1 and 0.1 mm using a stopped wing ruler and Vernier callipers respectively, the mass was taken to the nearest 0.5 g using a 50 g or 100 g Pesola spring balance. All measurements were taken twice and averaged prior to knowing the sex of each bird, which was later confirmed by molecular analysis of DNA for each bird. For DNA samples, we used a needle to prick the brachial vein of each adult mockingbird shortly after capture. Approximately 5 μL of blood was collected from each individual using a capillary tube (75 μL) and the blood was stored in a CryoTube™ vial with 1.0 ml of Queen's Lysis buffer. Vials were labelled with the respective metal band identity of each sampled bird. Blood samples were sent to the Equine Parentage and Animal Genetic Services Centre, Massey University, New Zealand for molecular analysis of the CHD gene of the avian sex chromosomes using a similar technique described in Norris-Caneda & Elliott (1998).

Analysis

Assumptions of normality were tested using a Shapiro-Wilk Test in R (R Core Team, 2013). All variables met the condition of normality so no

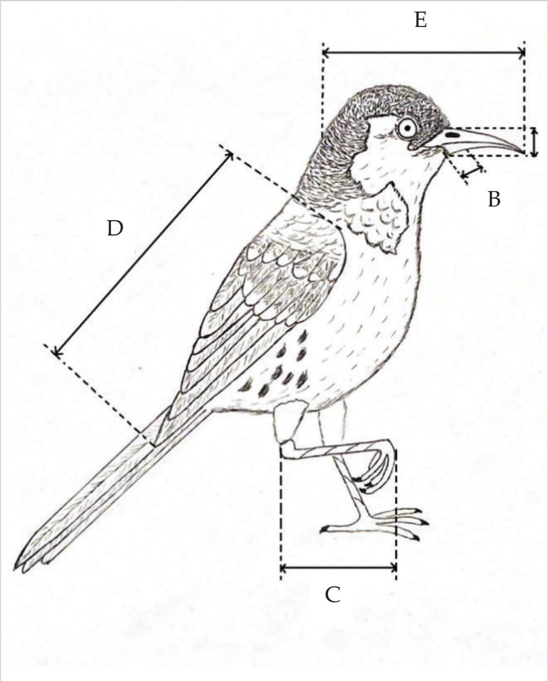

Figure 3. Description of morphological measurements used for the sexing of the Floreana mockingbird (*Mimus trifasciatus*). A) beak depth, b) beak width, c) tarsus length, d) wing length, and e) head-beak length. Drawing by: Enzo M. R. Reyes.

transformation was carried out. To test for inter-sexual differences among the molecular sexed birds, we used an unpaired t-test for each pair of measurements. Moreover, for each measurement, we calculated the percentage of sexual dimorphism using the formula described in Holmes & Pitelka (1968): 100x(m-f)/m, where m and f are the mean values of the male and female respectively. DFA of the measurements of the known sex birds were then conducted to determine which measurements were most reliable for classifying individuals either as male or female. Wilks' lambda (ƛ) statistics was used as a variable selection criterion. The accuracy of our discriminant functions were determined by the percentage of known sex individuals correctly classified using all the individuals. In addition, we applied a jack-knifing prediction procedure in which each case was reclassified by repeatedly removing a single individual and then classifying this individual based on the discriminant function generated by the remaining birds. When we obtained the best discriminant functions, we then calculated the threshold of probabilities of being a male or female through a decision tree analysis which predict an outcome based on a set of predictors classifying particular variables higher than some threshold. The analyses were run on R (R Core Team, 2013) using the packages MASS for the DFA calculations, rrcov for the multivariate lambda values and packages rpart, GGally, and tidyverse for the decision tree analysis. Univariates lambda values were extracted from SPSS software (IBM, 2020).

RESULTS

We sampled 14 birds from Champion (nine males, five females) and 27 birds from Gardner (15 males, 12 females). Morphological measurements from the 41 birds that were molecularly sexed showed that males and females overlapped but generally males were larger than females revealing sexual dimorphism by size (Table 1; Fig. 4). The mean values for five traits: mass, beak depth, tarsus length, head-beak, and wing length, were significantly larger in males than in females. Coefficient of sexual dimorphism shows that mass, beak depth, and wing length are the most dimorph traits. The DFA shows that the wing trait performs the best as a single variable classifying birds correctly 98% of the time (Table 2). Because of this, we created four discriminant functions using a combination of wing length and other variables: wing length + mass, wing length + tarsus length, wing length + all beak, and all measurements combined. From this, wing + mass and wing + tarsus length classified birds correctly 98% of the time in both cases and had a greater discriminatory power based on the Wilks' Lambda values (Table 2). As wing length performed the best as a univariate, the calculated cut-off point by a decision tree analysis was 119.5 mm. The probability of correctly classifying as a female was 94% under the threshold of 119.5 mm, and 100% probability of correctly classifying as a male when the wing length is equal or larger than 119.5 mm. The cut-off point for tarsus length was 39.9 mm. The probability of correctly classifying as a female was 85% under the threshold of 39.9 mm, and 79% probability of correctly classifying as a male when the tarsus length is equal or greater than 119.5 mm. Furthermore, for mass, we obtained two cut-off points: 61.6 g and 56.7 g. Birds under 61.6 g and 56.65 g could be classified as females with 59% and 77% probability, respectively. Meanwhile, birds equal or greater than 56.65 and 61.6 g could be classified as males with 56% and 100% probability, respectively.

DISCUSSION

In this study, we investigated whether *Mimus trifasciatus* can be correctly classified as a male or female by morphological measurements and, if so, which morphological traits are the best to assign

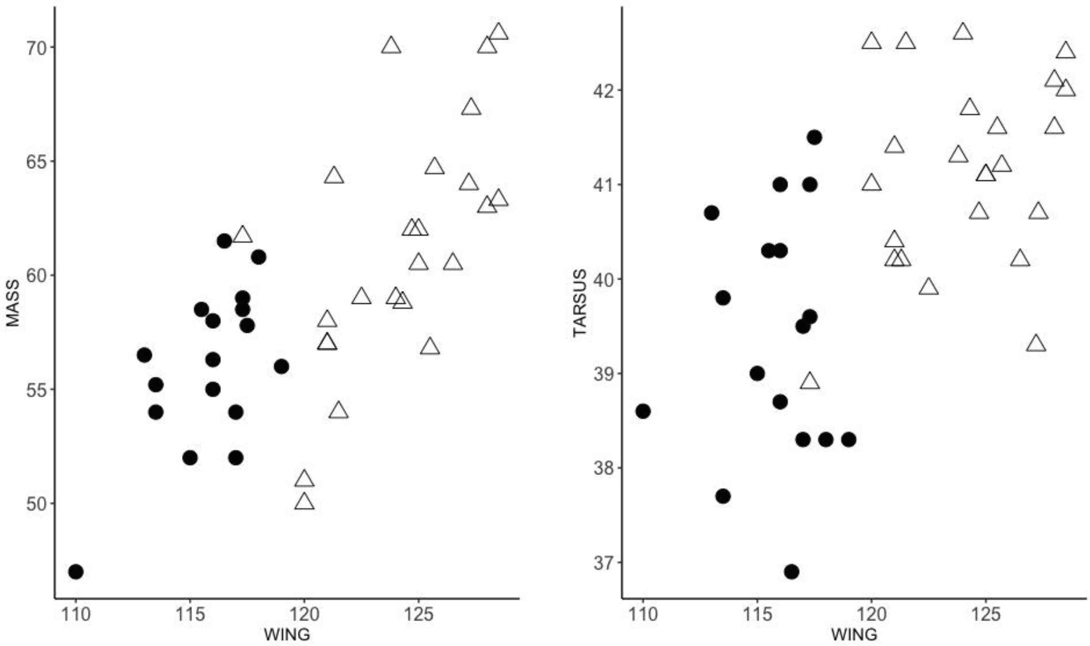

Figure 4. Plot of the measurements used as discriminant functions that best predict the sex of the Floreana mockingbird (*Mimus trifasciatus*). A) Wing length and mass and B) wing length and tarsus length measurements for male (open triangles) and females (closed circles) Floreana mockingbird. Wing length and tarsus length measures are given in mm, while mass is given in g.

an accurate classification. We concluded that male and female *M. trifasciatus* can be easily identified using simple morphological measurements. Our results confirm the assumption of Deem *et al*. (2011) that these monochromatic species present sexual dimorphism evident in morphological traits. Males were significantly larger than females in five of six morphological traits except beak width; similar features have been present in two other mockingbird species: *Mimus saturninus* and *Mimus triurus* (Fuchs & Montalti 2016). However, while mass appeared to be the more dimorphic trait, when using the coefficient of sexual dimorphism mass differences were not enough to correctly assign sex using the DFA. Male and female *M. trifasciatus* can be distinguished with 98% accuracy using only wing length or a combination of wing length, mass, and tarsus length.

Despite the widespread use of DFA, some factors can affect its performance. One is the

Table 1. Morphological measurements of 41 Floreana mockingbirds (*Mimus trifasciatus*) sexed using molecular methods and percentage of dimorphism for each morphological trait. Unpaired *t-test* values (*t*), df and significant values are given for comparison of variables between sexes. NS = not significant. Length measurements are given in mm, while mass is given in g.

	Males			Females			Males vs Females			
	$\bar{x} \pm sd$	Range	n	$\bar{x} \pm sd$	Range	n	*t*	*p*	*df*	% Dimorphism
Mass	61.0 ± 5.5	50.0–70.6	24	56.0 ± 3.6	47.0–61.5	17	3.6	<0.001	38.9	8.2
Head-beak length	59.3 ± 1.2	56.2–61.0	24	57.9 ± 0.7	57.0–59.1	17	4.3	<0.001	37.0	2.1
Beak width	7.1 ± 0.5	6.4–8.1	24	6.9 ± 0.4	6.4–7.6	17	1.5	NS	38.1	2.7
Beak depth	6.6 ± 0.4	6.0–7.6	24	6.2 ± 0.3	5.7–7.0	17	3.9	<0.001	38.8	6.3
Tarsus length	41.1 ± 1.0	38.9–42.6	24	39.4 ± 1.3	36.9–41.5	17	4.6	<0.001	29.0	4.2
Wing length	124.1 ± 3.1	117.3–128.5	24	115.8 ± 2.2	110.0–119.0	17	9.9	<0.001	39.0	6.7

Table 2. Accuracy in assigning sex of Floreana mockingbirds (*Mimus trifasciatus*) using a discriminant function analysis, denoted by Wilks' Lambda (ƛ) using single variables and combined functions of the variables.

		Proportion correct			Proportion jack-knifing		
Variable	ƛ	Female (17)	Male (24)	Overall	Female	Male	Overall
Mass	0.78	0.58	0.83	0.71	0.59	0.75	0.68
Head-beak length	0.72	0.65	0.79	0.73	0.65	0.79	0.73
Beak width	0.95	0.41	0.83	0.66	0.41	0.83	0.66
Beak depth	0.74	0.82	0.75	0.78	0.82	0.75	0.78
Tarsus length	0.63	0.65	0.88	0.77	0.64	0.88	0.78
Wing length	0.31	1	0.96	0.98	1	0.95	0.98
Wing length + mass	0.28	1	0.96	0.98	1	0.96	0.98
Wing length + tarsus	0.29	1	0.96	0.98	1	0.96	0.98
Wing length + all beak	0.29	1	0.96	0.98	0.94	0.88	0.90
All variables	0.51	1	0.96	0.98	0.94	0.92	0.93

consistency of the observer when taking the morphometric measurements. Some studies of sexing by morphological traits have found that this parameter can create bias in the results (Henry *et al*. 2015). Here, our morphological measurements were taken by a single observer at both sites during the same period of time, thus reducing the likelihood of introducing bias to our analysis. Other disadvantages are that DFA can only be applied in populations with a small degree of geographic variation and only over a certain time frame due to the potential for temporal instability (Ruiz *et al*. 1998; Shealer & Cleary 2007). In the case of the *M. trifasciatus*, although there was a difference in morphology between populations (Reyes *unpubl. data*) most of the significant differences were related to the beak measurements, hence the usefulness of using wing length as a sexing method for both populations. However, our results may lose efficacy in the future if temporal variation in morphometric traits occurs, a factor that has been shown in other Galápagos passerines (Gibbs & Grant 1987).

We recommend the use of wing length as a simple trait because the accuracy of classification was over 90% and because this measurement has been widely used in other mockingbird species (Kinnaird & Grant 1982; Curry 1988; 1989; Curry & Grant 1989; Martínez-Gómez & Curry 1996; 1998; Fuchs & Montalti 2016). We note that tarsus has been used in other birds to classify sex but it was less effective in our study (Taylor & Jamieson 2007; Montalti *et al*. 2012). Additionally, we do not recommend the use of mass alone as a discriminant for sex because mass may vary daily and seasonally depending on, for example, reproduction status, resource availability, and time of day measurements are taken (Lehikoinen 1987). Nevertheless, the use of a single measurement has the added benefit of minimising handling time which reduces stress, an important factor when handling endangered species (Dechaume-Moncharmont *et al*. 2011; Currylow *et al*. 2017). Moreover, the wing is an easy trait to measure because the landmarks are well-defined and because of its size in comparison with other morphological traits in passerine birds. Bigger traits are easy to measure regardless of the observer's experience reducing measurement errors (Yezerinac *et al*. 1992). One caveat is that our results can only be applied in non-moulting adults when using the wing only. Although not yet reported for *M. trifasciatus*, some passerine species show differentiation between the wing size of juvenile individuals, which have shorter and rounded wings when compared to adults (Norman 1997; Green *et al*. 2009).

The main goal of this study was to develop a tool that could be easily interpreted and applied by the personnel of the Galápagos National Park. This tool does not rely on equations of the discriminant functions but instead, a cut point on key measurements, easy to record and quick to apply on the field. Monitoring of *M. trifasciatus* and access to the study sites are restricted due to the conservation status of this species. Access to scientists only occurs for a limited number of days and a limited number of people. Meanwhile, park-rangers of the Galápagos National Park have free access to monitor the study sites and hence the need for an easy and quick tool for the monitoring of this endangered species.

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SHORT NOTE

Adelie penguins (*Pygoscelis adeliae*) in New Zealand

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Before 2021, there had been only two reports of Adelie penguin (*Pygoscelis adeliae*) reaching New Zealand shores (Kennington 1963; Cossee & Mills 1993). We here report three additional records from late 2021, bringing the total number of New Zealand records of Adelie penguins to five.

An adult Adelie penguin came ashore at Birdlings Flat, Canterbury, on the evening of 11 November 2021. Harry Singh reported the event on Facebook, and notified Christchurch Penguin Rehabilitation, as he was concerned for the penguin's well-being. The bird was taken into care overnight, and released at Magnet Bay, Banks Peninsula (3 km east of the capture site) the following morning (Fig. 1) by Allanah Purdie and Anita Spencer, Department of Conservation (DOC). The bird swam out to sea, and was not reported subsequently. An Unusual Bird Report (UBR) was submitted by Anita, and accepted by the Birds New Zealand Records Appraisal Committee (RAC), as UBR 2021-065.

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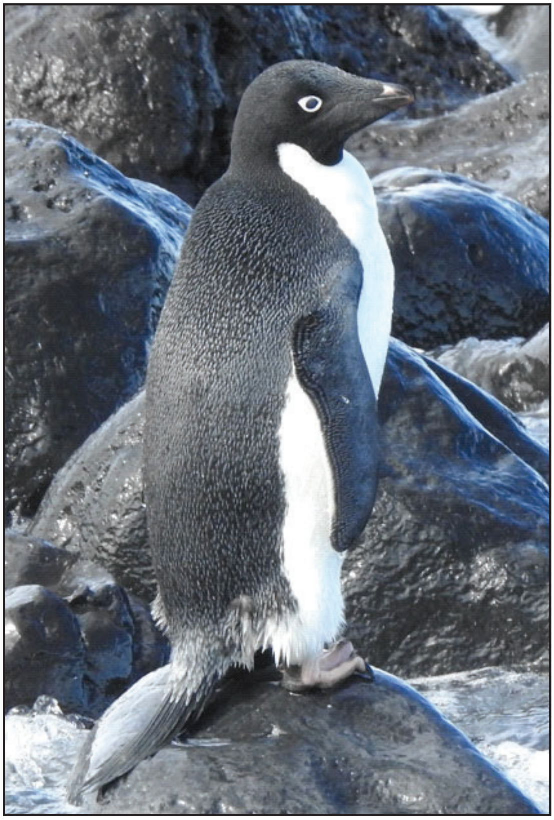

Figure 1. Adult Adelie penguin (*Pygoscelis adeliae*) after its release at Magnet Bay, Banks Peninsula, 12 November 2022. Photograph: Allanah Purdie, Department of Conservation.

Later that day (12 November 2021), an adult Adelie penguin was photographed north of the Rangitikei River mouth, Manawatu (Fig. 2). This is approximately 445 km north-east of Magnet Bay, and 470 km by the most direct swimming route. The bird was not handled, and was not reported subsequently. Michael Szabo submitted a UBR for the bird based on an image (by Kelsi Walker) posted on Facebook by Malcolm Dellow, and this record was also accepted by the RAC, as UBR 2022-001.

The third record of an Adelie penguin from New Zealand in 2021 was a headless corpse found on Masons Bay beach, Rakiura/Stewart Island, by Colin Miskelly on 31 December. The bird was estimated to have been dead for at least two weeks, and was recognised at the time as being either an Adelie penguin or a chinstrap penguin (*P. antarctica*), based on its relatively large size (larger than a crested penguin *Eudyptes* spp.), black dorsal plumage, and long tail. A flipper and the tail were retained, and are now in the Te Papa bird collection (NMNZ OR.031108). DNA extracted from these confirmed the identity of the bird as an Adelie penguin (Lara Shepherd *pers. comm.* to CMM, and see Te Papa blog 'Whose body is that? The case of the missing penguin head', published 5 May 2022). The record was accepted by the RAC, as UBR 2022-044. This was the second Adelie penguin recorded in the Ornithological Society of New Zealand's Beach Patrol Scheme (Powlesland 1984).

Adelie penguins have a mean swimming speed of 2.1 m.s^{-1} (=7.6 km.h^{-1}; Sato *et al*. 2010). If sustained for 24 hours, this equates to a straight line distance of 181 km. Based on this swimming speed (and without allowance for tidal currents through Cook Strait), it would take at least 2.6 days for an Adelie penguin to swim directly from Magnet Bay to the Rangitikei River mouth. Therefore, the Adelie penguin photographed near the Rangitikei River mouth must have been a different individual from the Canterbury bird. Unfortunately, no genetic samples were retained from these two birds, and so it is not possible to determine whether the Stewart Island corpse was of one of the live birds seen seven weeks earlier.

The two previous records of Adelie penguins from New Zealand were a dried corpse of an adult bird found north of the Flaxbourne River mouth,

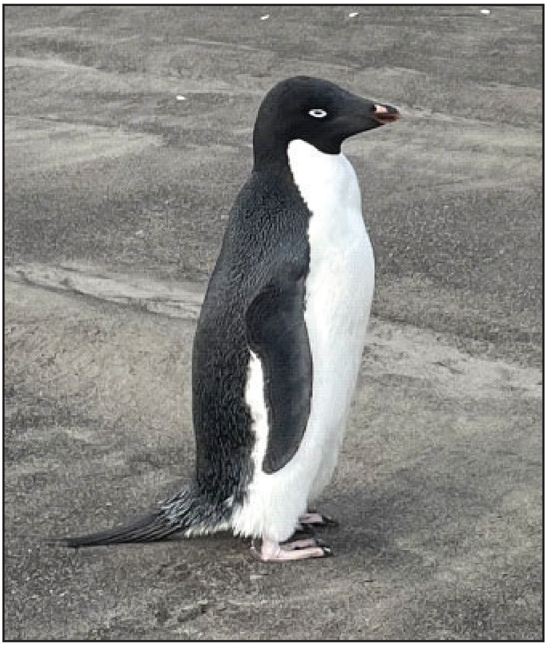

Figure 2. Adult Adelie penguin (*Pygoscelis adeliae*) at Scotts Ferry, Rangitikei River, Manawatu, 12 November 2022. Photograph: Kelsi Walker.

Marlborough, on 22 December 1962 (Kennington 1963; Powlesland 1984), and a live adult on Kaikoura Peninsula on 30 December 1992 (Cossee & Mills 1993). The only Australian record was a second-year bird from Fortescue Bay, Tasmania, in late December 1983 (Tuffy & Fazackerly 1984; Woehler 1992).

There is no obvious explanation for why two or more Adelie penguins would have reached New Zealand in late 2021. Sea surface temperatures south of New Zealand were warmer than average during October to December 2021 (NIWA data, https://niwa.co.nz/climate/sea-surface-temperature-update/, viewed 14 July 2022), and the 2021 Antarctic sea ice cover was considered 'normal' (Ocean and Sea Ice Satellite Application Facility data, https://www.eumetsat.int/state-arctic-and-antarctic-sea-ice-2021, viewed 14 July 2022). There has been no reported correlation in the occurrence of vagrant Antarctic penguins and seals in New Zealand in the past (Miskelly *et al.* 2012; Miskelly 2015), and there were no known occurrences of vagrant Antarctic seals from New Zealand in November or early December 2021 (Hannah Hendriks, DOC, *pers. comm*.). A total of four crabeater seals (*Lobodon carcinophaga*) and three Weddell seals (*Leptonychotes weddellii*) were reported from New Zealand during February 2020 to April 2022. The nearest occurrences to the Adelie penguins chronologically were a Weddell seal on Rangatira Island, Chatham Islands on 16 September 2021, and a probable crabeater seal at Titahi Bay, Wellington, on 21 December 2021 (Hannah Hendriks *ibid*.). However, we note that both of the live Adelie penguins were found by non-birders, and reported via social media. As with vagrant Antarctic seals, it is possible that higher reporting rates of Antarctic penguins in recent years has been driven more by the ease of reporting them rather than by any increase in actual rates of vagrancy (Miskelly 2015; Hannah Hendriks *ibid*.).

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We thank Peter & Kelsi Walker for permission to reproduce their photograph of the Scotts Ferry bird, Harry Singh and Malcolm Dellow for reporting the Adelie penguins that they encountered on social media, Hannah Hendriks (DOC) for information on vagrant Antarctic seals recorded in New Zealand since 2015, and Lara Shepherd, Te Papa, for genetic identification of the headless penguin from Stewart Island.

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SHORT NOTE

Molecular analysis confirms the occurrence of *Thalassarche steadi* in Argentinian waters

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Before the current availability of molecular methods for separating shy (*Thalassarche cauta*) and white-capped albatrosses (*T. steadi*) (Abbott & Double 2003), it was accepted that these two ´shy-type albatrosses´ (see Brooke 2004, Penhallurick & Wink 2004; Onley & Scofield 2007) along with Chatham albatross (*T. eremita*) and Salvin´s albatross (*T. salvini*) were historically placed under a single polytypic species: the shy albatross (*Diomedea cauta*) (Marchant & Higgins 1990; Carboneras 1992). In modern days the shy albatross complex is divided into four species placed in the genus *Thalassarche* based on morphometric, phylogenetic, and population genetics studies (Robertson & Nunn 1998; Abbott & Double 2003; Sangster *et al*. 2015). Albeit this taxonomy has been adopted by leading organizations such as the Agreement on the Conservation of Albatrosses and Petrels – ACAP (Taxonomy Working Group 2006; ACAP 2011) and BirdLife International (2022), some authors show discrepancies (see Brooke 2004; Onley & Scofield 2007). In this paper we follow ACAP (2011) and BirdLife International (2022) in considering *T. steadi* as a separate species.

Thalassarche steadi, a New Zealand breeding endemic species, breeds on Auckland Islands, Antipodes Islands, and occasionally on the Chatham Islands (ACAP 2011). The vast majority of these birds (up to 90%) breed on Disappointment Islands (50°44’S, 166°06’E). *Thalassarche steadi* is regarded as a biennial breeder with a total population estimated at 203,600 mature individuals (BirdLife International 2022). Population trends of the species show strong inter-annual fluctuations, and despite further data needed to confirm the population trend, this parameter is currently considered as declining (BirdLife International 2022). Currently, *Thalassarche steadi* is listed as ´Near Threatened´ due to a combination of at-sea (mainly fisheries bycatch) and on land (chiefly invasive non-native species) threats (Taylor 2000; Baker *et al*. 2007; Francis 2012).

Thalassarche steadi has an almost circumpolar distribution outside the breeding season, showing westerly dispersal directions (Shirihai 2008; Howell & Zufelt 2019), mainly reaching productive waters off South Africa, particularly on the Atlantic side, a well-established key foraging area for over-wintering and non-breeding individuals (Baker *et al*. 2007; Petersen *et al*. 2009 and references therein). There, the species is bycaught in large numbers by longline fisheries operating off South Africa (Baker *et al*. 2007; Petersen *et al*. 2009). Still, other

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productive areas included in the range of *T. steadi* during its early stages of life and/or during the non-breeding season are the Argentine Continental Shelf and its shelf-break (White *et al*. 2002; Favero & Silva Rodríguez 2005; Seco Pon & Tamini 2013). This area has long been regarded as an ecosystem of global importance, offering abundant food for a number of local and migratory marine megafauna, including seabirds (Croxall & Wood 2002; Favero & Silva Rodríguez 2005). In other areas of the south-western Atlantic, the species may reach waters off Uruguay (Jiménez *et al*. 2009) and southern Brazil (Pereira *et al*. 2016). Further south, white-capped albatrosses have been sighted at Malvinas/Falkland Islands (White *et al*. 2002) and at Georgias del Sur/South Georgia (Phalan *et al*. 2004).

Although *T. steadi* is listed within known Argentine bird checklists (de la Peña & Rumboll 1998; Narosky & Izurieta 2010; MADYS 2017; Pearman & Areta 2020), to date the occurrence of the species is based on at-sea observations of birds attending commercial fisheries (Seco Pon & Tamini 2013) and a single specimen found stranded in northern Patagonia (40°45′S, 64°57′W) (Savigny & Carabajal 2015). Due to the great resemblance between white-capped and shy albatrosses, especially at sea (see Abbott & Double 2003; Double *et al*. 2003), the study by Seco Pon & Tamini (2013) did not attempt to identify individuals at the specific level. On the other hand, the study by Savigny & Carabajal (2015) suggests the occurrence of the species based solely on biometric data and plumage colouration. According to Double *et al*. (2003), *T. steadi* is on average larger than *T. cauta*, and discriminant functions involving body measurements may assist in the identification. However, *T. steadi* can be accurately separated by a fixed substitution in Domain I of the mitochondrial DNA control region (Abbott & Double 2003). In this paper, we confirm the occurrence of the species in Argentina based on molecular techniques.

On 09 March 2019, a dead shy-type *Thalassarche* albatross on the beach at Punta Mogotes (38°02′55′′S, 57°31′52′′W), Mar del Plata city, located in the south-eastern Buenos Aires Province, Argentina was reported to one of the authors (JPSP). Prior to the necropsy, morphometric measurements were taken (following Double *et al*. 2003) (using Vernier calliper with an accuracy of ±0.1 mm and digital scale with precision ±1 g), and primary, tail, and body (head, back, and belly) moult was evaluated (after Ginn & Melville 1983). Body moult was defined as active if at least five growing feathers were found; otherwise body moult was treated as inactive (see Bugoni *et al*. 2015). Upon necropsy, muscle tissue samples were preserved in absolute ethanol.

The carcass was found showing a slight decomposition (i.e. with intact internal organs, some rotten smell). No oil stains were noted on feathers or skin of the specimen. The bird had a grey head and neck; its crown and chin were white with little to no pale grey. The rump and undersides were white, and the upper wings black; white underwings with narrow black margins and pale primary flight feather bases (Fig. 1). The bill was pale grey with a blackish tip on the mandible. No primary or tail feathers showed active moult, but body feathers were moulting.

Figure 1. *Thalassarche steadi* found stranded in Mar del Plata, Buenos Aires Province, Argentina. Photographs: Marco Favero.

Morphometric measurements of the specimen are as follows: head length, 77.2 mm; maximum head width, 65.6 mm; culmen length, 131.5 mm; upper bill depth, 31.5 mm; basal bill depth, 50.1 mm; basal bill width, 35.7 mm; middletoe (without nail), 126.2 mm; middletoe nail, 19.0 mm; tarsus, 90.3 mm; wing cord, 584.0 mm; and tail length, 245.0 mm. By applying the discriminant function developed by Double *et al*. (2003) – which correctly identifies both the sex and species of 84% of specimens from a sample size of 70 birds previously recognized using molecular techniques - the bird was classified as a female *T. steadi*. The specimen was then sexed by dissection and direct examination of gonads as an immature female.

Total genomic DNA was isolated from a portion of pectoral muscle using an adaptation of Chelex DNA extraction method (Walsh *et al*. 1991; Phillips *et al*. 2012). A small fraction of muscle, *c*. 5 x 5 mm, was placed in a 1.5 ml tube with 200 µl of Chelex 100 resin™ Matrix (BioRad) 5%. The sample was then incubated at 55°C for 30 minutes, followed by 8 minutes at 100°C. Molecular species identification was done through the PCR amplification of a 325bp fragment of the Domain I of the mitochondrial control region following Abbott & Double (2003). Primers GluR7 and SPECF2 (Abbott & Double 2003) were used. The PCR product was visualized on a 1.5% agarose gel, posterior purification of the PCR product and sequencing was performed at Macrogen Inc. (Seoul, Korea). The sequence was aligned with MUSCLE within the program Mega X (Kumar *et al*. 2018) together with 15 and 23 sequences for shy and white-capped albatrosses, respectively, uploaded from GenBank. The individual was identified as *Thalassarche steadi* based on a single nucleotide polymorphism (SNP), an Adenine to Guanine substitution, detected at the 121 nucleotide position, which corresponds to a fixed difference diagnostic for the species (Abbott & Double 2003). The sequence is deposited in GenBank under accession number OP832372.

From molecular determination we can confirm that the stranded bird analyzed corresponded to a *Thalassarche steadi* individual. This identification method has been previously implemented in the molecular determination of shy-type albatrosses stranded on coastal areas and/or by-caught in fisheries operating in the region (Jiménez *et al*. 2009; 2015; Pereira *et al*. 2016). Molecular techniques as the one used here have been largely applied to the identification of seabirds incidentally killed in fisheries and/or stranded on coastal areas (Abbott *et al*. 2006; Burg *et al*. 2017; Baetscher *et al*. 2022; among others). To our knowledge this would be the first study to identify *T. steadi* as a non-breeding visitor in Argentinian waters.

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Keywords: Argentina, molecular analysis, *Thalassarche steadi*, southwest Atlantic Ocean

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SHORT NOTE

The 1962 record of a long-tailed cuckoo (*Eudynamys taitensis*) parasitising a New Zealand fantail (*Rhipidura fuliginosa*)

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The range of species of passerine hosts parasitized by each species of parasitic cuckoo may be wide or narrow (Payne 2005). The long-tailed cuckoo (koekoeā, *Eudynamys taitensis*), which breeds only in New Zealand, principally parasitizes the three species of *Mohoua*, namely whitehead (pōpokotea, *M. albicilla*), yellowhead (mohua, *M. ochrocephala*), and brown creeper (pīpipi, *M. novaeseelandiae*) (Oliver 1955; Gill 2022). These three host species constitute a family (Mohouidae) endemic to New Zealand.

Fledglings of parasitic cuckoos in general, are large (relative to hosts), with large gapes and noisy begging. This can represent a super-stimulus to passing birds of any species (Davies 2000: 80–81). Unconnected birds may divert to feeding the begging cuckoo fledgling if they pass by while carrying food intended for their own offspring. This means that seeing a species feeding a fledgling cuckoo is not evidence that the species was parasitized. However, observing a growing cuckoo nestling in the nest of a species constitutes firm evidence of parasitism.

In a review of evidence for long-tailed cuckoo hosts (Gill 2022), there were only three detailed and

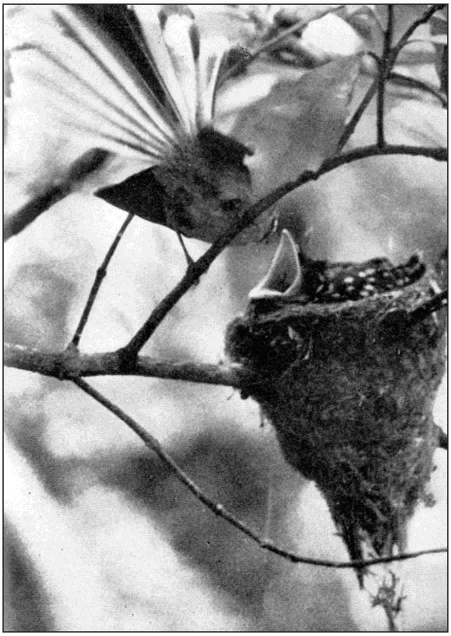

Figure 1. The original printed image of the cuckoo in a New Zealand fantail (pīwakawaka, *Rhipidura fuliginosa*) nest, as scanned from the page in *Notornis* (volume 10, page 173; Roberts 1963).

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Figure 2. Scans of two additional photographic prints of the New Zealand fantail (pīwakawaka, *Rhipidura fuliginosa*) nest identified by Roberts (1963). In the upper image the fantail seems to hold a small food item in its bill. Photo 21-273 (above) and 21-274 (below); Tauranga City Libraries.

reliable records of cuckoo nestlings seen in nests of non-mohouid passerines. Evidence for parasitism of the New Zealand fantail or pīwakawaka (*Rhipidura fuliginosa*) rests on a stand-alone photograph, and accompanying caption, published in *Notornis* in 1963 (Roberts 1963; scanned from the printed page and reproduced here as Fig. 1).

The *Notornis* photograph, attributed to P.M. Roberts, has the following caption:

"Young Long-tailed Cuckoo (*Eudynamis* [*sic*] *taitensis*) in nest of Fantail (*R. fuliginosa*), placed at about 5½ft. [1.7 m] in a pigeonwood [*Hedycarya arborea*] at Pye's Pa Bush, near Tauranga. Is this combination unique?"

The photograph shows a fantail advancing towards the open gape of a long-tailed cuckoo nestling in what is clearly a typical fantail nest. The neat rounded rim raised above the supporting twigs, and the "tail" below are characteristic of fantail nests (Heather & Robertson 1996). The cuckoo nestling is well-feathered, at least two-thirds of the way through its nestling period, and has the pale dorsal spots characteristic of an immature long-tailed cuckoo. The cuckoo fills the nest and appears to be the sole occupant. The image was in the issue of *Notornis* published in March 1963, so the photograph was presumably taken in summer (December to February) of 1962–1963, the months when long-tailed cuckoos would be at the nestling stage (see Gill & Hauber 2013).

Philip Murray Roberts (1922–2015) was Works Manager at the Bay of Plenty Farmers Fertiliser Co-Op. His wife Patricia Ruth Roberts (née Monckton; 1922–2016) was an OSNZ member. Both Philip and Ruth were keen photographers. Ruth had a Leica camera with a telephoto lens. Philip used an enlarger and developed his own black and white photographs.

In April 2021, Elizabeth Simm, daughter of Mr and Mrs Roberts, presented to Tauranga City Libraries two of her parents' photographic prints (Fig. 2; see blog by PC on the Tauranga City Libraries website, "The cuckoo of Pye's Pa bush", published 10 May 2021). The additional photographs (monochrome prints measuring 212 x 165 mm) are different from the *Notornis* photograph but show activity at the same nest. All three images were taken from the same, or similar, camera angle, and each shows a slightly different moment as a fantail delivers food to the cuckoo while perched on a twig adjacent to the nest. Figure 2 (upper) seems to show a small, rounded food item in the fantail's beak.

Mrs Roberts must have sent a photograph of the nest to the ornithologist R.A. Falla. In a letter to her dated 21 December 1962 (held by Rosemary Sargison, another daughter of Mrs Roberts), Falla commented on the importance of the observation. This dates the photographs to late 1962.

The image published in 1963 now seems a little crude by today's standard of photographic reproduction. The purpose of this note is to reproduce the two additional images to give clearer photographic evidence of this unique record of brood-parasitism.

It remains to be seen whether parasitism of fantails by long-tailed cuckoos is observed again. Such a finding would warrant close observation to see if fantails are capable of raising the chick to fledging, and of caring for the fledgling to independence. The exact location of the nest depicted in the photographs is not known, but it may have been on land, now cleared of bush, south-west of the Pye's Pa School (which is at 37.819°S, 176.126°E). Bird-watchers in the Tauranga area should pay special attention to fantail nests in case a lineage (host-specific race or gens) of fantail-parasitising long-tailed cuckoos is active in the area.

ACKNOWLEDGEMENTS

We thank Elizabeth Simm for placing the additional photographs of the cuckoo chick in a public collection; the Heritage & Research Team, Tauranga City Libraries, for scanning them; and Rosemary Sargison for retrieving Falla's letter to her mother.

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Keywords: brood parasitism, secondary host, historic photographs

OBITUARY

KERRY-JAYNE WILSON MNZM
6 March 1949 – 29 March 2022

Leaving Bluff, 27 November 2013. Kerry-Jayne Wilson on the rear deck of MV Akademik Shokalskiy.

In Kerry-Jayne Wilson's passing, just before dawn on 29 March 2022, the natural world lost a resolute friend and immersive story-teller. A dignifying lens of research and commentary is missing from this country's ornithological bedrock today.

Over five decades, Kerry-Jayne dedicated her natural talents as a research ecologist, teacher and author to conserving the biological systems and species to which she was drawn intuitively, even as a young child. She pursued her ambitions for greater human sensitivity to what she termed 'our fellow-travellers on this planet' by connecting people with the wilderness through her science. Hers was a restless energy to do so. It went hand in hand with her longing for adventure. Her abiding affection for birds conveyed her, often alone, to wild places on all continents, some exceedingly remote, with researching and teaching on many continents. The great southern oceans and Antarctica were particularly treasured destinations.

Kerry-Jayne grew up in Dunedin where the birdlife of the Otago Peninsula's placid harbours and tumultuous ocean coasts awakened her interests in the natural world. She determined in her teens that her future lay in Antarctic exploration. Today, books of Antarctic and Arctic exploration populate much of her library, a not-so-vicarious link with the frontier research hardships she herself embraced.

Later, in her Waikato adolescence, she plunged into what became a lifelong interest in caving. She pioneered courageous subterranean routes for which she is still warmly appreciated by New Zealand's caving community. At the University of Canterbury, leading petrel scientist Dr John Warham dispatched her to the Snares Islands as his undergraduate field assistant for the 1969–71 summers. There, for the first time, she became immersed in the richly enigmatic world of oceanic seabirds and their isolated, wild islands. Friend Paul Sagar says of her work there; "During her time at the University of Canterbury Kerry-Jayne spent the summers of 1969–70 & 70–71 on the Snares Islands, completing field work on sooty shearwaters and mottled petrels, at the request of Dr John Warham (Warham & Wilson 1982; Warham *et al.* 1982). In addition to these major efforts, Dr Warham also requested that Kerry-Jayne catch 100 Snares crested penguins, and record a series of specific measurements, providing Kerry-Jayne with printed forms on which to record the data. In due course, Kerry-Jayne set aside time at the Snares to complete this task. Like all crested penguins, the birds at the Snares are strong and vigorously object to being handled, and so need to be firmly restrained. Kerry-Jayne set about catching penguins, one bird at a time, sitting down with the penguin's body and flippers held between her legs whilst she used her hands to hold the head and used vernier calipers to take measurements of the beak, which were duly recorded on the printed forms. Everything went well until bird 65 when, perhaps due to a moment's distraction, the penguin freed its head from Kerry-Jayne's restraint and shot its beak up her nose, tearing the internal septum between her nostrils in the process. Tears, blood and no doubt a good dose of Anglo-Saxon flowed copiously as Kerry-Jayne retired to the hut to self-administer first aid. Sometime later she returned to the colony and completed measuring the penguins.

Sometime after the expedition Kerry-Jayne was at her desk in the Zoology Department, University of Canterbury, when Dr Warham appeared with a printed sheet liberally spattered with blood and queried Kerry-Jayne about why there were some measurements missing from bird 65, to which Kerry-Jayne gave a full explanation. Having heard this, Dr Warham explained that the first priority of research was to maintain the quality of the data, the second priority was the welfare of the birds, leaving Kerry-Jayne to conjecture that perhaps the third priority was the welfare of the researcher!"

This scarring experience did not deter Kerry-Jayne from learning more about penguins. She devoted much of her research time and blood to these birds throughout her life, first in Antarctica and, in her last decade, to the little penguins breeding in decreasing numbers near her home at Charleston on the West Coast.

As a postgraduate student, she mapped fur seal distribution in the New Zealand region (1971–74). Expeditions along remote ocean coasts were often hazardous and physically demanding, though none was a match for her determination, as some of her field companions attest. By 1974, field work had also taken her to Antarctica and the challenging Solander Islands. Graeme Taylor relates that "Kerry-Jayne later told a story about how she was dropped off alone at the rugged Solander Islands by a small fishing boat. All her gear was piled into a rowboat and she set off to land at the nearby beach. The fishing boat left with Kerry-Jayne paddling furiously. However, the beach was impossible to land on with the swells and large rocks. So, she had to row around the 120 ha island to the far side in rather rough seas and found refuge on a rocky beach with a sea cave."

Between 1975–77, she worked alone in very isolated Newfoundland communities, recording Canadian seabird distribution and abundance. Later she spoke affectionately of the locals who came nightly to watch her write up her notes, a skill that most in that community at that time did not possess or need to. From 1977 to 1987, she was censusing populations of Adélie penguins (*Pygoscelis adeliae*) at Cape Bird and Cape Hallett. Studies at both locations investigated penguin responses to intrusive human activities (Davis *et al.* 1994).

She joined the International Survey of Antarctic Seabirds as an expert observer during this period. Her six cruises with the Survey extended knowledge of seabird distribution and abundance in the New Zealand/Ross Sea sector of the Southern Ocean (Bassett & Wilson 1983; Harper *et al.* 1984). The biological datasets she and later colleagues compiled annually – first by groundwork, later by aerial photography – help us understand today how climate change affects seabirds and the Antarctic ecosystem.

In 1986, Lincoln University appointed her to lecture in ecology. Her tenure concluded in 2009 when she retired from the position (though inevitably, not from teaching). In that year, the Students' Association celebrated her talents with its Green Award for Excellence in Teaching and

Support. She brought inspiring qualities to her teaching, for which her students remember her warmly. She was a natural historian, a vanishing class of biologist in an increasingly reductionist world. She tolerated statistics but only as a tool to complement direct observation and deduction. Many will recall her caution against seductive mathematical paths to explaining natural phenomena: 'Be sure to test your elegant models against what you see before you. Observation is key'. Not surprisingly then, she remained an outspoken advocate for field ecology as a necessity for undergraduates. Her lecturing and mentoring drew compellingly from her own innate sense of connection and compassion for the natural world. She allowed stories to say how things were. She was passionately an applied ecologist, resolutely dedicated to seeing science serve conservation. She cared as much for her students' intellects as for their souls. She gave everyone a chance, nurturing their particular talents. In return, she challenged her students and colleagues to be critical thinkers and to publish. Through these qualities, and the research she guided, Kerry-Jayne defined what it meant to be a conservation biologist.

She was capable of inspired innovation. Her interest in petrels led to her supervising a series of student projects on the impacts of broad-billed prions on Chatham petrels. Graeme Taylor recalls how Kerry-Jayne pondered for some time on how to exclude prions from the similarly sized burrows of the critically endangered petrel. Prion invasions had seemed an intractable threat to overcome. "Finally, she dreamt up the idea of a neoprene burrow flap with a narrow slit to allow tight access into burrows. We tested this on one of my expeditions to the Mercury Islands to test these flaps on the close relative Pycroft's petrels (*Pterodroma pycrofti*). The flaps worked exceptionally well. The petrels kept breeding and when used on Chatham petrel burrows, most prions were deterred. It was a major breakthrough in the management of these species, allowing for greatly reduced "hands-on" management of the prion competition."

In her professional life and in a very great deal of her own time, Kerry-Jayne worked tirelessly to clarify the biology and status of native bird species in New Zealand. Her ornithological compass was broad and diverse. She researched and supervised projects from the mountains to the oceans, throughout New Zealand and overseas. Whatever and wherever her species of interest, she exemplified the virtues of learning, recording, and reporting systematically. She supervised students and other projects in Germany, Malaysia, Sarawak, Cook Islands, Columbia, Mongolia, and the United States. She was the logical choice to be Lincoln University's developer and director of the Masters in International Nature Conservation, co-taught with Germany's Georg-August University in Göttingen (2002–09).

Kerry-Jayne's recognition of the need for an integrated approach to conserving kererū (*Hemiphaga novaeseelandiae*) on Banks Peninsula illustrates the reach and conviction of her applied-science thinking. She took a leading role in creating the Kaupapa Kererū programme, which brought together Ngāi Tahu, Lincoln University, Department of Conservation, Landcare Research, and the Banks Peninsula community (see for example Norton *et al.* 2005). She supervised much of the post-graduate and post-doctoral research underwriting the programme. Topics included studies of seasonal food preference, analysis by radio telemetry of kererū movements, predator impacts, feral cat ecology, and community-based survey methods. The research revealed that exotic plants, in particular tree lucerne, are important as kererū food and that kererū are seemingly able to raise chicks on plant foliage and are not obligate consumers of higher-quality foods such as fruit, as previous studies had concluded.

Kerry-Jayne's impressive publication record in Notornis (appended below), her broad teaching and supervising interests, and her deepening interest in the future of the swiftly evolving new direction in Kiwi guardianship of our natural heritage attest to the diversity of her research.

Kerry-Jayne employed the instinct and ability of the natural historian to interpret her knowledge and discoveries for specialist and lay audiences alike, in terms and language accessible to all. Fully aware of the cost to her academic publishing record, she chose to translate her science for the lay public through books rather than papers. Flight of the Huia, her impressive review of our natural heritage, was the first book to traverse the history of faunal change in New Zealand. It reviewed the ecology and conservation of those animals and was a finalist in the 2005 Montana Book Awards. Her West Coast Walking: A naturalist's guide (co-authored with the late David Given) reveals her sweeping knowledge of our remarkable biota and its places. Her final book, New Zealand Seabirds: A natural history, is a simply prodigious work whose writing she sustained through formidable willpower as her health deteriorated.

The Ornithological Society of New Zealand benefited significantly from her sense of vocation and her leadership as a mentor and researcher. She served in governance roles as South Island Vice President of the Society (1997–2003), was the inaugural Convenor of the Society's Scientific Committee (2001–2004), and represented the Society's oceanic seabird interests in the Australasian region as the Society representative on the Australasian Seabird Group. She compiled and edited the State of New Zealand Birds reports from 2005 to 2009. She joined the local organising committee for the 20th International Ornithological Congress in Christchurch. From 2001–2010, she represented the Society on the organising committee for Australasian Ornithological Conference's (AOC). She chaired the organising group for the Blenheim AOC in 2005. Kerry-Jayne was always alert for candidates not yet aware of tasks they were uniquely suited to perform. An innocent comment at the 2003 AGM resulted in Bruce McKinlay being tasked to support Tom and Hazel Harty in their organising of the Scientific Day at Oamaru's 2004 conference.

After retiring to her charming house above the Tasman Sea in Charleston, Kerry-Jayne pursued her seabird interests through founding the West Coast Penguin Trust. She chaired the Trust until her health began to fail but remained its scientific advisor throughout. Here, in the final chapter, her duty to conserve as well as observe, was fully formed. Kerry-Jayne insisted on evidence-based approaches to Trust projects and was integral to everything the Trust did. This was literally mud-and-blood devotion to her beloved penguins and petrels, from rough-country field work in the middle of the night to retrieving data-loggers from penguins, managing research projects, advancing expert evidence in resource consent hearings, and all the day-to-day decisions and operations in-between.

Under her guidance, the Trust extended its original focus on little penguins/kororā to Fiordland crested penguins/tawaki, Westland petrels/taiko and other threatened seabirds. At the same time Kerry-Jayne downloaded a lifetime of experience and expertise to a series of significant reviews on seabirds (e.g. Wilson & Croxall 2012; Wilson & Waugh 2013; Rodriguez *et al*. 2016; Jamieson *et al*. 2016). Thomas Mattern, a colleague from the Tawaki Project recalls, 'What I admired most about Kerry-Jayne was that she would never give up. She just kept on going. Her resilience and – let's call it – stubbornness allowed her to achieve incredible if under-appreciated successes that most of us can only dream of – burrow flaps (for Chatham petrels) and initiating work on Westland petrels are just two examples that come to mind'. Thomas recalls that Kerry-Jayne's encouragement especially during and after the first year of the Tawaki Project was crucial for the project to carry on against all odds. She was always part of the first discussions to fathom what it all might mean.

Kerry-Jayne's achievements acquired due recognition over the years. The Society nominated her for the Robert Falla Memorial Award in 2012. She was honoured by the Queen as a Member of the New Zealand Order of Merit for services to seabird conservation in 2019. However, as Thomas Mattern observes, Kerry-Jayne regarded awards and recognitions as by-products of her purpose in life and she would have been more happy to trade them for a better understanding and protection of seabirds.

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With contributions from: Thomas Mattern, Paul Sagar, Graeme Taylor

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APPENDIX: List of Publications by Kerry-Jayne Wilson in *Notornis* and *Southern Bird.*

Campbell, K.L.; Schotborgh, H.M..; Wilson, K-J.; Ogilvie, S. 2008. Diet of kereru (*Hemiphaga novaeseelandiae*) in a rural-urban landscape, Banks Peninsula, New Zealand. *Notornis 55*: 173–183.

Campbell, K.L.; Wilson, K-J.; Ogilvie, S. 2008. Notes on the breeding biology of kereru (New Zealand pigeon, *Hemiphaga novaeseelandiae*) on Banks Peninsula, South Is, New Zealand. *Notornis 55*: 98–100.

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