

Pest mammal eradication leads to landscape-scale spillover of tūī (*Prosthemadera novaeseelandiae*) from a New Zealand mainland biodiversity sanctuary

NEIL FITZGERALD*

JOHN INNES

NORMAN W.H. MASON

Manaaki Whenua – Landcare Research, Private Bag 3127, Hamilton 3240, New Zealand

Abstract: Maungatautari is a 3,240 ha pest-fenced ecosanctuary free of virtually all mammalian predators in Waikato, New Zealand. We used triennial 5-minute counts within the ecosanctuary and biennial surveys of residents up to 20 km from the perimeter pest fence to measure spillover of tūī from Maungatautari into the surrounding area over a 9-year period (2006–2014) following pest eradication. Following pest eradication in the ecosanctuary, tūī relative abundance increased there and in the surrounding largely unmanaged area. The mean number of tūī per 5-minute count within the ecosanctuary was 2.23 (se = 0.163) in 2005 and increased following predator eradication in 2006 to 3.33 (se = 0.206) in 2008, 3.76 (se = 0.193) in 2011, and 2.68 (se = 0.279) in 2014. The mean maximum number of tūī at one time observed by residents in the largely unmanaged area increased from 4.4 (max = 47, n = 320) in 2006 to 15.6 (max = 300, n = 138) in 2014. Tūī numbers in both the ecosanctuary and the surrounding area were positively correlated with time since pest eradication. In the largely unmanaged area surrounding Maungatautari, tūī numbers were also positively correlated with provision of artificial food, and negatively correlated with distance from the ecosanctuary. Wind was negatively correlated with the number of tūī recorded in 5-minute counts at Maungatautari. Our findings show that pest-free ecosanctuaries can facilitate increased abundance of volant birds in surrounding landscapes if habitat is available.

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INTRODUCTION

Tūī (*Prosthemadera novaeseelandiae*) is an iconic New Zealand honeyeater (Meliphagidae), widespread throughout most of the country but sparse in dry, eastern, deforested parts of the South Island and some highly pastoral areas of the North Island (Higgins *et al.* 2001; Robertson *et al.* 2007). Before 2006, when we began this study, tūī were uncommon in central Waikato compared with many other parts of New Zealand (Robertson *et al.* 2007).

During the breeding season (October–February in Waikato; *unpubl. data*) tūī movement is restricted to a foraging range of approximately 500 m (Bergquist 1985). However, they may forage widely (tens of km) during the non-breeding season, crossing large gaps of non-woody habitat (Craig *et al.* 1981; Stewart & Craig 1985; Higgins *et al.* 2001; Innes *et al.* 2005).

The diet of tūī includes nectar and fruit of a wide variety of native and introduced plants (Higgins *et al.* 2001). This, combined with their ability to move large distances, makes tūī ecologically important pollinators and seed dispersers (Castro & Robertson

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*Correspondence: fitzgeraldn@landcareresearch.co.nz

1997; Robertson *et al.* 2008; Kelly *et al.* 2010) able to exploit novel environments such as urban and rural residential gardens.

Globally, invasive alien species have been the most important driver of bird extinction over the past 500 years, and mammals are the most important group of invasive alien species causing declines in extant birds, primarily through reduced reproductive success and direct predation (del Hoyo *et al.* 2010). This is particularly true in New Zealand, where introduced mammalian predators are the primary factor limiting endemic forest bird abundance in large forest tracts by predation of eggs, chicks, and incubating adults. Therefore, bird populations frequently recover after pest predator control (Innes *et al.* 1999; Moorhouse *et al.* 2003; Smith & Westbrooke 2004; Armstrong *et al.* 2006; Innes *et al.* 2010). In the absence of effective ship rat (*Rattus rattus*) and brushtail possum (*Trichosurus vulpecula*) management, tūi nesting success in the Waikato is poor (Innes *et al.* 2005; Innes *et al.* 2015). When the densities of these key introduced predators are reduced, tūi is one of the most conspicuously responsive species (Saunders 2000; Innes *et al.* 2004; Fitzgerald & Innes 2014; Miskelly 2018).

Being conspicuous and easily identifiable, with a propensity to range widely and respond rapidly to mammalian predator control, tūi provide an opportunity to investigate native biodiversity 'spillover' – where the benefit from a reserve extends beyond its boundary into non-target habitat (Brudvig *et al.* 2009). We used 5-minute counts of tūi at Maungatautari – a fenced ecosanctuary (Campbell-Hunt & Campbell-Hunt 2013) – and surveys of residents within 20 km of Maungatautari, over a 9-year period following pest eradication, to determine if tūi numbers increased in the ecosanctuary, and if there was evidence of spillover of tūi into the surrounding, largely unmanaged, non-target area.

METHODS

Study area

Maungatautari (175.574°E, 38.025°S) is an extinct andesite volcano, approximately 30 km SE of Hamilton city in central Waikato, New Zealand, with contiguous native forest cover from 240 to 797 m above sea level. The forest ranges from lowland rimu (*Dacrydium cupressinum*)/tawa (*Beilschmiedia tawa*) forest to montane forest dominated by tāwari (*Ixerba brexioides*), kāmahī (*Weinmannia racemosa*), and tāwheowheo (*Quintinia serrata*) (Clarkson *et al.* 2002). Construction of a 47 km pest-resistant fence encircling 3,240 ha of the forest was completed in August 2006 and eradication of all pest mammals except house mice (*Mus musculus*) commenced in November 2006 (Speedy *et al.* 2007). This created

the largest area of virtually pest-free forest on the New Zealand mainland.

Our study area included the pest-fenced Maungatautari ecosanctuary and a near-circular largely unmanaged zone extending 20 km out from the perimeter pest fence (Fig. 1). Land use within this 171,960 ha unmanaged zone is predominantly intensive agriculture (88%; 150,970 ha) with fragments of exotic forest and scrub (5%; 7,870 ha), indigenous woody vegetation (4%; 7,650 ha), and urban and other built-up areas (<2%; 2,850 ha; Land Cover Database version 4.1). Indigenous vegetation and built-up areas are not distributed uniformly across the study area; 51% of the indigenous vegetation occurs 15–20 km from Maungatautari, and 96% of urban and built-up areas are 10–20 km from Maungatautari (Fig. 1).

Maungatautari is not the only project focusing on mammalian predator control in the region, but it is by far the largest and most comprehensive. The most significant other project in our study area is Waikato Regional Council's 'Hamilton Halo' project, which began in 2007 with the aim of increasing tūi abundance in Hamilton by reducing the abundance of ship rats and possums in surrounding forest. 'Halo' in this instance refers to a conceptual ring of protected habitat surrounding the area of intended benefit (Hamilton), which is different from other definitions of the term (e.g. Birt *et al.* 1987; Brudvig *et al.* 2009; Glen *et al.* 2013). The Hamilton Halo project was guided by research identifying movement and factors limiting numbers of tūi in the greater Hamilton area (Innes *et al.* 2005; Fitzgerald *et al.* 2015) and involves periodic ship rat and possum control at three sites totalling 518 ha of native forest, 6.8% of the indigenous woody vegetation within our study area (Te Tapui Scenic Reserve, Maungakawa Scenic Reserve, and Tirohanga Road Reserve; Innes *et al.* 2013). Pest management techniques varied from site to site and year to year, but typically consisted of poison bait stations on a 75 m grid with brodifacoum, diphacene, pindone, or cholecalciferol to target both species on 3-years-on and 2-years-off regime that aimed to have both pest species below target levels by the onset of each tūi nesting season (October to January). Target residual pest abundances 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. Most (383 ha) of this pest mammal control was >15 km from Maungatautari.

Resident survey method

We surveyed residents within 20 km of Maungatautari biennially about their recollection of tūi presence and abundance at their property.

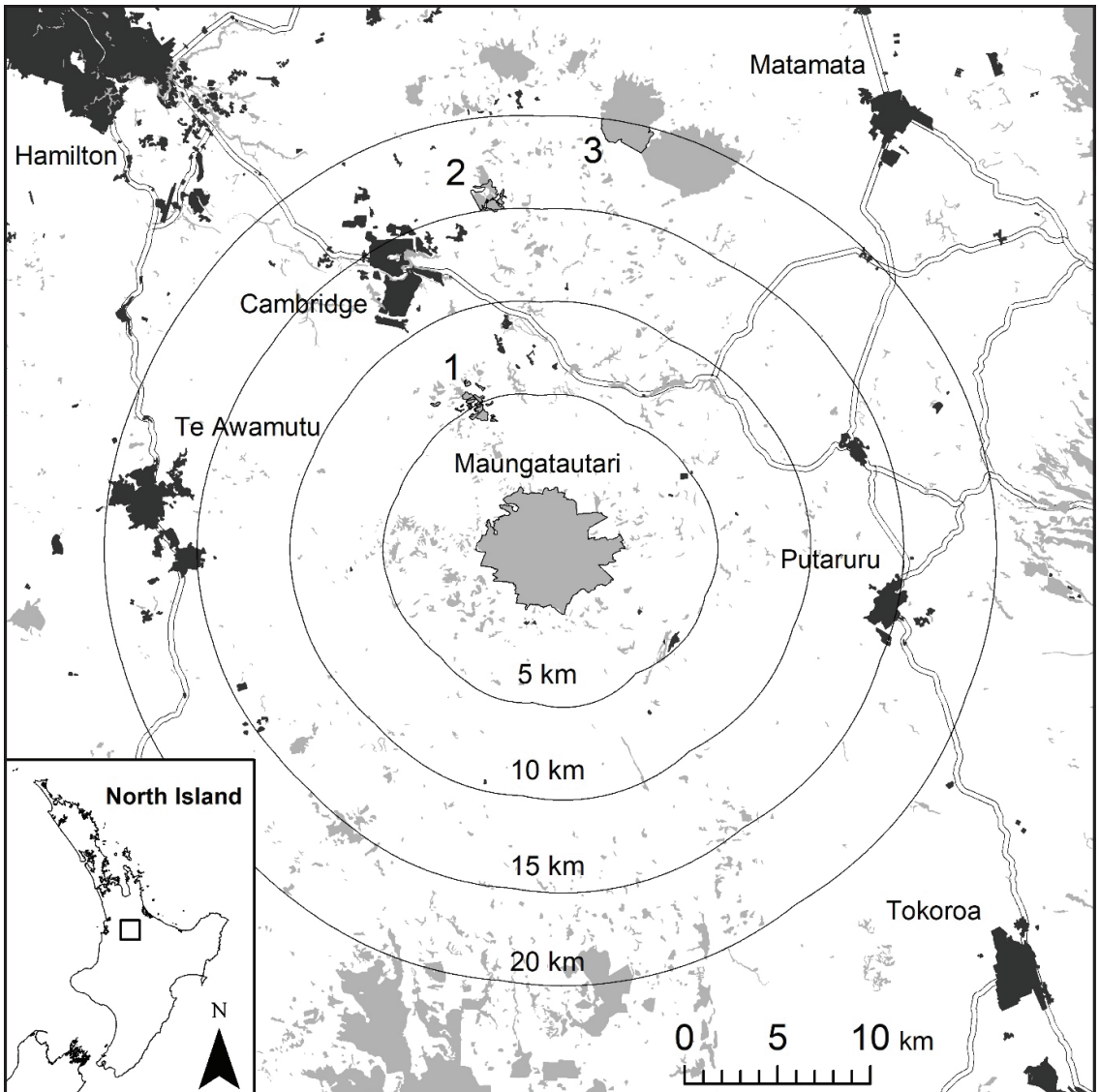


Figure 1. Study area showing distances from the Maungatautari perimeter pest fence. Urban and other built-up areas are shown in black and indigenous forest in grey. State highways are indicated with narrow parallel lines. Numbers indicate sites of episodic ship rat and possum control undertaken by Waikato Regional Council in the 'Hamilton Halo' project. 1 - Tirohanga Road Reserve, 2 - Maungakawa Scenic Reserve, 3 - Te Tapui Scenic Reserve.

Surveys were conducted in January–March 2007–2015 and referred to the preceding calendar year (2006–2014). To avoid self-selection, the survey questionnaire was delivered to mailboxes of 2,000 residents in January 2007, distributed proportionately by area in 5 km bands from the pest fence (0–5 km, $n = 232$; 5–10 km, $n = 407$; 10–15 km, $n = 589$; 15–20 km, $n = 722$). In subsequent surveys, questionnaires were delivered by post or email to all respondents who had participated in a previous survey and provided a valid address.

In each survey, participants were asked: 1) What was the maximum number of tūi you saw at one time at your property during the previous year?; 2) In what month(s) did this occur?; 3) Do you think tūi have increased, decreased, or stayed the same since the previous survey?; 4) Are tūi present at your property during summer (December–February, the main breeding season)?; and 6) Do you regularly put out food for tūi?

We used tūī as a focal species because it is a conspicuous iconic species, and one of the native birds most familiar to members of the public. The maximum number of birds seen at one time was chosen as a measure of abundance as non-breeding congregation at preferred food sources is a conspicuous characteristic of tūī behaviour (Higgins *et al.* 2001; Lyver *et al.* 2008). It is also a simple and probably memorable measure that anecdotal reports suggested was often noted by the public without requiring specific instruction from us.

Bird counts

We undertook 5-minute bird counts every third year at Maungatautari from 2002 using methodology based on Dawson & Bull (1975). All 5-minute counts were done by experienced observers at least 1 hour after sunrise and 1 hour before sunset, over a 17–31-day period in November–December each survey year. Observers recorded all birds seen or heard during a 5-minute period while stationary at each count station. Observers also recorded estimates of i) cloud cover (0; none–2; rain), ii) rain (0; none–4; heavy), iii) wind (0; calm or leaves move silently–3; strong), and iv) other noise (0; none–2; loud) that could affect bird detection. Counts were not done in rain (scored ≥ 3) or strong wind. Count stations were spaced at least 200 m apart along lines following existing tracks, and counts were bounded at 100 m to minimise repeated counting of birds in different counts. The analyses presented are based on a subset of 5-minute bird counts undertaken in 2005, 2008, 2011, and 2014, covering the same period as the surveys of residents in the surrounding landscape. In 2005 and 2008, 35 count stations were used, each separated by approximately 15 min walk (mean 315 m apart), and count stations were visited twice, each time by a different observer on a different day. From 2011, the number of count stations was increased to 50 but visited only once each survey year to provide a larger sample size with similar counting effort as earlier surveys. The count stations used from 2011 were at new locations (mean separation of 208 m) along the same tracks used in previous surveys. The 5-minute counts were undertaken during the tūī breeding season, so reflect changes in birds established there, rather than transient birds from other sources. In total, 231 separate 5-minute counts were used for analysis of the change in tūī relative abundance at Maungatautari.

Analysis

Resident surveys

We used a generalised linear mixed model (GLMM) with a negative binomial error distribution and a log link function to test the effect of time (years since

the first survey), distance from Maungatautari, the interaction between distance and time, and the provision of supplementary food on maximum tūī counts. We initially specified a Poisson distribution for this model but this produced unreliable estimates due to over-dispersion which was resolved by using a negative binomial distribution.

We used a GLMM with a binomial distribution and logit link function to test the effect of time, distance from Maungatautari, and the interaction between time and distance on the occurrence of tūī breeding activity. We included a unique identifier for each survey respondent as a random effect in both models fitted to the data from resident surveys to account for non-independent repeated surveys of the same people. Two of the survey questions referred to tūī abundance, and two asked about evidence of breeding. We expected the related questions to give similar results if they were equally reliable. To test this we used Pearson's correlation tests in the base R package to check that changes in the maximum number of tūī (question 1) were consistent with impressions of whether tūī had increased, decreased, or stayed the same (question 3), and whether the presence of tūī during the breeding season (question 4) and observation of breeding (question 5) were correlated. The correlation between questions 1 & 3 was not strong ($r = 0.35$; 95% CI 0.28–0.42) so we did not use the reported impression of change in tūī abundance in analyses as it is less informative and likely less reliable as it requires respondents to recall two time periods rather than one. Correlation between presence during the breeding season and observed nesting was also low ($r = 0.23$; 95% CI 0.17–0.29). We consider both the presence of tūī during the breeding season and observation of nesting behaviour to be reliable indicators of breeding activity (but with differing conspicuousness) so we combined these measures to produce a single variable for analysis.

Five-minute counts

We used a GLMM with Poisson error distribution and a log link function to test the effect of time (years), cloud, rain, wind, other noise, and time of day on counts of tūī at Maungatautari between 2005 and 2014. The log of the number of times a station was counted in a year was included as an offset in the model to adjust for the different number of times some stations were counted (Hutchinson & Holtman 2005), and we included a unique identifier for each observer and station as random variables in the model to account for the repeated measures design.

We used the sjstats package (Lüdecke 2019) to calculate variance inflation factors (VIF) to check for multicollinearity between model variables. Maximum VIF did not exceed a conservative

threshold of 2 (Zuur *et al.* 2010), so we retained all variables.

We assume that all the effects included in the models are real, whether statistically significant or not, so we estimate parameters from the full models rather than alternative approaches such as backward stepwise regression or information-theoretic tools (Bolker *et al.* 2009).

We used the glmmTMB package (Brooks *et al.* 2017) in the R statistical computing environment (3.5.2; R Core Team 2018) to fit GLMMs to the data using maximum likelihood estimation. We tested all GLMMs for potential misspecification, such as using an inappropriate error distribution, indicated by residual over- and under-dispersion, zero-inflation, and residual outliers using a simulation-based approach with 10,000 iterations using the DHARMA package (Hartig 2019).

RESULTS

The relative abundance of tūi counted within the ecosanctuary increased significantly with time following predator eradication (Table 1). The mean number of tūi per 5-minute count was 2.23 (se = 0.154) in 2005, 3.23 (se = 0.219) in 2008, 3.76 (se = 0.193) in 2011, and 2.68 (se = 0.279) in 2014. The effect of wind (mean score 0.94) and other noise (0.08) was negatively correlated with tūi counts. Cloud cover (mean 0.78), rain (mean 0.07), and time of day were not significantly correlated with differences in tūi relative abundance.

We received 320 responses to the 2,000 questionnaires delivered in the 2006 survey, and 225, 205, 167, and 138 for the 2008, 2010, 2012, and 2014 surveys respectively. Where respondents gave additional information on the location of their observations, these typically described rural and urban gardens.

Table 1. Generalised linear mixed model log estimates of fixed effects and fit statistics for modelled change in the relative abundance of tūi within Maungatautari ecosanctuary following predator eradication. Estimate values give the log of the expected relative change in the number of tūi per 5-minute count when a fixed effect increases by one and all other fixed effects are held constant

Response	Fixed effect	Estimate	Standard Error	z-value	P-value
Tūi count	Time (yr)	0.114	0.013	8.959	<0.001
	Cloud	0.029	0.094	0.311	0.756
	Rain	0.073	0.136	0.536	0.592
	Wind	-0.233	0.053	-4.387	<0.001
	Other noise	-0.327	0.161	-2.023	0.043
	Time of day	0.050	0.028	1.779	0.075

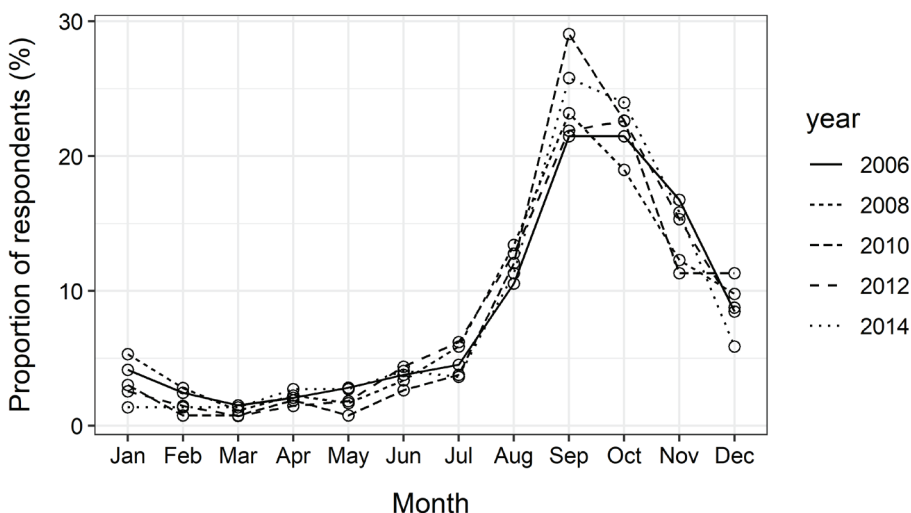


Figure 2. Months in which survey respondents recorded maximum tūi counts as a proportion of all responses each survey year, 2006–2014.

Means (and maxima) of the maximum number of tūi reported at each property within the whole study area in 2006, 2008, 2010, 2012, and 2014 were 4.4 (47), 5.5 (55), 8.6 (60), 11.7 (300), and 15.6 (300) respectively. Tūi aggregations were largest in spring (September–October) and smallest in early autumn (March; Fig. 2). We received six reports of large congregations of ≥ 100 birds from five residents (2 in 2012 and 4 in 2014).

The maximum number of tūi reported by residents in the study area increased significantly

with time and the provision of artificial food and decreased with distance from Maungatautari (Table 2; Fig. 3). Including an interaction between time and distance in the model resulted in significant deviation between observed and expected residuals, so we did not include the interaction in the full model.

There was some evidence for an increase in tūi breeding occurrence in the largely unmanaged area with time, but distance and the interaction between time and distance were not significant (Table 2)

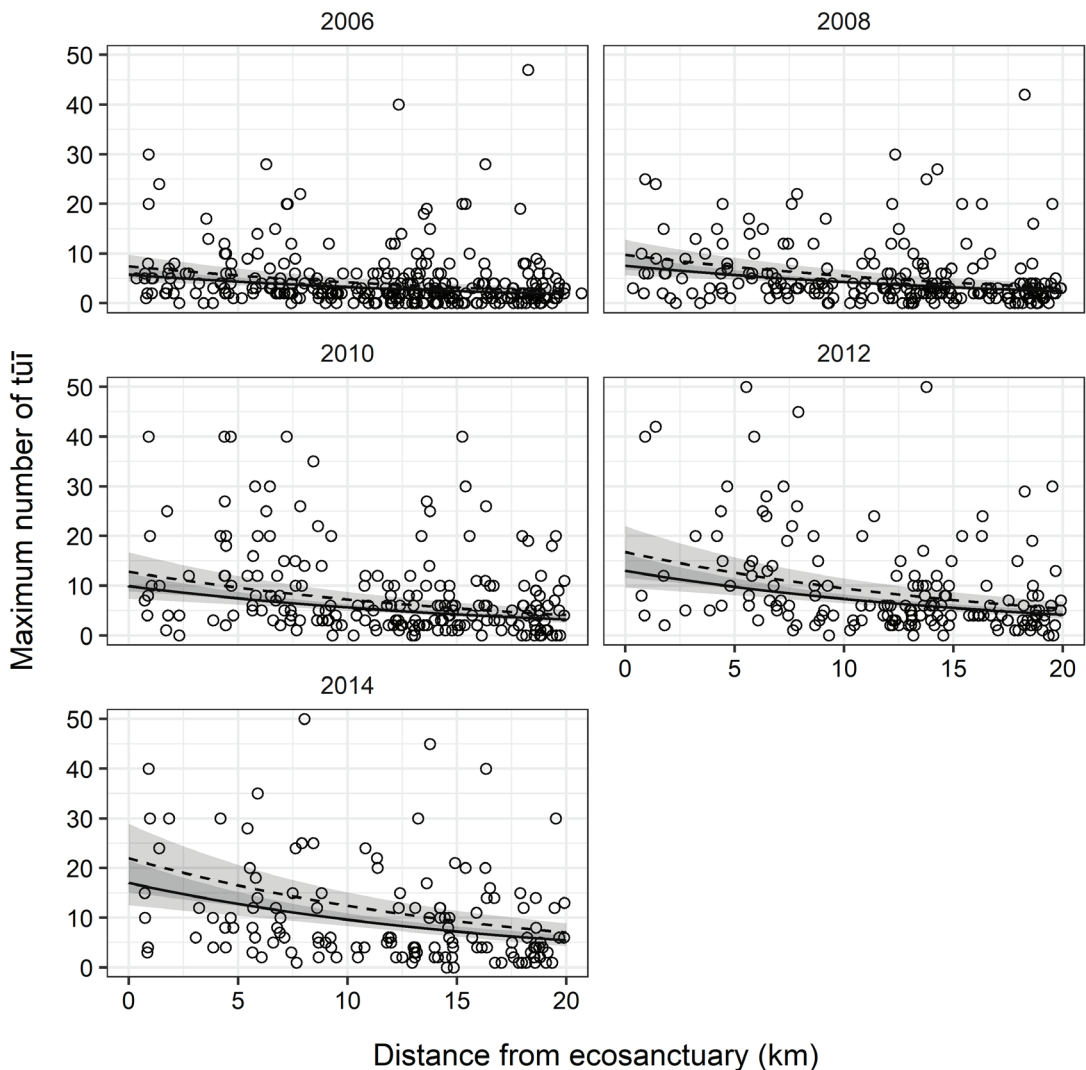


Figure 3. Maximum counts of tūi (circles; values >50 are not shown) reported by residents up to 20 km from Maungatautari ecosanctuary, and modelled change in maximum counts of tūi over time with distance from the ecosanctuary, with (dashed line) and without (solid line) provision of artificial food. Shaded areas show 95% confidence intervals around the predicted value for each distance.

Table 2. Generalised linear mixed model log estimates of fixed effects and fit statistics for modelled change in maximum counts of tūi and change in breeding occurrence within 20 km of Maungatautari sanctuary following predator eradication within the ecosanctuary. Estimate values give the log of the expected relative change in the response variable when a fixed effect increases by one and all other fixed effects against which it is modelled are held constant

Response	Fixed effect	Estimate	Standard Error	z-value	P-value
Maximum tūi count	Time (yr)	0.136	0.008	17.886	<0.001
	Distance (km)	-0.057	0.010	-5.681	<0.001
	Provision of food	0.256	0.098	2.600	0.009
Breeding	Time (yr)	0.159	0.083	1.919	0.055
	Distance (km)	-0.047	0.034	-1.398	0.162
	Time × Distance	0.005	0.006	0.741	0.459

DISCUSSION

Tūi increased at Maungatautari after pest eradication, as well as in the surrounding largely unmanaged area where counts of tūi were larger closer to the ecosanctuary. Together, these changes in tūi relative abundance are evidence of spillover of tūi from Maungatautari into the surrounding landscape, which has important biological and social implications.

Increase in tūi abundance within the ecosanctuary

We found that tūi relative abundance within pest-fenced Maungatautari increased following the eradication of all mammalian predators except mice from the sanctuary in 2006. This increase is consistent with independent non-temporal measures from Maungatautari (Iles & Kelly 2014; Bombaci *et al.* 2018), and data from other sanctuaries, such as Zealandia, Wellington (Miskelly 2018).

Hartley (2012) suggested that the effect of weather variables and noise on 5-minute counts should be investigated. We avoided counting birds in rain, strong wind, or other noisy conditions, but there was still strong evidence that the moderate wind and other noise during which we undertook some counts had substantial negative effects on the number of birds counted. We suggest that wind and other noise at least be included in analyses of 5-minute counts to control for their potential effects on bird counts and, therefore, on the inferences drawn from them.

Tūi spillover into the surrounding landscape

We found that tūi relative abundance increased at residential properties in the non-target landscape surrounding Maungatautari over the same period in which tūi increased within the ecosanctuary. Brudvig *et al.* (2009) note that spillover is largely a function of within-patch processes and is greatest from patches with greater density of the taxa

of interest. This conceptual model implies that temporal increases in within-patch density, as seen with tūi at Maungatautari, will also result in increasing spillover. We found maximum congregations of tūi were larger with proximity to the sanctuary, which is also evidence of spillover of indigenous biodiversity into the wider landscape (Brudvig *et al.* 2009; Tanentzap & Lloyd 2017). The known mobility and life-history of tūi, and increases in their relative abundance, together with the scale of the Maungatautari project suggest that significant landscape-scale spillover of tūi is occurring from this mainland biodiversity sanctuary.

The maximum tūi count data from resident surveys are strongly right-skewed, with a small number of very large aggregations of tūi. Congregations of 100 or more tūi were reported 6 times. Such exceptional congregations of tūi have not been previously reported in Waikato. In late-August 2015, we visited the property where the largest number (300) had been reported in both 2012 and 2014. This property was a large (approximately 10 ha) rural garden 6.7 km from Maungatautari. The landowners noted that there were fewer tūi present that day than at the peak. Despite this, we estimated from counts and photographs that there were at least 210 tūi present, mostly in approximately 100 mature flowering Taiwan cherry trees (*Prunus campanulata*) from which they were feeding on nectar. This property demonstrates the potential for very large ephemeral congregations of tūi at sites with abundant food resources.

Maximum counts of tūi at rural and urban residences were most often observed in spring, immediately before the breeding season. This is consistent with previous reports of pre-breeding congregation of tūi at preferred nectar sources (Bergquist 1985; Stewart & Craig 1985; Higgins *et al.* 2001) as well as of Australian Meliphagidae (Pyke 1980; McGoldrick & Mac Nally 1998). In the Waikato, these preferred food sources are typically coastal banksia (*Banksia integrifolia*), followed by

kōwhai (*Sophora* spp.), flowering cherry (*Prunus* spp.), rewarewa (*Knightia excelsa*), camellia (*Camellia* spp.), and eucalypts (*Eucalyptus* and *Corymbia* spp.; Innes *et al.* 2005).

Evidence for increased occurrence of nesting in gardens in the landscape surrounding Maungatautari during our study was not as strong as for non-breeding change. This is unsurprising, as tūi are often relatively inconspicuous when breeding, and the natal philopatry shown by Bergquist (1985) suggests that most of the tūi that disperse seasonally from Maungatautari will return there to breed.

Limitations of the study

Pest control involving periodic targeting of ship rats and possums at the Hamilton Halo sites within and beyond our study area is also likely to have contributed to increased tūi abundance. However, this effect is likely to be modest compared with the influence of Maungatautari, where there has been sustained eradication of the full suite of mammalian predators, except mice, over a much larger area.

The survey respondents may not be representative of all residents in the study area, and the locations of the counts they recorded represent a small, non-random subset of the available habitat in the study area. The survey data therefore provide a measure of tūi relative abundance at the survey sites (residents' gardens), not an overall measure of abundance in the study area.

Our study lacks spatial replication, as it is focussed on a single ecosanctuary, so the results apply only to the study area. However, the inferred movement of tūi in this study is entirely consistent with other studies (Craig *et al.* 1981; Bergquist 1985; Stewart & Craig 1985; Higgins *et al.* 2001; Innes *et al.* 2005). The relative isolation of Maungatautari from other mammalian predator-control sites was advantageous for this study, but the large size (3,240 ha) of the reserve precluded replication. Repeating the study elsewhere is needed to determine if the results are more widely applicable.

Biological and social importance of tūi spillover

Scofield *et al.* (2011) suggested that, in many cases, degraded habitat outside pest-fenced ecosanctuaries will never be able to sustain the species found within the ecosanctuaries. The 'habitat' of a species refers to the resources and conditions present in an area that produce occupancy, including survival and reproduction (Hall *et al.* 1997). In situations described by Scofield *et al.* (2011), emigration from a fenced ecosanctuary may create a source-sink dynamic, where species are able to occupy the low quality "degraded" habitat but reproductive success there is less than within-habitat mortality

(Pulliam 1988; Faaborg *et al.* 2010). Predator abundance is an important attribute of habitat, and the relatively unmanaged area surrounding Maungatautari is likely to be sink habitat for species that are highly vulnerable to mammalian predation (e.g. hihi *Notiomystis cincta*, kōkako *Callaeas wilsoni*, and tieke *Philesturnus rufusater*; Innes *et al.* 2010; Norbury *et al.* 2015). A sink population relies on immigration to persist, but despite low rates of reproductive success, sink habitat can contribute to larger total population size as offspring from the source can disperse and produce some offspring in sinks (Pulliam & Danielson 1991). It is also possible for sink habitat to have high population density due to immigration, so density can be a misleading discriminator of source and sink habitat (Van Horne 1983; Pulliam 1988; McArthur *et al.* 2019). It is unknown to what extent tūi that emigrate permanently from Maungatautari can breed successfully outside the sanctuary, and therefore whether it is sink habitat for this species, but the tūi we studied were undertaking winter-spring (non-breeding season) movement. Most tūi originating from the ecosanctuary may return there to breed (Bergquist 1985), which is when they are most vulnerable to mammalian predation (Innes *et al.* 2010). The increased presence of tūi in the wider landscape will help restore indigenous dominance in ecosystem processes such as pollination and seed dispersal. Furthermore, public awareness, engagement, and acceptance of pest mammal control are improved when people experience tangible benefits of restoration, such as tūi visiting their properties (Campbell-Hunt 2002).

Connectivity between habitat patches (so-called 'corridors') is a key factor in spillover (Brudvig *et al.* 2009), and the rescue-effect that can maintain species and genetic diversity in fragmented landscapes (Brown & Kodric-Brown 1977; Piessens *et al.* 2004). Habitat is a species-specific concept, so it is important to frame connectivity and spillover in the context of the taxon of interest. It is also important to clarify which movement processes are of interest, e.g. seasonal movement, breeding dispersal, natal dispersal, or post-translocation dispersal, and to recognize the limitations in the understanding of many of these. Seasonal movement is important for enabling birds to access food resources that may be absent from remaining, often fragmented habitat, and breeding and natal dispersal are key to colonisation of the landscape surrounding sanctuaries, but these processes are poorly known for many New Zealand birds. Post-translocation dispersal (Richardson *et al.* 2015) may be somewhat better known because monitoring is frequently mandated by the NZ Department of Conservation in translocations, which are very common (Miskelly & Powlesland 2013).

The habitat matrix surrounding Maungatautari, and detailed studies of tūi movement (Bergquist 1985; Stewart & Craig 1985; Innes *et al.* 2005), suggest that tūi readily cross pasture gaps of at least several kilometres, and this has potential for positive social and biodiversity gains over a considerably larger area than the fenced ecosanctuary alone.

Biodiversity spillover is a key to achieving widespread benefit from the long-term goal to make New Zealand predator-free (Russell *et al.* 2015; Parkes *et al.* 2017), but few studies have shown empirical evidence of biodiversity spillover from pest-fenced ecosanctuaries in New Zealand (Tanentzap & Lloyd 2017). Overall, our results provide strong evidence that predator exclusion from the Maungatautari ecosanctuary has enhanced tūi visits to the surrounding landscape via spillover. We predict that this will lead to more tūi breeding in the surrounding landscape, as in Hamilton City (Innes *et al.* 2015), and this could be enhanced further by management to reduce the abundance of mammalian predators there during the tūi breeding season. Reducing the abundance of predators in the landscape surrounding the ecosanctuary may also provide scope for 'evolutionary rescue' of some species (Urlich 2015). Our results also show that maximum counts of tūi can provide an effective way to engage citizen science to monitor landscape-scale population dynamics of conspicuous, iconic species.

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