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Increasing urban abundance of tūī (*Prosthemadera novaeseelandiae*) by pest mammal control in surrounding forests

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Abstract: Public and our observations during 1999–2004 suggested that tūī (*Prosthemadera novaeseelandiae*) visited the city of Hamilton during March to October only, outside the nesting season. From 2004 onwards, we captured and banded 51 adult tūī and fitted radio transmitters to 41 in Waikato urban areas to locate nests. We directly observed 15 nests to determine nesting success and gather evidence of any predation events. Tūī moved 5–23 km from urban areas to surrounding native forests at the onset of nesting, but only four (29%) of 14 unmanaged nests fledged young, due mostly to predation by ship rats (*Rattus rattus*), swamp harriers (*Circus approximans*), and brushtail possums (*Trichosurus vulpecula*). Subsequent effective pest mammal control in forests around Hamilton was associated with greatly increased year-round tūī abundance and nesting in Hamilton. These results confirm previous findings that tūī move widely in winter; that they readily cross pasture in the absence of forest corridors, and that they will permanently inhabit urban areas. Provided adequate food is available, effective control of ship rats and possums can rapidly (1–4 years) increase tūī visits and nesting within 20 km of managed sites, enabling recolonisation of proximate urban habitats by this iconic endemic taxon, despite previous evidence for natal philopatry.

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INTRODUCTION

Tūī (*Prosthemadera novaeseelandiae*) is an endemic honeyeater (Meliphagidae) found throughout most of New Zealand. Although it is not threatened

(Robertson *et al.* 2017), it is sparse in deforested regions, especially east of the central Southern Alps in the South Island, and in the Manawatu, south Taranaki, and central Waikato in the North Island (Higgins *et al.* 2001; Robertson *et al.* 2007). Tūī is an iconic New Zealand species with distinctive appearance and song and is important

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for pollination and seed dispersal of native trees and shrubs (Kelly *et al.* 2010). Although tūī live mainly in native forest and shrublands, it has also readily adapted to feeding on the nectar and fruit of planted exotic trees and shrubs in rural and urban gardens and parks (Higgins *et al.* 2001; Spurr 2012; Robertson 2013). Being iconic, ecologically important, and regularly encountered by people, tūī often attract the focus of community conservation initiatives such as planting of food trees and control measures to reduce pest predator populations (Bergquist 1989).

Sexual size dimorphism in tūī is extremely high for a socially monogamous passerine, with mean weight of males up to 50% higher than females (Wells *et al.* 2015). There are also differences in male and female diet, which are most pronounced in spring and autumn, when males feed more on nectar and less on arthropods (Bergquist 1985a). Tūī can have small ranges (*c.* 1 km across; Bergquist 1985b) in the summer when nesting, but in the non-breeding season they forage widely to feed on dispersed and irregular sources of nectar, sometimes in family groups (Craig *et al.* 1981; Bergquist 1985b; Bergquist & Craig 1988; Guest & Guest 1993; Higgins *et al.* 2001). Male tūī may generally move larger distances than females, due to their larger size and greater reliance on nectar (Craig *et al.* 1981). Our surveys, and reported sightings from the public, verified that this pattern of range size varying with nesting status applied to Hamilton in the central Waikato during 1999–2004 (Innes *et al.* 2005). During the breeding season (late October–February) in these years, all except two tūī sightings were confined to the few central Waikato native forest areas larger than *c.* 100 ha (Fig. 1). However, during March–October tūī were frequently reported in rural gardens away from native forests, and in urban Cambridge and Hamilton (Innes *et al.* 2005; authors *unpubl. data*).

Where vegetation type and cover are adequate, local populations of New Zealand forest birds are limited primarily by predation at nests by introduced predatory mammals (Innes *et al.* 2010). In these situations, native bird populations frequently recover after control measures reduce pest predator densities (Innes *et al.* 1999; Moorhouse *et al.* 2003; Armstrong *et al.* 2006; Innes *et al.* 2010; Miskelly 2018; Binny *et al.* 2021), and tūī are among the most responsive species to such control (Graham *et al.* 2013; Miskelly 2018; Fitzgerald *et al.* 2019).

We therefore hypothesised that the number of tūī in Hamilton could be increased, at least seasonally, by reducing densities of predatory pest mammals in native forests 10–20 km from the city. To test this hypothesis we, i) identified tūī breeding sites near Hamilton by radio telemetry, ii) measured unmanaged nesting success at those sites, iii) subsequently undertook control of mammalian

predators near nesting sites while continuing to monitor nesting success, and iv) monitored changes in tūī relative abundance in Hamilton.

METHODS

Study sites

A programme of pest mammal management by Waikato Regional Council began in 2007 in native forest in the central Waikato (Waikato Regional Council 2015). By 2009, the programme comprised six large (>100 ha) native forest remnants – Maungakawa Scenic Reserve (at the time, part of Te Tapui Scenic Reserve), Old Mountain Road East and West, Pukemako Historic Reserve (at the time, Maungakawa Scenic Reserve), Te Miro Scenic Reserve and Tirohanga Road Bush – and one smaller site (39 ha; Pukemokemoke Bush Reserve). The programme was branded ‘Hamilton Halo’ because the remnant forests surround Hamilton in a circle (Fig. 1). All Halo sites occurred in Waikato lowlands (40–340 m a.s.l.) in an area approximately bounded by Huntly in the north, Matamata in the east and Te Awamutu in the south. Several other large native forest areas close to Hamilton were not included in the Hamilton Halo programme (Hakarimata Range, Kakepuku, Maungatautari, and Pirongia; Fig. 1) but received variable pest management through other means.

We counted birds from 2004–2012 in Hamilton remnant native forests, gullies, and urban sports and amenity parks (collectively ‘green’ areas), and in four residential areas in Hamilton. Hamilton (11,080 ha) has <20 ha of high-quality native-dominated remnant forest remaining, but the vegetation of about a quarter of its 750-ha network of steep-sided gullies that drain into the Waikato River provides a mix of native and exotic forest/scrubland vegetation with some value to wildlife (Clarkson & McQueen 2004). This gully vegetation has been subject to a programme of restoration by the Hamilton City Council, private citizens and restoration groups since *c.* 2000 (Clarkson *et al.* 2007; Wallace *et al.* 2017). The residential areas we sampled were away from main roads, with uniform-sized (median 775 m²) sections dominated by houses and lawns, frequent shrubs, and small trees but few large (>12 m tall) trees.

Tūī capture and radio-tracking

Fifty-one adult and subadult tūī were captured in or near Hamilton, Cambridge, and Te Awamutu (Fig. 1) between November 2003 and August 2007. These birds were caught using mist-nets at food trees with playback of locally recorded tūī song. Captured tūī were marked with one metal band and up to three Darvic® wrap-around colour bands, and 41 had VHF radio transmitters attached. After

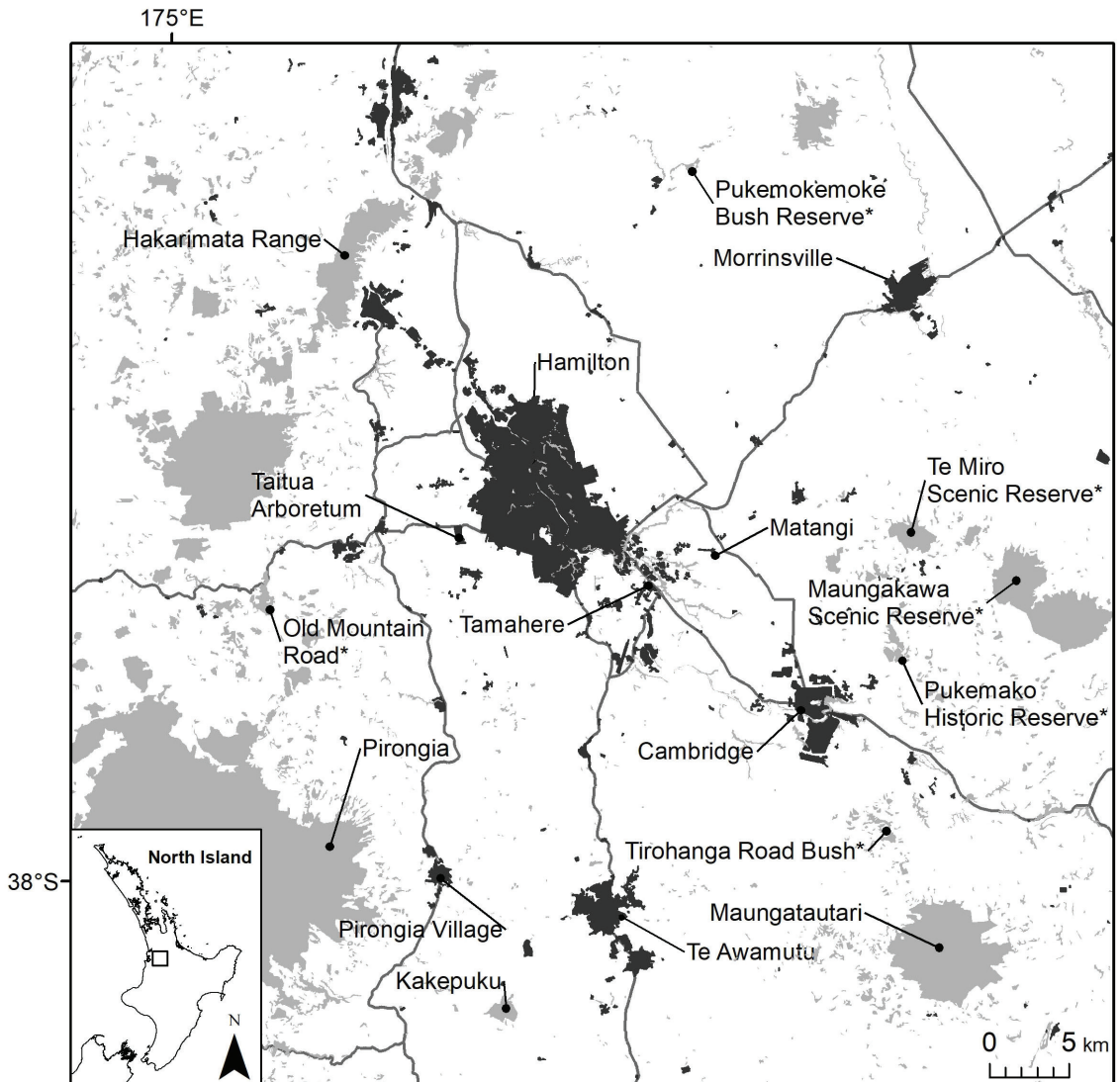


Figure 1. Central Waikato, North Island, New Zealand, showing Hamilton and other urban areas (black) and indigenous forests (grey). Sites that were subject to pest control under Project Halo during 2007–2012 are asterisked.

capture, each bird was fed with sugar-water at the beginning and end of handling, then released at the same site. Subadult (first year) tūi were identified by the lack of a slot on the inner web of the eighth primary feather (Onley 1986).

Transmitters were placed on 25 tūi (21 males, four females) during Sep–Oct 2004; on eight tūi (seven males, one female) during Aug–Sep 2005, and on a further eight tūi (seven males, one female) in Jun–Aug 2007.

Transmitters (BD-2, Holohil Systems Ltd, Ontario, Canada) weighed 1.8 g and had expected

battery life of 14 weeks. We tied (dental floss) and glued (ethyl cyanoacrylate ‘superglue’) transmitters to the two central tail feathers of both male and female tūi after an initial trial with two captive male tūi at Hamilton Zoo in July 2004.

Tūi were primarily tracked from the ground with initial general location established from widely scattered hilltops with TR4 receivers (Telonics, Arizona, USA) and Yagi (Sirtrack, Havelock North, NZ) aerials, followed by closer searching from vehicles and on foot. In 2004, we attempted to locate all transmitters weekly; using

them primarily to look for nests. In 2005 and 2007 we focused on determining spring movement, so attached transmitters from June to September. We aimed to follow each tūi at least once per week for 24 hours, from noon to dusk and then from dawn to noon the next day.

On 20 December 2004, we looked for missing radio-tagged tūi from the air in a Cessna fixed-wing aeroplane with two 3-element, Strongline Yagi antennae attached to wing struts, a programmable Telonics TR5 receiver, a SPO-22 Transcom aircraft intercom system and a Sigtronics helicopter headset. The aeroplane was flown with one observer (NF) at 460 m above ground with a maximum groundspeed of c. 200 kph and in flight-lines c. 8 km apart over likely areas.

'Locations' of tūi referred to in results are patches of woody vegetation that were physically separated from each other.

Nesting success

We looked for tūi nests primarily at Pukemako Historic Reserve from December 2003 to November 2005 by following flight paths of females (2003–2005) and radio-tagged birds (2004–2005). Nesting females usually flew low into trees adjacent to the nest tree, or to the nest tree itself, and then made short flights and hops to the nest, although they tended to fly directly from the nest when leaving. Following radio-tagged males (85% of our radio-tagged sample) did not yield nest locations because male visits to nests were too brief. We monitored nests by observation from the ground every 2–3 days and climbed to all failed nests to search for evidence to help determine the cause of failure. There was no pest predator control (e.g. trapping or poisoning) at Pukemako Historic Reserve during this period. We also monitored one nest in November 2005 at Taitua Arboretum, where Hamilton City Council staff undertook some control of ship rats (*Rattus rattus*) and brushtail possums (*Trichosurus vulpecula*; hereafter 'possums') using poison bait stations.

We placed continuous time-lapse video cameras at some nests. We used fixed-focus, fixed-focal length (3.6, 6, or 8 mm) weatherproof cameras (PIH-0022) with infrared diodes (peak wavelength 850 nm) connected to 12-volt, time-lapse Panasonic AG-TL550 or Sanyo TLS-1600P video cassette recorders. At most nests, we examined footage only to view failure or fledging events. However, video from one nest was monitored in detail for data on incubation, brooding times and visit rates by the male and female through the nesting cycle. There were 24 cassette tapes collected at this nest, spanning the hatching to fledging period (23 days). Timing of the beginning and end of incubation and brooding sessions by the female, and feeding visits to the nest

by male and female were noted in detail from all odd-numbered tapes.

Pest control at Halo sites

Waikato Regional Council engaged pest control contractors to reduce ship rat and possum densities at seven 'Halo' forest sites. All sites were targeted in a pulsed, 3-years-on and 2-years-off regime that aimed to have both pest species at low levels by the onset of each tūi nesting season (October–January). Target residual pest densities were assessed by standard indexing techniques, namely <5% residual trap catch (NPCA 2011) for possums and <5% tracking rate (Gillies & Williams 2013) for ship rats. Old Mountain Road East (pest control area 195 ha) and Old Mountain Road West (167 ha) sites were first targeted in spring 2007; Te Miro Scenic Reserve (684 ha) and Pukemako Historic Reserve (78 ha) commenced in 2008; and Tirohanga Road Bush (136 ha), Pukemokemoke Bush Reserve (39 ha), and Maungakawa Scenic Reserve (997 ha) began in 2009.

Pest control techniques varied from site to site and year to year, although most sites had poison bait stations on a 75 m grid with brodifacoum, diphaceneone, pindone, cholecalciferol, or pre-fed 1080 poison in cereal pellets to target both species. Sometimes possums were targeted separately with leghold traps or cyanide. Pre-fed aerial application of 1080 bait (0.08%, Wanganui No. 7 baits) was used at the Old Mountain Road West site during 2007–2009.

Counting tūi in Hamilton

Five-minute bird counts

Five-minute bird counts (Dawson & Bull 1975) were used to obtain abundance indices of all species present and to allow comparisons with many other counts made around the Waikato and New Zealand (Hartley 2012). During each five-minute count, terrestrial birds seen or heard within 100 m of the stationary observer were recorded. The technique does not determine absolute density of birds, but can provide repeatable indices of abundance if counts are made by experienced observers at the same time of year in conditions of little or no wind or rain (Hartley 2012).

In 2004 we established count stations at least 200 m apart in representative green and residential areas in Hamilton. Counts in residential areas were made from street footpaths. We avoided establishing count sites on main roads to minimise traffic noise, and we avoided counting at all stations during moderate or strong winds or rain.

Counts were undertaken every two years from 2004–2012. Green sites (99–101 stations) were

counted in late winter (August) and late spring (November). Residential sites (106 stations) were counted in late spring (November). The late winter counts were undertaken to monitor changes in the relative abundance of tūī visiting Hamilton at that time, as preliminary survey and public reports indicated presence then. The number of green stations counted differed slightly in some years due to instances of flooding making some stations inaccessible. Observers recorded estimates of semi-quantitative indices of cloud cover (0–2), rain (0–4), wind (0–3) and other noise (0–2) with each count. Birds were counted between 0800 h and 1700 h in August and between 0800 h and 1830 h in November to avoid significant changes in conspicuousness that may occur around sunrise and sunset.

Slow-walk transects

We conducted 'slow-walk transect counts' in which all terrestrial birds within 10 m each side of the observer's path were recorded while slowly walking a fixed-length line (Handford 2000; Morgan *et al.* 2012). Two transects, separated by at least 40 m, were counted at each of five green sites (Hammond Park, Jubilee Park, Mangaiti and Tauhara Parks, Taitua Arboretum, Waiwhakareke Heritage Park). Transect length (mean 417 m, range 245–500 m) was restricted by the size of some of the green sites. Eight of the ten transects were in areas where five-minute counts were also conducted. These transects give an estimate of absolute density of birds in some small areas (unlike five-minute counts) but described bird distribution poorly, because there were few transects. Transect counts were repeated three times (no more than once per day) in November, biennially from 2004–2012 (same times as five-minute counts).

Analysis of count data

To test whether tūī counts increased with time in Hamilton during the period when pest control was carried out at Halo sites, we fitted generalized linear mixed models (GLMMs) to the count data. We fitted models separately for each season (spring and summer), area (green and residential), and count method (five-minute counts and slow-walk transects). For each of these subsets we attempted to fit GLMMs using four error distributions appropriate for count data — Poisson, Conway–Maxwell–Poisson, negative binomial with variance increasing linearly with the mean, and negative binomial with variance increasing quadratically with the mean (Shmueli *et al.* 2005; Brooks *et al.* 2017). The number of tūī in each count was modelled with a log link function against time (years since the first survey). Wind and other noise can affect the number

of tūī recorded in five-minute counts (Fitzgerald *et al.* 2019), so we included these and other variables (cloud, rain, time of day, and observer) in the models as fixed effects so their influence on counts could be separated from the main effect of interest (time). We assumed that all the effects included in the models were real, whether statistically significant or not, so we estimated parameters from the full models rather than alternative approaches such as backward stepwise regression (Bolker *et al.* 2009). Count station, and transect repeat count number (i.e., first, second, or third repeat in a season) nested within each transect, were included as random effects to account for non-independence of the repeated counts of these locations. The log of transect length was included as an offset in the models of transect counts (Hutchinson & Holtman 2005).

We used the glmmTMB package (Brooks *et al.* 2017) in the R statistical computing environment (3.6.2; R Core R 2019) to fit GLMMs to the data using maximum likelihood estimation. We tested all GLMMs for potential misspecification, such as inappropriate error distribution, using a simulation-based approach with 10,000 iterations using the DHARMA package (Hartig 2019). We used Akaike Information Criterion (AIC) to compare goodness of fit of all appropriately specified models. Models with similar weighting ($\Delta\text{AIC} < 2$) were averaged using the MuMIn package (Barton 2020).

Public observations

Citizen observations of tūī in Hamilton were requested and recorded by Waikato Regional Council starting in 2007. We summarise these data from the available full winter–winter years, 2008/09–2012/13.

RESULTS

Locating tūī with colour bands and transmitters

Unsurprisingly, radio-tracking yielded many more separate locations of tūī than banding alone. Radio-tracking produced a mean of 18.1 locations per bird located at least once after release (median 6, range 1–111, $n = 33$), while band sightings resulted in a mean of 3.6 post-release locations per bird located at least once after release (median 2, range 1–18, $n = 28$). Band recoveries also tended to be by the same people at the same places, either in gardens by owner-occupiers or at banding locations by us. Banding enabled movement data to be obtained over longer time periods (up to 11 years) than radio transmitters. However, even tūī with transmitters often could not be found. Twelve of 51 tūī were not subsequently located after initial capture, either by band resighting or radio transmitter,

perhaps because the birds moved beyond where we searched or they were in a location such as an urban area or forested valley with limited signal range. Of these 12 missing tūī, 8 had transmitters. While no transmitters were known to have failed, 12 were known to have fallen off the tūī to which they were attached in 2004 after 7–113 days (mean 39 days), yielding some movement information. Of these losses, three were caused by tail feathers pulling out, five by glue failing, and three by unknown causes. No transmitters fell off in 2005 or 2007, presumably reflecting our improved skill and experience at attaching transmitters.

The range at which transmitters could be detected varied enormously, depending on the environment, signal interference, receiver system (land or aeroplane), bird location, and behaviour. Maximum range achieved by ground observers on rural hilltops was about 20 km but was less than 100 m in urban locations with substantial signal reflection and attenuation, and radio interference. Large radio transmission towers on some hilltops such as at Pukemako Historic Reserve caused significant radio interference. Reference transmitters placed in known locations on the ground during the December 2004 flight indicated a maximum detection distance from the air of 2.5 km.

Tūī movements

While neither banding nor radio-tracking was likely to have revealed full home ranges in any season, our 2004–2007 data showed large movements in spring (August to October; mean range length 6,045 m, median 2,305 m, *se* 1,176 m, max. 24,111 m, $n = 34$) compared with winter (May to July; mean range length 3,719 m, median 1105 m, *se* 1,986 m, max. 10,241 m, $n = 5$) and summer (November to January; mean range length 347 m, median 210 m, *se* 131 m, max. 1,205 m, $n = 8$). However, these range lengths were derived from few locations in summer (mean 3.6 locations per bird, range 2–9) compared with spring (mean 77.6 locations per bird, range 2–556) and winter (mean 53.6 locations per bird, range 2–135).

Eight of 15 radio-tagged tūī moved at least 4.5–15.5 km within one or more 24-hour periods in 2005 and 2007, often travelling over pasture between areas of native forest where they roosted at night, to rural and urban areas where they fed during the day.

Nine tūī radio-tracked for at least four weeks starting in August–October moved 5–19 km from urban areas to surrounding native forests, while three tūī did not move away from urban areas during the period they were radio tracked (Fig. 2). These

movements were mostly made by September or October at the onset of nesting. Another tūī, tracked for only 16 days in September, moved 24.1 km from urban to native forest areas. In contrast, of the tūī radio-tracked from spring in areas dominated by native forest (Pukemako Historic Reserve) for at least four weeks, one moved to an urban area and seven remained within 500 m of the capture location during the period they were radio tracked.

Only one banded bird yielded long-distance movement information. An adult male tūī banded at Cambridge in October 2004 was seen near Huntly 53 km away a year later and remained there until at least July 2011.

Tūī nesting and nesting success

Only four (29%) of the 14 unmanaged nests located between December 2003 and February 2008 successfully fledged young (Table 1). Of the remainder, one was deserted at the chick stage, and the rest were preyed on by ship rats (three nests at egg stage), swamp harriers (*Circus approximans*; one nest at egg stage and one with chicks), possums (one nest at chick stage), or an unknown predator (one nest at egg stage and two with chicks). A nest at Taitua Arboretum fledged young when ship rats and possums were controlled using poison bait stations. The first nest we detected in Hamilton itself was at Hamilton Gardens in October 2007 and failed due to an unidentified predator.

The mean height of 14 tūī nests located during October–February of 2003–2008 was 16.1 m, and nests were near the top of their mostly exotic host trees (mean height 18.7 m; Table 1).

Sex ratio, longevity and death of banded tūī

Only 10% of adult tūī ($n = 41$) we caught were female, compared with 40% of first year tūī ($n = 10$) and 50% of sexed nestlings ($n = 6$).

The maximum tūī longevity we recorded was of a male that was initially captured as an adult in October 2004 and observed at the same location in September 2015, meaning it was at least 12.5 years old when last seen. When observed in 2015, this individual had lost one colour band, but the numbered metal band was clearly legible in photographs.

Four tūī were recovered dead during this study, between six weeks and 2.7 years after initial capture and banding. One female was found dead at a nest and a male died while fighting with another tūī when they fell on a concrete footpath with interlocked feet. The cause of death of two tūī (one female and one male) could not be determined.

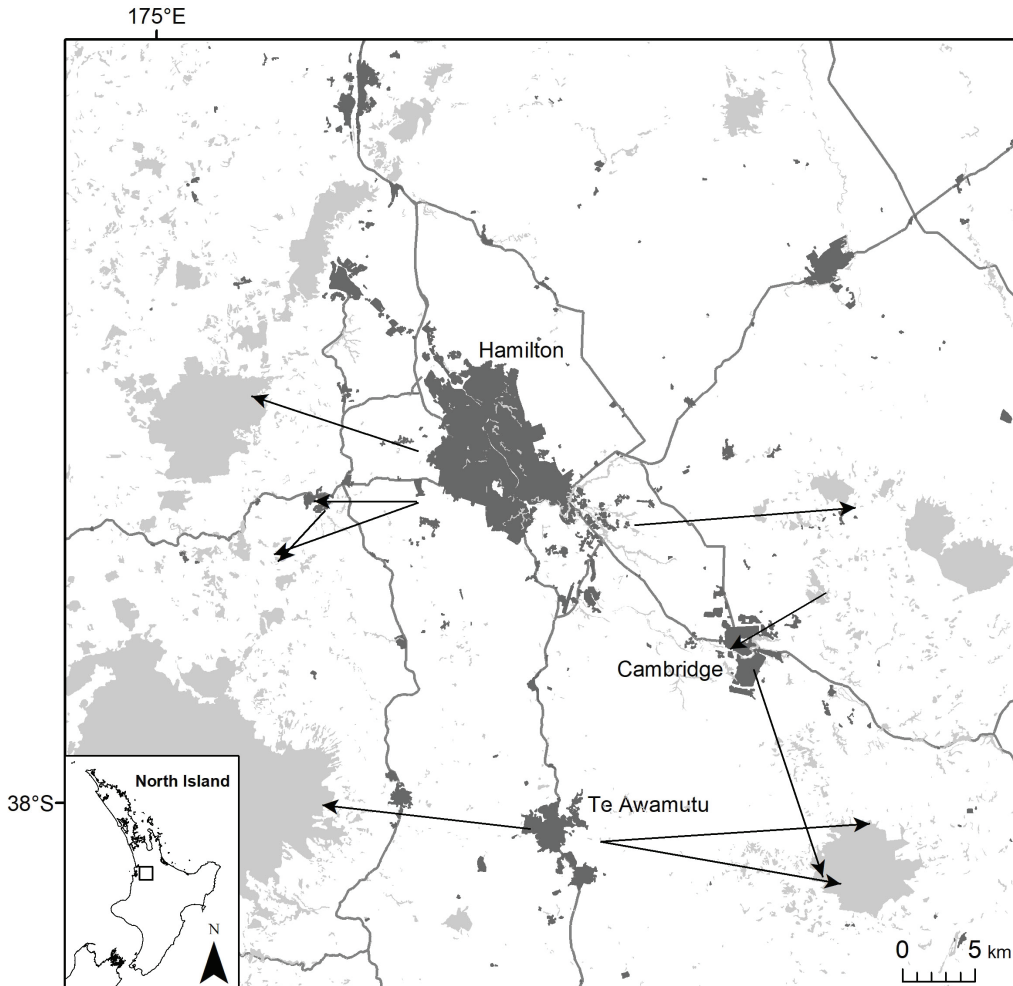


Figure 2. Spring movements of 10 Waikato tūi radio-tracked for at least four weeks starting in August–October during 2004–2007. Ten tūi meeting these criteria remained near their capture locations during the period they were monitored and are not shown here.

Pest control outcomes at Halo sites

Control of ship rats and possum populations in Halo sites was highly effective. The mean post-control residual trap-catch index of possum abundance during 2007–2012 was 1.2% (*se* 0.7%, $n = 15$). The index exceeded 2% in only one block in one year (Old Mountain Road East in 2007; RTC 11%). The mean ship rat tracking index during October–January (when tūi nest), in the years control was undertaken at pest-managed sites from 2007/8 to 2011/12, was 2.7% (*se* 0.91, $n = 33$), whereas the mean index from October 2007 to January 2012 in the years pest control was not undertaken was 28.6% (*se* 3.3, $n = 41$).

Tūi relative abundance in Hamilton 2004–2014

The empirical mean abundance of tūi in Hamilton green areas increased in August and November counts from 2004 to 2014 (Fig. 3). Tūi were recorded in counts in residential areas for the first time in 2012.

Generalized linear mixed models fitted to the data show that the increases in tūi over time (separated from differences related to weather, noise, and observers) were significant in five-minute counts in green areas in August ($P < 0.001$) and November ($P < 0.001$), and in November transect counts ($P = 0.007$). Model estimates and fit statistics are given in Appendix 1. There were too few tūi

Table 1 Attributes and fates of 15 tūī nests located from December 2003 to February 2008 in the central Waikato, New Zealand. Pred = depredated, unk. = unknown.

Location & date found	Stage when found	Host species	Nest height (m)	Host height (m)	Nest fate (cause)
Pukemako Historic Reserve					
3 Dec 2003	Building	<i>Agathis australis</i>	17	18	Fledged
18 Dec 2003	Building	<i>Araucaria heterophylla</i>	10	20	Pred. (harrier)
6 Jan 2004	Incubating	<i>Chamaecyparis lawsoniana</i>	25	27	Deserted
12 Jan 2004	Fledging	<i>Chamaecyparis lawsoniana</i>	unk.	10	Fledged
2 Nov 2004	Building	<i>Agathis australis</i>	15	18	Pred. (unk.)
10 Nov 2004	Chicks	<i>Cupressus macrocarpa</i>	30	31	Fledged
2 Dec 2004	Building	<i>Cupressus macrocarpa</i>	30	36	Pred. (unk.)
10 Jan 2005	Building	<i>Dacrydium cupressinum</i>	15	20	Pred. (harrier)
19 Jan 2005	Chicks	<i>Dacrydium cupressinum</i>	9	12	Pred. (possum)
Taitua Arboretum					
21 Nov 2004	Unknown	<i>Cryptomeria japonica</i>	12	16	Pred. (ship rat)
24 Nov 2005	Incubating	<i>Populus</i> sp.	20	10	Fledged
7 Feb 2008	Building	<i>Quercus robur</i>	10	12	Pred. (ship rat)
Whatawhata					
7 Dec 2004	Building	<i>Pittosporum eugenioides</i>	8	8.75	Pred. (ship rat)
Hamilton Gardens					
24 Oct 2007	Incubating	<i>Cupressus macrocarpa</i>	15	17	Pred. (unk.)
1 Dec 2007	Building	<i>Bambusa</i> sp.	10	12	Fledged

counted in residential areas to model change in the residential counts.

The number of observations of tūī recorded by members of the public on Waikato Regional Council's public website increased greatly in 2009/10 then remained relatively constant, as did both the mean and maximum number of birds seen (Table 2).

DISCUSSION

Tūī increases in relation to pest control

Five-minute bird counts, slow-walk transect counts, public reports to the Waikato Regional Council

website, and numerous other unpublished personal communications and media reports all documented significant or substantial increases in tūī abundance in and around Hamilton after the Hamilton Halo project began in 2007. The small increases in tūī counts in 2006 (before the Halo project started) were perhaps due to the progeny of a single pair of tūī nesting successfully at Taitua Arboretum. Our data suggest that limited local breeding and dispersal to Hamilton started before Hamilton Halo pest control began. However, the marked increases after 2009 are consistent with the expansion of management to reduce pest populations from just two sites in 2007/08 to five in 2008/09. Tūī were absent from

Table 2. Number of citizen reports of tūī in Hamilton and near surrounds (excluding Cambridge, Whatawhata, Ngaruawahia, Huntly, King Country and beyond) to the Waikato Regional Council website, and mean (*se*) and maximum number reported, 2008/09 to 2012/13

Years (winter to winter)	2008/09	2009/10	2010/11	2011/12	2012/13
No. reports	34	490	331	313	544
Mean no. tūī per report	1.0 (0)	1.8 (0.07)	2.1 (0.12)	1.9 (0.12)	2.5 (0.11)
Maximum no. tūī reported	1	18	20	20	15

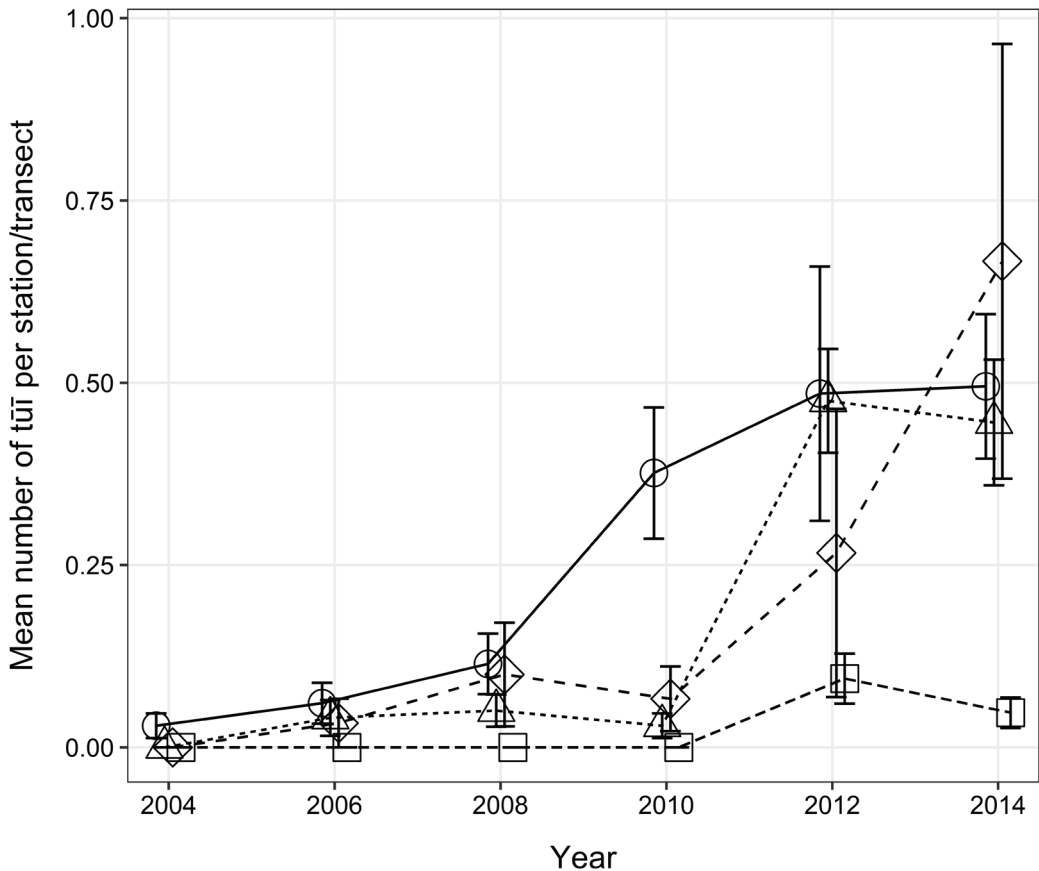


Figure 3. Mean (error bars = *se*) number of tūī counted per five-minute count in Hamilton green areas (August, circle; November, triangle), residential areas (November, square), and per transect (green areas, November, diamond), from 2004 to 2014.

Hamilton in 1993 (Day 1995) and scarce during 2000–2004 (our data; Robertson *et al.* 2007). Despite some restoration of gullies to native vegetation, it is unlikely that sudden increases in food supply in Hamilton either occurred or could explain the tūī increase. We did not measure food availability but observed throughout this research that many preferred food trees (e.g., coastal banksia, *Banksia integrifolia*; Taiwan cherry, *Prunus campanulata*; and kōwhai *Sophora* spp.) were not visited by any tūī at all, suggesting that food was never in short supply. Tūī have also increased at other sites after pest control, including Motatau, Northland (Innes *et al.* 2004), Wellington and Zealandia Sanctuary (Miskelly *et al.* 2005; Miskelly 2018), Maungatautari, Waikato (Fitzgerald *et al.* 2019), and in Department of Conservation’s Mainland Islands at Tounson Kauri Park (Northland), Otamatuna (northern Te Urewera National Park) and Boundary Stream

(Hawkes Bay; Saunders 2000), but not at Pureora (Smith & Westbrooke 2004).

Pest management by Waikato Regional Council described here was not the only forest bird restoration initiative in the Waikato during our monitoring period. Other pest control sites included Kakepuku, Pirongia, and Maungatautari. Maungatautari is a pest-fenced 3,240 ha forested reserve between Te Awamutu and Tirau (Fig. 1) that is completely free of ship rats and possums (Speedy *et al.* 2007; Burns *et al.* 2012). We radio-tracked tūī from Te Awamutu (15 km away) and from Cambridge (11 km away) but never from Hamilton (29 km away) going to Maungatautari (Fig. 2). It is likely that tūī and other forest bird species will undertake seasonal and dispersal radial movements from all these managed sites into the wider rural and urban Waikato landscape (Hanski & Simberloff 1997; Fitzgerald *et al.* 2019).

The number of citizen observation reports of tūī received may be some artefact of publicity, but the large increase in number of reports from 2009/10 onwards is consistent with simultaneous increases in the mean and maximum number of tūī per report.

Tūī is one of the taxa listed by Robertson *et al.* (2007) as having increased in national distribution between 1979 and 2004, from 47% of squares in the first atlas of New Zealand bird distribution (Bull *et al.* 1985) to 60% of squares in the second (Robertson *et al.* 2007). This was probably due to a combination of widespread and increasing mammalian pest control (Parkes & Murphy 2003) and the propensity of tūī to fly over and live in rural and urban environments without the need for forested or any other kind of movement corridors.

The relationship between pest mammal density and impacts on forest birds is poorly known for most New Zealand species (Norbury *et al.* 2015). Our work has not substantially clarified targets of residual abundance for key nest predators (ship rats and possums) for tūī, but the mean post-control ship rat tracking index of 2.7% and mean post-control possum residual trap catch index of 1.2% achieved by Halo contractors appear to be adequate to recover tūī numbers in this context. This response is consistent with levels of residual abundance (<5% by each measure) recommended for recovery of North Island kōkako (*Callaena wilsoni*; Innes *et al.* 1999), kererū (*Hemiphaga novaeseelandiae*; Innes *et al.* 2004), and North Island robin (*Petroica longipes*; Armstrong *et al.* 2006).

Our results suggest that large-scale intensive control of ship rats and possums to protect tūī nests will rapidly increase tūī abundance within a radius of about 20 km from the pest control site. Tūī will initially be autumn-spring visitors and then may remain to nest, resulting in year-round presence.

Tūī nesting and nest predation

The tūī nest success rate we found in the absence of mammalian predator control (29%) was consistent with the mean 27% for New Zealand forest birds in unmanaged forests reported by Innes *et al.* (2010).

Tūī nests were difficult to find in the podocarp-broadleaved forest of this region because of the complexity and height of the forest, and because nesting females were cryptic and furtive, and visits by males were brief (<1 minute) at all stages of the nesting cycle. Most (85–88%) tūī with transmitters in all years in our study were male, so that transmitters generally failed to help us find nests. The easiest times to find tūī nests were during building and chick-feeding, when adults were carrying nest material or food directly to the nest.

Dilks (2004) suggested that backpack and tail-mounted transmitters appeared to discourage

female Chatham Island tūī (*P. n. chathamensis*) from nesting. Although our sample is small, all three of the radio-tagged females for which we got >1 post-release tracking location nested, one twice, suggesting that tail-mounted transmitters did not inhibit attempts to breed in our study.

The sex ratio of tūī in our study was increasingly male-biased with age. Bergquist's (1985b) banded sample was similarly biased, with females comprising 60% of chicks ($n = 5$) and 30% of adults and first year birds ($n = 79$). Paucity of the incubating sex is a characteristic attribute of predation-vulnerable forest bird populations in New Zealand (Innes *et al.* 2010). Female tūī are probably vulnerable while nesting, and in our study a female was killed at one of the 15 nests we monitored. Alternatively, an excess of males may be a bias of capture technique, or perhaps more male than female tūī left Waikato forest fragments to visit Hamilton and other urban sites, although we made no observations that support these suggestions.

Predator behaviour and prey remains that we observed at tūī nests were consistent with previous accounts at nests of other forest bird species, and studies using artificial nests in North Island podocarp-broadleaved forest (Innes *et al.* 1996; Brown 1997; Boulton & Cassey 2006; Lewis *et al.* 2009). Filming revealed brief predation events that would otherwise not have been identified. A ship rat was filmed eating a single freshly laid tūī egg before incubation even began, and a harrier was filmed removing three tūī eggs in a few seconds with no shell remaining in the nest. Harriers were predators at two of the six nests with identified predators and have been significant in other studies (Innes *et al.* 1996; Boulton & Cassey 2006; Morgan *et al.* 2006).

Tūī movements

Banding alone produced few locations for most tūī in this study. Although radio-tagging generally allowed many more observations to be made, this method was limited by relatively short tag life, variable range, and the large distances and speed of some tūī movements. Nevertheless, our observations concur broadly with Bergquist (1985b), who studied tūī on Auckland's North Shore, and Stewart & Craig (1985) on Tiritiri Matangi Island. Across these different landscapes, tūī consistently have large, but variable, winter-spring ranges (1–30 km) compared to summer breeding ranges (0.5 km). Some Waikato tūī that we followed regularly commuted 5–17 km in a day between roosts and feeding sites, similar to the distances Stewart & Craig (1985) reported from Tiritiri Matangi Island. Large movements enable tūī, like many Australian Meliphagidae, to locate and exploit nectar sources

that are widely dispersed and often asynchronous (Keast 1968; Bergquist 1985b; Stewart & Craig 1985; Higgins *et al.* 2001).

We expected tūi visiting in winter to increase rapidly in Hamilton with pest mammal control in surrounding forests, but the speed with which substantial numbers of birds remained to nest in the city was a surprise, given the strong natal philopatry shown by Bergquist (1985b). Counts of non-breeding tūi in Hamilton green areas increased steadily within 3 years of the start of the Halo project, but counts at nesting time suggest that tūi began to nest in the city in substantial numbers within 5 years after release from chronic predation pressure at distant nesting sites.

Natal philopatry, the tendency for individuals to first breed at or near their site of origin (Greenwood 1980), is reported as common in both sexes of tūi (Stewart 1980; Bergquist 1985b; Stewart & Craig 1985). Although it is possible that the tūi that nested in Hamilton in 2012/13 had themselves fledged cryptically in the city in previous years, we think that the rapid increase in numbers suggests that they came from elsewhere.

Although dispersal is predominantly a trait of juveniles (natal dispersal), adult birds may also change breeding sites (breeding dispersal; Greenwood 1980; Greenwood & Harvey 1982). The extent to which breeding dispersal occurs in tūi is unknown and estimates of tūi natal dispersal may have been previously underestimated due to small sample sizes and difficulty locating birds that breed away from study areas. In birds, natal and breeding dispersal are both biased towards females (Greenwood 1980), particularly where the adult sex ratio is male-biased (Végvári *et al.* 2018). If tūi dispersal is similarly female-biased, mammalian predation of nesting females (Innes *et al.* 2010) and reduced ability of female tūi to move large distances due to their much smaller size compared with male tūi (Craig *et al.* 1981), could have restricted colonisation of Hamilton by tūi before pest mammal control. Whatever the underlying mechanisms and demographic characteristics, any tendency towards natal philopatry in tūi was not a barrier to them colonising and breeding in an urban centre.

We did not attempt to estimate natal dispersal distances and it is likely that published accounts of dispersal distances are biased by researchers limited ability to survey possible post-dispersal settlement sites. More accurate estimates of natal and subsequent adult dispersal by forest birds is an important research priority if biodiversity restoration is to become large-scale and undertaken effectively across landscapes (Paradis *et al.* 1998; Glen *et al.* 2013).

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Appendix 1. Generalised linear mixed model estimates and fit statistics for modelled change in the relative abundance of tūī in Hamilton, 2004–2014. Estimate values give the log of the expected change in the number of tūī per count when that fixed effect increases by one and all other fixed effects against which it is modelled are held constant.

Survey	Fixed effect	Estimate	Standard Error	z-value	P-value
Green areas, August (5-minute counts)					
	Time (yr)	0.238	0.039	6.166	<0.001
	Cloud	0.283	0.223	1.269	0.204
	Rain	0.302	0.400	0.756	0.450
	Wind	-0.287	0.182	-1.579	0.114
	Other noise	-0.213	0.305	-0.696	0.486
	Time of day	-0.007	0.049	-0.141	0.888
	Observer 2	0.834	0.599	1.391	0.164
	Observer 3	0.627	0.585	1.072	0.284
Green areas, November (5-minute counts)					
	Time (yr)	0.314	0.051	6.102	<0.001
	Cloud	0.409	0.239	1.710	0.087
	Rain	-0.294	0.514	0.572	0.567
	Wind	-0.035	0.167	0.209	0.835
	Other noise	-0.617	0.277	2.220	0.026
	Time of day	0.018	0.053	0.344	0.730
	Observer 2	2.285	0.776	2.941	0.003
	Observer 3	1.700	0.822	2.064	0.039
	Observer 4	1.613	1.258	1.279	0.201
Green areas, November (slow-walk transects)					
	Time (yr)	0.402	0.147	2.708	0.007
	Cloud	0.106	0.538	0.195	0.845
	Rain	0.212	1.037	0.203	0.839
	Wind	-0.149	0.322	0.461	0.645
	Other noise	-0.381	0.569	0.664	0.507
	Time of day	0.032	0.071	0.449	0.653
	Observer 2	-1.53	1.011	1.499	0.134
	Observer 3	0.380	0.853	0.443	0.658