Notornis, 2022, Vol. 69: 243-255
0029-4470

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.

Miskelly, C.M.; Beauchamp, A.J.; Oates, K.E. 2022. Changes in the Mana Island, New Zealand, bird community following mouse (*Mus musculus*) eradication. *Notornis 69(4)*: 243–255.

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 &

Received 22 August 2022; accepted 23 September 2022
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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°05ʹS, 174°47ʹE) 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

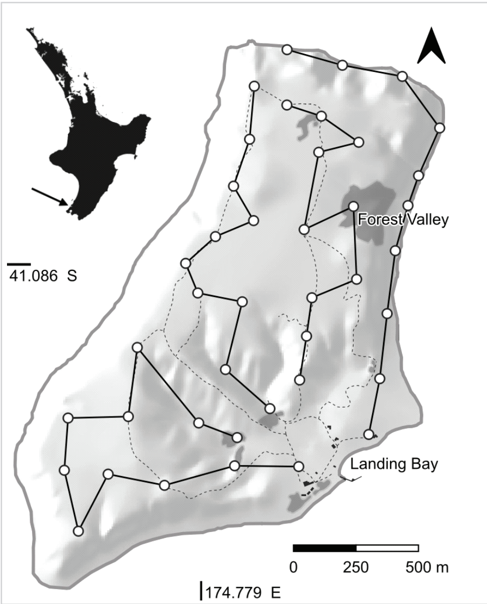

Figure 1. Bird count station locations on Mana Island (Wellington, New Zealand) during 1987–93. Black = buildings; dark grey = trees (macrocarpa *Cupressus macrocarpa* stands, apart from Forest Valley, which was predominantly kānuka *Kunzea robusta*). Dashed lines are farm tracks based on a 1987 aerial 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

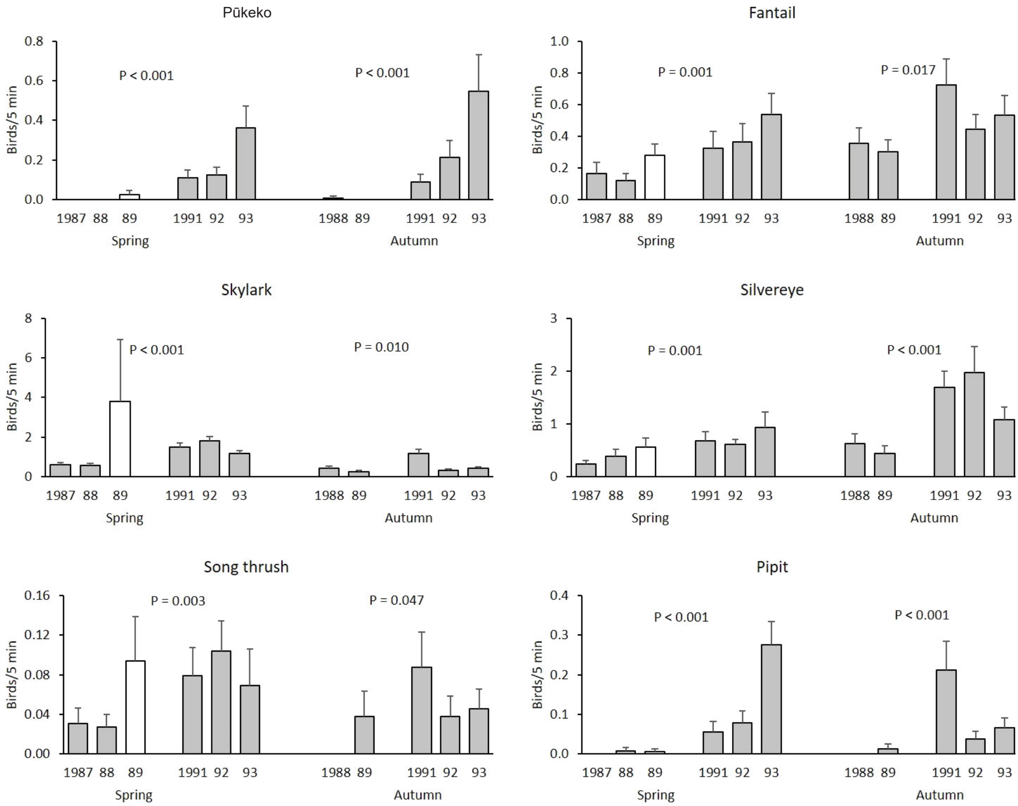

Figure 2. Bird species that had higher counts in both spring and autumn after mice were eradicated from Mana Island. Spring 1989 counts (when rodenticide was present, shown as a white bar) were excluded from the statistical analyses presented in this Figure. The data presented are birds per 5-minute 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).

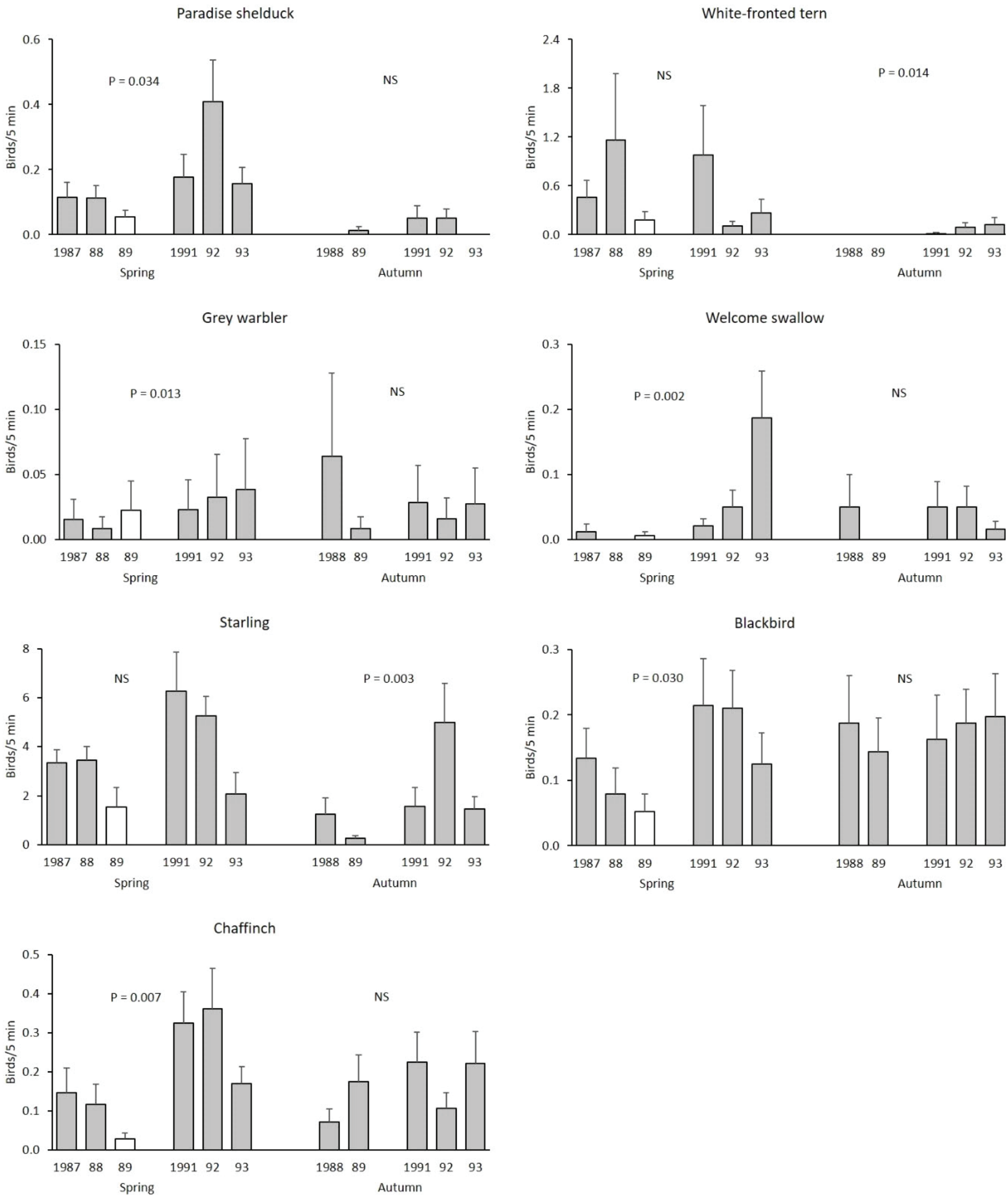

Figure 3. Bird species with significantly higher counts in one of two seasons after mice were eradicated from Mana Island. Spring 1989 counts (when rodenticide was present, shown as a white bar) were excluded from the statistical analyses presented in this Figure. The data presented are birds per 5-minute 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).

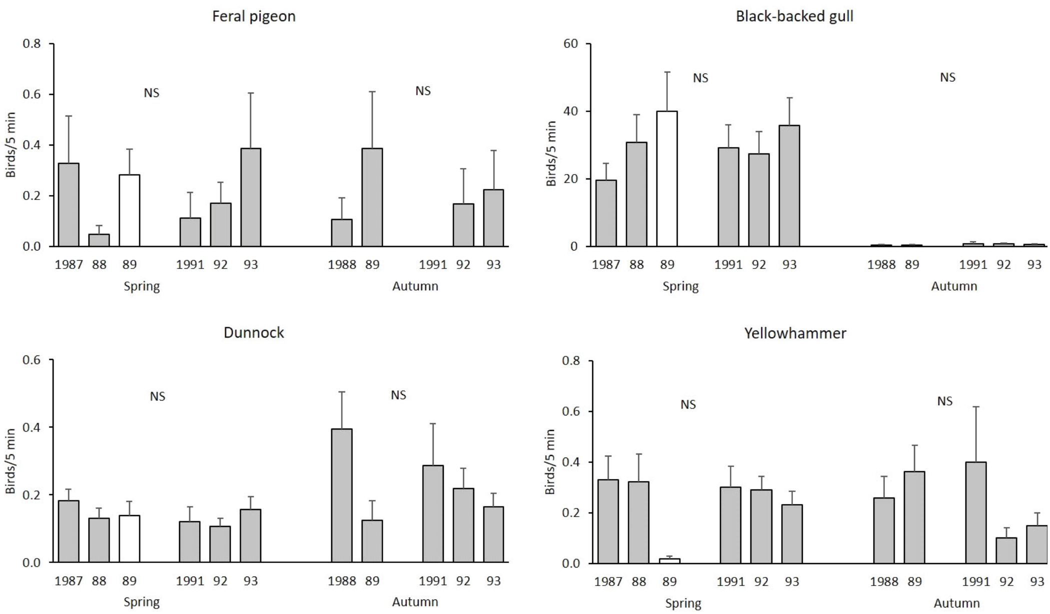

Figure 4. Bird species that had no significant difference in both spring and autumn counts after mice were eradicated from Mana Island. Spring 1989 counts (when rodenticide was present, shown as a white bar) were excluded from the statistical analyses presented in this Figure. The data presented are 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.

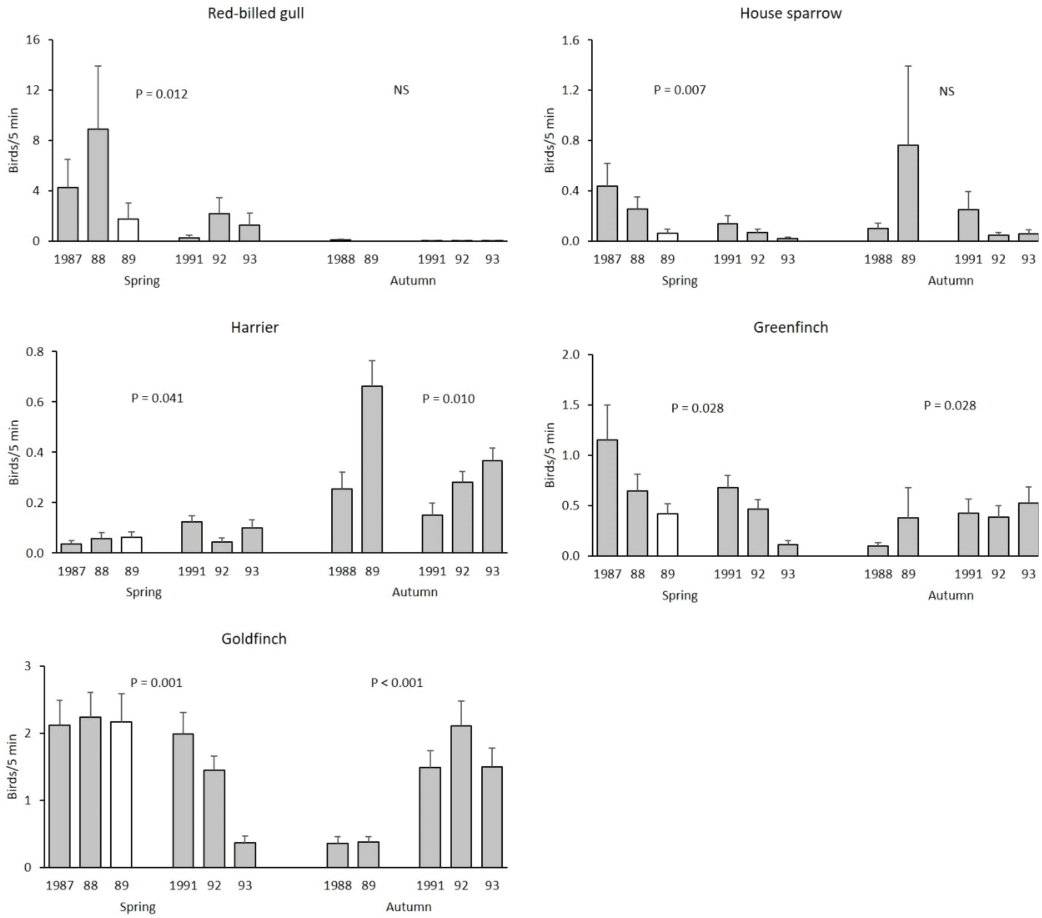

Figure 5. Bird species that had significantly lower counts in one of two seasons after mice were eradicated from Mana Island. Spring 1989 counts (when rodenticide was present, shown as a white bar) were excluded from the statistical analyses presented in this Figure. The data presented are birds per 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.

ACKNOWLEDGEMENTS

We thank Department of Conservation staff (particularly island rangers Trevor Hook and Phil Todd) for their support for this bird monitoring project, including permitting overnight stays on Mana Island. Phil Todd also provided much detail about the mouse eradication programme. Our appreciative thanks to the many Ornithological Society of New Zealand members and associates who undertook the surveys reported here, including Dave Bell, Enfys Graham*, Roy Slack, Julia Brooke-White, Don Stracey, Linda Hayes, Mike Bell, Judy Philpott, Gavin Woodward*, Rod Hitchmough, Olga Vincent, Ros Batcheler, Rick Bell, Allan Munro, Molly Neill*, Jim O'Malley, Jim Sinner, Derek Batcheler, Kingsley Brown*, Geoff de Lisle, Muriel Stracey, Louise Bell, Jim Jolly, Alan Tennyson, Russell Thomas*, and Mark Simmonds. We also acknowledge the crucial role of the Friends of Mana Island executive committee (particularly Brian Bell and Dale Shirtliff), who recognised the value of surviving copies of many of the original datasheets, and saved them from the recycling skip. The map was skilfully prepared by Jaz Hamilton. This manuscript was greatly improved by comments received from Graeme Elliott, James Russell, and Craig Symes.
*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