DISSERTATION

RESTORING ISLAND BIRDS AND SEED DISPERSAL IN NEW ZEALAND'S FENCED MAINLAND ISLAND SANCTUARIES

Submitted by

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ABSTRACT

RESTORING ISLAND BIRDS AND SEED DISPERSAL IN NEW ZEALAND'S FENCED MAINLAND ISLAND SANCTUARIES

Island ecosystems are global biodiversity hotspots, but many island species face population declines and extinction. These losses are mainly driven by invasive mammals that consume or compete with native animals and degrade their habitats. The decline of island animal populations may also impact ecosystem processes that depend on them, e.g. seed dispersal, pollination, and nutrient cycling. The island nation of New Zealand has pioneered a unique solution – fenced mainland island sanctuaries – which exclude invasive mammals from natural habitats and provide opportunities to restore native birds and other wildlife. Yet, critics question whether sanctuaries, which are costly and require continuous maintenance, effectively conserve birds and ecosystems, given minimal research on sanctuary project outcomes. I assessed if sanctuaries are an effective conservation tool for restoring birds and seed dispersal in New Zealand. I compared bird population densities and bird-mediated seed dispersal in three fenced sanctuary sites to three paired reference sites (with minimal mammal control). From January-April 2016 and 2017, I set seed traps to measure dispersed-seed abundance, conducted focal tree observations to determine foraging rates for six tree species, and used distance sampling-based point counts to survey birds at randomly placed sampling locations within each site. I supplemented my bird surveys with a paired acoustic sampling method that uses acoustic recorders to increase survey sample size when estimating population densities with distance sampling. I tested the effectiveness of paired acoustic sampling for monitoring New Zealand forest bird populations by assessing whether density estimates from acoustic data were biased relative to densities estimated from human point counts, and by assessing whether the paired acoustic sampling method corrects bias from acoustic data, when present. Thus, the objectives of this dissertation were to assess 1) whether audio data could be used to estimate population densities for New Zealand forest birds (Chapter 1), 2) whether fenced mainland island sanctuaries increase the density of native or introduced bird species relative to unprotected areas in New Zealand (Chapter 2), and 3) whether sanctuaries enhance bird-mediated seed dispersal (foraging rates and dispersed-seed abundance) relative to unprotected areas (Chapter 3). I found that acoustic recorders underestimated bird population densities for four bird species but incorporating statistical offsets from the paired sampling method in generalized linear mixed models corrected the bias for all four species. Across both years, I found 0.27 to 9.00 more birds/ha on average for nine of twelve native bird species (including seven frugivores) in sanctuaries compared to unprotected sites, and no difference in mean population densities for three introduced bird species (two frugivores) and three biogeographically recent native species (one frugivore). Mean foraging rates and dispersed seed counts were also higher (0.1-0.6 more fruits consumed/observation period; 2-22 more seeds dispersed/plot) in sanctuary sites for several native tree species. Frugivore density, or both frugivore density and fruit abundance were significant positive predictors of foraging rates and dispersed seed counts for most tree species. Finally, native bird densities were correlated with foraging rates and dispersed seed counts for most tree species, but introduced bird densities were rarely correlated with foraging or dispersed seed counts. Thus, higher densities of native frugivorous birds in sanctuary sites appears to have resulted in increased fruit removal and dispersed seed counts for several native tree species. My study is one of the first to demonstrate that fenced mainland island sanctuaries, which require a substantial investment of conservation funds, are meeting ecological objectives. Furthermore, I demonstrate that paired acoustic sampling can be used to produce unbiased population density estimates from acoustic data, relative to human point counts, which holds great promise for increasing the scope and efficiency of bird population monitoring in New Zealand. I show that sanctuaries increase bird population densities for several native bird species and have no effect on introduced and biogeographically recent native species. These findings support predictions made over a decade ago on the potential ‘winners’ and ‘losers’ of mammal eradication and offer evidence that fenced sanctuaries effectively conserve New Zealand’s native bird populations. By increasing bird densities and seed dispersal, fenced mainland island sanctuaries could be a viable tool for restoring other island and mainland ecosystems under threat from invasive mammals.

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PREFACE

This dissertation is organized around three chapters that are each intended to be published as articles in peer-reviewed journals. Formatting, organization, and terms may therefore differ among chapters. Each article will have one or more co-authors, so I use the pronoun ‘we’ throughout the dissertation. Chapter one was recently submitted for publication in the *New Zealand Journal of Ecology*. Chapter two will be submitted to *Conservation Biology* or a similar conservation journal. Chapter three is intended for *Science*, *PNAS*, or a similar short-format high-impact journal, and is therefore written in the format used by these journals (i.e. Merged Introduction, Results, and Discussion; Methods presented at the end of the article). Chapter titles and authors are listed below.

Chapter 1. **Using paired acoustic sampling to enhance population monitoring of New Zealand’s forest birds.**

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Chapter 2. **Fenced mainland island sanctuaries: an effective tool for bird conservation in New Zealand.**

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Chapter 3. **More birds and seeds dispersed in a novel network of fenced ‘mainland island’ sanctuaries.**

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CHAPTER ONE

USING PAIRED ACOUSTIC SAMPLING TO ENHANCE POPULATION MONITORING OF NEW ZEALAND'S FOREST BIRDS

Introduction

Sustained monitoring is critical for evaluating how animal populations respond to land use change and conservation interventions, especially when monitoring is designed to address specific *a priori* hypotheses (Bart 2005, Nichols and Williams 2006, MacLeod et al. 2012). In New Zealand, management actions frequently focus on reducing the abundance of invasive mammals (e.g. ship rats *Rattus rattus*, Norway rats *R. norvegicus* mustelids *Mustela spp.*, possums *Trichosurus vulpecula*) (Parkes and Murphy 2003, Towns et al. 2013). These actions are meant, in part, to reduce mammal predation on native forest birds and browsing-related impacts to their habitats (Towns et al. 2013). Although scientists are proposing monitoring programs to provide robust measures of population changes across multiple species in response to invasive mammal removal or other conservation management actions (MacLeod et al. 2012), to our knowledge, a robust multi-species national monitoring program has not yet been realized. Citizen science-based data repositories (e.g. New Zealand eBird) provide valuable and verified monitoring data useful for addressing questions about species distributions and occurrence patterns, but these data do not account for imperfect detection or differences in observer effort, and thus cannot be used to provide measures of absolute abundance or population densities, or relate changes in these population parameters to conservation management actions (MacLeod et al. 2012, Scofield et al. 2012). In some cases, indices that do not account for detection bias can generate spurious conclusions that may have serious consequences for species management (Greene and Pryde 2012). Further, citizen science monitoring programs often over-sample accessible areas near urban centers and under-sample remote areas with challenging terrain, which limits the value of these data for assessing nation-wide population trends (MacLeod et al. 2012).

The lack of robust monitoring may limit the ability of conservation managers and researchers to explore how native bird populations respond to predator control across different temporal and landscape scales, predator management levels, and ecological contexts. Consistent bird monitoring programs with well-defined objectives may provide key insights to guide future predator management actions and can facilitate adaptive conservation management of mammalian predators (Innes et al. 1999, Nichols and Williams 2006, Macleod et al. 2012). Furthermore, monitoring has historically been limited to rare and endangered species in New Zealand (Innes et al. 2010); yet, common species may play important roles in maintaining ecosystem functions and the public is often interested in the population status of more common and familiar birds (MacLeod et al. 2012). Thus, monitoring of common species should also be prioritized (MacLeod et al. 2012).

Distance sampling (Buckland et al. 2001) and time removal sampling (Farnsworth et al. 2002, Sólymos et al. 2013) methods are frequently used to estimate bird population densities and monitor changes in bird populations, but these methods require observers to collect additional information during bird counts (i.e. distance between the observer and the detected bird or time-of-detection) that require extra training for observers to meet analytical assumptions. Distance sampling analysis also demands numerous observations per species to allow proper estimation of the detection function (Buckland et al. 2001). The need for reliable distance and/or time-of-detection measurements and abundant data can limit the usefulness of these techniques for monitoring bird populations in New Zealand, where the terrain is often steep, thickly vegetated, and difficult to traverse (MacLeod et al. 2012, Allen et al. 2013). Thus, sending trained observers to multiple points distributed across the landscape, or to the same points over repeated visits to acquire sufficient survey data for distance or removal sampling may be costly or impractical. Furthermore, some bird species that are present, but difficult to detect using standard point counts, e.g. nocturnal residents, human-sensitive species, and migrants, may not be recorded by transient observers (Steer 2010, Van Wilgenburg et al. 2017). Alternative population monitoring solutions that address these challenges are needed to facilitate a robust population monitoring program in New Zealand.

A potential tool for increasing the efficiency, and spatial and temporal coverage of bird population monitoring efforts across New Zealand is the use of autonomous recording units (ARUs). ARUs have been used in New Zealand and elsewhere to supplement data collected by human observers (Haselmayer and Quinn 2000, Hobson et al. 2002, Francis et al. 2009, Steer 2010, Klingbeil and Willig 2015, Van Wilgenburg et al. 2017). ARUs may provide a cost-effective population monitoring solution because they only require humans to visit a location once to deploy the ARU and once to retrieve it (Yip et al. 2017). The ARU can be programmed to collect repeated surveys following almost any protocol, and thus can increase the quantity of data collected in an area substantially with relatively little extra field effort (Steer 2010, Van Wilgenburg et al. 2017). Acoustic recording files also provide a permanent record that can be verified by multiple experts, facilitating accurate and reproducible research (Steer 2010). Lastly, software is available to aid in bird call identification (e.g. Raven Pro, Bioacoustics Research Program 2014) and advances in machine learning will soon enable accurate automated identification of bird calls from audio recordings (Brandes et al. 2008, Acevedo et al. 2009, Digby et al. 2013, Stowell and Plumbley 2014).

Most detections of forest birds in point count surveys are auditory (Haselmayer and Quinn 2000, Hutto and Stutzman 2009), so it is reasonable to assume that the data collected using ARUs and human-based surveys would be comparable in these habitats. In fact, point count data collected by ARUs and human observers has frequently produced comparable abundance and diversity estimates (Hobson et al. 2002, Blumstein et al. 2011, Venier et al. 2012, Klingbeil and Willig 2015). However, these two approaches do not always produce similar outcomes (Hutto and Stutzman 2009, Venier et al. 2012), and the efficacy of ARUs has rarely been evaluated for New Zealand birds (MacLeod et al. 2012 - but see Steer 2010 and Digby et al. 2013). A potential shortcoming of using ARUs is that biases in detection of song cues between human observers and ARU-based point counts may occur due to differences in the detection radius for each method, which could lead to biased abundance estimates if not corrected for (Van Wilgenburg et al. 2017).

A novel study design and analytical approach was recently developed to allow ARU data to be calibrated with human point count data to estimate bird densities/abundance from both types of surveys, while accounting for imperfect detection and species availability (Van Wilgenburg et al. 2017). By conducting synchronous point count and ARU surveys, researchers can estimate statistical offsets that account for the differences in detection radius between human observers and ARUs when estimating population densities (Solymos et al. 2013, Van Wilgenburg et al. 2017). There is potential for integration of paired ARU sampling with established citizen-science monitoring programs (e.g. eBird https://ebird.org/newzealand/home, and The Cacophony Project https://cacophony.org.nz/). Scientists or trained citizen scientists could conduct paired ARU and human observer sampling across different regions that can be used to correct acoustic data from citizen science repositories.

To evaluate the potential for ARUs to be used to improve bird population monitoring in New Zealand, we conducted a field test with the following objectives: 1) to assess whether human point count surveys and ARU-based surveys produced similar density estimates for multiple New Zealand forest bird species, and 2) to test whether the sampling framework of Van Wilgenburg et al. (2017) removes bias in estimated densities between the two approaches, when it occurs. We hypothesized that ARU-based surveys would underestimate forest bird densities relative to human point counts because the detection radius for ARUs is smaller than for human point counts for other forest bird species (Van Wilgenburg et al. 2017, Yip et al. 2017). We further hypothesized that the paired acoustic sampling approach (Van Wilgenburg et al. 2017) would correct ARU underestimation of densities, when it occurs.

Materials and Methods

Study Area

Our study was conducted at six sites on the North Island of New Zealand, including two sites in each of Auckland, Waikato, and Taranaki regions (Figure 1.1), which ranged in size from approximately 100 ha to 3300 ha, and included three fenced mainland island sanctuaries (Tawharanui Regional Park 36°22’18” S, 174°50’33” E, Maungatautari Ecological Reserve 38°02’58” S, 175°33’36” E, and Rotokare Scenic Reserve 39°27’14” S, 174°24’35” E), and three forest patches with minimal predator control (McElroy Scenic Reserve 36°27’32” S, 174°41’32” E, Te Tapui Scenic Reserve 37°48’38” S, 175°37’23” E, and Tarata Conservation Area 39°10’05” S, 174°21’24” E). We included fenced sanctuary sites in our study design to obtain data for rare species, i.e. North Island Robin *Petroica longipes*, North Island Saddleback *Philesturnus rufusate*, Whitehead *Mohoua albicilla*.

Figure 1. The six study areas (black triangles) where we conducted bird point counts to assess the effectiveness of autonomous recording units (ARUs) relative to human observers for estimating bird densities in New Zealand. Study areas: Tawharanui Regional Park (1), McElroy Scenic Reserve (2), Te Tapui Scenic Reserve (3), Maungatautari Ecological Reserve (4), Tarata Conservation Area (5), and Rotokare Scenic Reserve (6).

Forest cover was dominated by manuka (*Leptospermum scoparium*) mixed with other indigenous trees in Tawharanui Regional Park and McElroy Scenic Reserve, and Tawa (*Beilschmiedia tawa*)-Rimu (*Dacrydium cupressinum*) mixed indigenous forest in Maungatautari Ecological Reserve, Te Tapui Scenic Reserve, Tarata Conservation Area, and Rotokare Scenic Reserve. Median annual total rainfall ranged from 1200 mm to 1800 mm, median annual mean temperature ranged from 13°C to 16°C (rainfall and temperature from National Institute of Water and Atmospheric Research 1981-2010 data), and mean site elevation ranges from 44m to 442m (Appendix 1.1).

Bird surveys

Surveys were conducted from January through April 2017 at 280 point count stations. Points were established at random locations > 200m apart (MacLeod et al. 2012, Allen et al. 2013) along randomly-selected pest monitoring lines (fenced sanctuary sites) or along randomly-placed transects (non-sanctuary sites). We revisited each sampling point an average of 2.99 (+/- 0.17 SE; range 2-11) times over the four-month sampling period for a total of 589 surveys. Surveys were conducted between 15 minutes and 5 hours after sunrise by one trained observer (SB). However, paired acoustic sampling can be used with data collected by multiple observers if the same person also transcribes the audio (Van Wilgenburg et al. 2017). The observer collected distance data following point transect distance sampling protocol (Buckland et al. 2001) and time-of-detection data following time removal sampling protocol (Farnsworth et al. 2002, Sólymos et al. 2013). Specifically, the observer recorded exact distances to detected birds using a rangefinder and recorded the minute interval of initial detection for each individual bird observation.

Before starting each point count, the observer placed an Olympus (Olympus Corporation, Center Valley, PA) DM-620 digital voice recorder with a built-in three microphone system in a quiet location approximately five meters away from the point location to avoid impacts to recording quality from noises made by observer movement. ARU settings were: MP3 file format at 320 kbps, all three microphones at high sensitivity, low cut filter off, and all other recording options set to defaults. We ran a pilot study in early 2016 to determine optimal ARU settings necessary to retain audio quality while minimizing memory requirements. We were able to detect the same individual birds in audio from an MP3 file format at 320 kbps as we could using a higher-quality uncompressed PCM file format (48 kHz -16 bit), so we chose to use the lower quality setting to reduce file size. The recorder was placed in a small plastic container to protect it from rainfall and moisture. The observer then started the audio recording and walked to the established point to immediately begin the point count survey. After the 5-min bird survey, the observer stopped the audio recordings.

Audio transcription

ARU recordings were transcribed by the same observer (SB), who listened to the audio and recorded detected species after the field season without access to field data, as recommended by Van Wilgenburg et al. (2017). We did not transcribe audio files with high sound interference (noisy) – i.e. when bird calls could not be heard well over background wind or other noise. Excluding noisy audio files reduced our dataset from 589 to 352 paired surveys. We chose to exclude noisy audio files from our analysis because they provided less data per effort, but they can be included if the transcriber incorporates a covariate to account for variation that arises from background noise, e.g. a categorical classification or direct measure of background noise (Van Wilgenburg et al. 2017). For each audio detection of individuals, the transcriber would record the species and exact time of detection. The transcriber could replay audio segments to confirm identifications. Times for both human and audio count data were later converted to three time intervals (0-2min, 2-4min, and 4-5min) for the time removal analysis (Farnsworth et al. 2002). We used Raven Software (Raven Lite 2.0.0, Bioacoustics Research Program 2014) to help distinguish cues made by different individuals of the same species. Birds of the same species singing at the same kilohertz (kHz) range and intensity were considered the same individual and thus ‘removed’ from being further detected.

Analysis Summary

To evaluate the efficacy of using ARUs for monitoring birds in New Zealand, we followed the framework of Van Wilgenburg et al. (2017) to generate maximum likelihood δ offsets that represent the relationship between ARU and human observer bird counts. We used δ estimates to assess bias in bird counts and density estimates derived from ARU data relative to human point count data, and we validated our findings using repeated random subsampling (Van Wilgenburg et al. 2017). In the section below, we provide a brief overview of the theoretical background of the paired sampling method. In the following section, we describe how we applied the method to assess ARU to human observer bias in New Zealand while noting any modifications we made.

Theoretical Background

The paired acoustic sampling approach (Van Wilgenburg et al. 2017) requires observers to conduct simultaneous audio and human point counts and collect time-of-detection and distance data during the human point counts. This method assumes that the population present in a surveyed area for a given species is equal for both the human observer and the audio recorder and that both are exposed to the same acoustic signals. Thus, differences between human and

ARU counts should arise chiefly from differences in the area sampled by the two methods (Van Wilgenburg et al. 2017).

Paired acoustic sampling allows biologists to produce population density or abundance estimates that incorporate two components of the detection process: 1) the probability that a bird in the survey area gives a visual or audio cue that is available to be detected (probability of availability, p), and 2) the probability that a bird was detected, given it was available for detection (probability of perceptibility, q) (Alldredge et al. 2007, Nichols et al. 2009, Van Wilgenburg et al. 2017). Availability (p) is estimated from the human point count data using removal or time-of-detection methods, and it is assumed that p will be equivalent for ARU count data (Farnsworth et al. 2002, Alldregde et al. 2007, Sólymos et al. 2013). Perceptibility (q) is estimated from the human point count data using distance sampling methods (Buckland et al. 2001) and modeled with a conditional maximum likelihood approach that accounts for differences in the area sampled, or effective detection radius (EDR), between human point counts and ARUs (Van Wilgenburg et al. 2017).

See Van Wilgenburg et al. (2017) for the complete theory but briefly, the expected value of a count from human observer data is represented as:

$$E[Y_H] = Np_{tj}q_{rk} \quad (1)$$

where Y_H is the count, N is the species' abundance, p_{tj} is the probability of species' availability given presence during the cumulative duration of the count (tj where t is total time and $j = 1 \ldots J$ time intervals), and q_{rk} is the probability a bird is detected in point count radius r ($k = 1 \ldots K$ distance intervals), given availability. This can be rewritten when assuming perfect perceptibility ($q = 1$) within the effective detection radius to:

$$E[Y_H] = Np_{tj}q_{rk} = DA_Hp_H \quad (2)$$

where D is the species' density at the point, and A_H is the area sampled in the human point counts, which can be estimated using distance sampling methods as $\hat{A}_H = \pi\hat{\tau}_H^2$, where τ = effective detection radius. Assuming equal density ($D_H = D_A = D$) and equal availability ($p_H = p_A = p$) among survey methods, and assuming perfect perceptibility ($q = 1$) within the effective detection radius, we can take the mean of the expected ARU to human observer counts to represent the relationship between the areas sampled between the two methods:

$$\frac{E[Y_A]}{E[Y_H]} = \frac{D\hat{A}_A p}{D\hat{A}_H p} = \frac{\pi\hat{\tau}_A^2}{\pi\hat{\tau}_H^2} = \frac{\hat{\tau}_A^2}{\hat{\tau}_H^2} \text{ (3)}$$

If we set $\delta = \frac{\hat{\tau}_A}{\hat{\tau}_H}$ then $\hat{\tau}_A = \delta\hat{\tau}_H$ and $\hat{\tau}_A^2 = \delta^2\tau_H^2$, so we could rewrite equation 3 as:

$$\frac{E[Y_A]}{E[Y_H]} = \frac{\delta^2\hat{\tau}_H^2}{\hat{\tau}_H^2} = \delta^2 \text{ (4)}$$

which is the squared scaling constant that relates the effective detection radius of the human count data to the unknown effective detection radius of the ARU. The δ^2 estimate can be derived as above, or as a maximum likelihood estimate that accounts for differences in sampling strategies, which is calculated by back-transforming a 'Survey Type' coefficient ($\delta^2 = \exp(\beta)$) in a Poisson or negative binomial regression model (Van Wilgenburg et al. 2017). Here 'Survey Type' is a fixed effect for ARU or Human surveys, with Human as the reference category, and $\delta^2 = \exp(\beta)$ represents the ratio of bird counts for a species between ARUs and human observers.

The δ^2 estimate is then included as a statistical offset in Poisson or negative binomial generalized linear mixed effects models (GLMMs) to model count data from both the human point counts and audio counts, where δ^2 accounts for the differences in the effective detection radius between both survey methods (Van Wilgenburg et al. 2017). The GLMM models also incorporate a random effect for the point transect and a statistical offset that accounts for imperfect detection across the different survey types through a correction factor ($C = \pi\hat{\tau}_H^2 p_H$), where τ and p are estimated from the human observer data using distance sampling and time removal sampling, respectively (Sólymos et al. 2013, Van Wilgenburg et al. 2017). The δ offset is fit with an indicator function (I_A) in the GLMM models that takes the value of zero for human observer data and a value of one for ARU data. Thus, the mean count for a point location *i* with the correction factor *C* and squared scaling constant δ is written as:

$$\log(\lambda_i) = \log(D_i) + \log(C_i) + I_A \log(\delta^2) \quad (5)$$

Data Analysis

We followed the approach described above and in Van Wilgenburg et al. (2017) to conduct our analyses for multiple forest bird species (see Appendix 1.2 for a list of species and scientific names), excluding those with less than 20 detections and those commonly detected as flyovers (e.g. New Zealand falcon *Falco novaeseelandiae*). We fit count removal models using the 'detect' package (Sólymos et al. 2016) in R (R Development Core Team 2008) with a 'Survey Type' factor to estimate availability (p) and assess differences in p between ARU and human point count data. We excluded species that did not meet the $p_H = p_A$ assumption (i.e. if the 95% confidence intervals between p_H and p_A did not overlap) from further analyses. We used p estimates from the remaining species' models to calculate the correction factor, *C*.

We used program Distance (Thomas et al. 2010) to estimate τ. Unlike Van Wilgenburg et al. (2017), we did not bin exact distance measurements into distance intervals. We fit models with the following key detection functions and series expansions: a half normal function with a hermite expansion, a hazard rate function with a simple polynomial expansion, and a uniform function with a cosine expansion. Models also included a survey effort correction to account for repeated visits to plots. Prior to analysis, we viewed detection function histograms and truncated data to visually identified distances when truncation improved model fit (i.e. increased the *p*-

value in Kolmogorov–Smirnov goodness-of-fit tests) over untruncated models. We used Akaike's Information Criterion with a small sample size correction (AICc) to identify the most parsimonious model (Burnham and Anderson 2002) and used the τ estimate from this model in the correction factor (C) calculation.

We used repeated random subsampling to validate the models and evaluate bias in density estimates, as in Van Wilgenburg et al. (2017). We randomly selected 70% of the point count locations over 50 iterations and used these subsamples to estimate δ^2 and 95% confidence intervals across the replicates using the GLMM modeling approach described above, where $\delta^2 = \exp(\beta)$. These δ^2 estimates were used in the same iteration with the remaining 30% data subset to fit models for the human observer and ARU data that included a statistical offset with both C and δ^2 incorporated. We also used the 30% validation data subsampled over 50 replicates to calculate δ^2 as an empirical ratio of mean bird count totals from ARU surveys to mean count totals from human surveys. We compared δ estimates and 95% confidence intervals for δ produced from maximum likelihood estimates using the full dataset to those produced with the 70% calibration data and to the empirical estimates produced with the 30% validation data subsample.

We also used the 30% subset validation data to evaluate bias in density estimates derived from ARUs vs. estimates derived from human point counts. Bias was calculated by subtracting predicted mean densities from human observer models from ARU data predicted mean densities ($\widehat{D}_A - \widehat{D}_H$). This was done for models that included a statistical offset for C only (i.e. equation 5 when I_A = zero), and for models that included a statistical offset with both C and δ^2 (i.e. equation 5 when I_A = one), where $\delta^2 = \exp(\beta)$ estimated from models fit to the 70% calibration data during the same iteration. The bias between ARU and human count densities for the models with the offset for C only was compared to the bias for the models with an offset for C and δ.

We also evaluated whether models with a 'Survey Type' effect were supported over null models for all species using AIC model selection to select the most parsimonious models (ΔAIC < 2.0; Burnham and Anderson 2002). The GLMM modeling approach described above can be adapted to include covariate effects (e.g. habitat type, background noise levels), and their relative importance can be assessed using AIC model selection (Van Wilgenburg et al. 2017), but this was not done in our study because counts were all conducted in indigenous forest habitat and only audio data with low background noise was used in our analysis.

Results

We detected 29 species across all sites (Appendix 1.2), of which 13 species met our selection criteria including the Australasian Magpie *Gymnorhina tibicen*, Bellbird *Anthornis melanura*, Chaffinch *Fringilla coelebs*, Common Myna *Acridotheres tristis*, Grey Warbler *Gerygone igata*, Kereru *Hemiphaga novaeseelandiae*, New Zealand Fantail *Rhipidura fuliginosa*, North Island Robin *Petroica longipes*, North Island Saddleback *Philesturnus rufusater*, Silvereye *Zosterops lateralis*, Tomtit *Petroica macrocephala*, Tui *Prosthemadera novaeseelandiae*, and Whitehead *Mohoua albicilla*. All species met the assumption of equal availability, (95% confidence intervals overlapped for p_H and p_A estimates), however two species, the Tomtit and Tui, had confidence intervals that only slightly overlapped for ARU and human observer estimates (Table 1.1). Removal model estimates of availability between human and ARU count data were highly correlated (Pearson's $r = 0.84$, $p = 0.0003$) across all species.

Table 1.1**.** Probability of availability estimates from simultaneous point counts conducted by autonomous recording units (ARUs) (p_A) and human observers (p_H) for 13 bird species detected across six native forest sites in 2017 on the North Island of New Zealand. Availability (p) was estimated using time removal methods (Farnsworth et al. 2002, Sólymos et al. 2013, Van Wilgenburg et al. 2017).

	LCL	p_H	**UCL**	**LCL**	p_A	**UCL**
Bellbird	0.861	0.923	0.964	0.873	0.934	0.972
Chaffinch	0.422	0.771	0.981	0.667	0.852	0.964

Fantail	0.835	0.915	0.966	0.909	0.954	0.981
Grey Warbler	0.779	0.868	0.933	0.737	0.837	0.915
Kereru	0.001	0.147	1.000	0.165	0.506	0.936
Magpie	0.819	0.922	0.978	0.747	0.879	0.961
Myna	0.607	0.868	0.987	0.868	0.968	0.997
N. Island Robin	0.536	0.788	0.956	0.715	0.887	0.977
N. Island Saddleback	0.527	0.766	0.940	0.717	0.854	0.947
Silvereye	0.320	0.509	0.732	0.477	0.638	0.796
Tomtit	0.663	0.820	0.933	0.903	0.948	0.977
Tui	0.730	0.817	0.891	0.890	0.929	0.958
Whitehead	0.610	0.839	0.971	0.360	0.672	0.938

The effective detection radius, τ, from the human observer data ranged from 16 to 85m (Appendix 1.3), and the scaling constant δ (a measure of the ratio of τ from ARU bird counts to human bird counts derived from the maximum likelihood coefficients in GLMMs) ranged from 0.814 to 1.247 (median = 0.954) (Figure 1.2, Appendix 1.4). Calibration δ estimates from the GLMMs fit to 70% of the data over 50 iterations were similar to the maximum likelihood estimates (range = 0.793 to 1.239; median = 0.943) (Appendix 1.4). A δ value of 1.0 indicates that ARU count data and human count data are the same, and values < 1.0 indicate that fewer birds were detected during ARUs than during human surveys. Most species' maximum likelihood δ estimates were just below 1.0, suggesting that they were detected slightly less during ARU surveys than human point count surveys (Figure 1.2, Appendix 1.4). However, the Bellbird, Kereru, and Silvereye were detected approximately 20% less in ARU recordings and the Tomtit and Chaffinch were detected 12% and 25% more in ARU recordings, respectively (Figure 1.2, Appendix 1.4). The confidence intervals from the maximum likelihood δ estimates overlapped 1.0 for nine of thirteen species (excluding the Bellbird, Kereru, Silvereye, or Tui) (Figure 1.2, Appendix 1.4). The empirical ratio δ ranged from 0.827 to 1.205 (median = 1.020) (Figure 1.2, Appendix 1.4). The confidence intervals around the maximum likelihood δ estimates overlapped with the confidence intervals for the empirical ratio δ estimates for all species except the Grey Warbler and the Silvereye (Appendix 1.4).

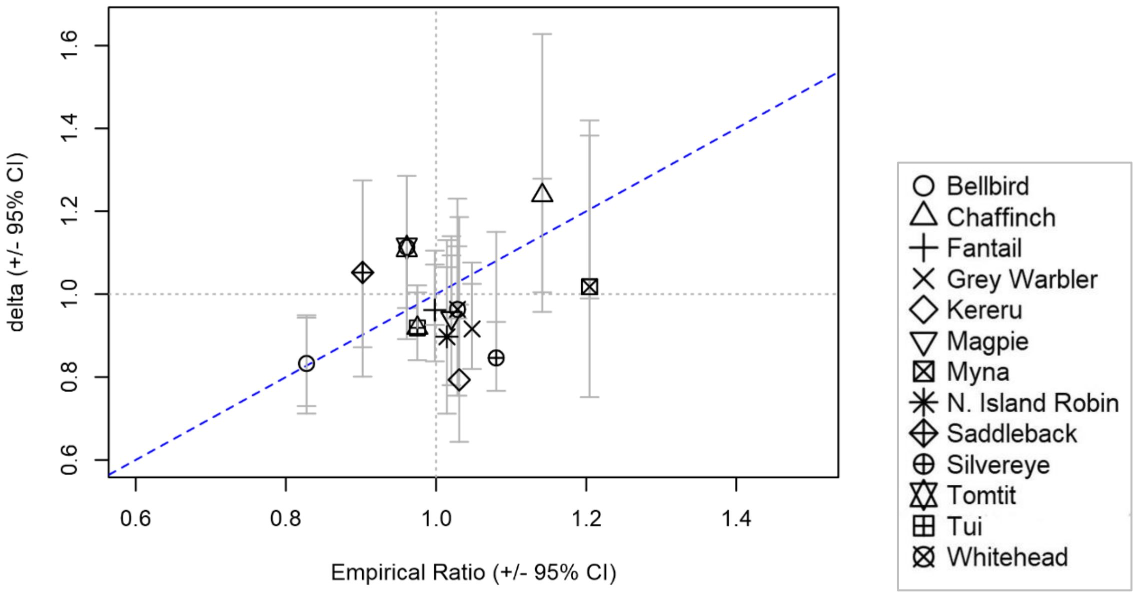

Figure 1.2. Comparison of maximum likelihood δ estimates (a measure of bias between ARU and human survey bird counts) produced using generalised linear mixed-effects models (GLMM; y-axis) and empirically-estimated δ values (x-axis). GLMM estimates are derived from Poisson model regression coefficients as $\delta = \sqrt{\exp(\beta)}$ from models fit to 70% of the data. Empirical estimates were produced using the withheld 30% validation data by taking the ratio of mean bird count totals from ARU surveys to mean count totals from human surveys. For both GLMM and empirical approaches, values < 1.0 indicate that fewer birds were detected using ARUs than during human surveys.

Models that included δ and C statistical offsets reduced bias in density estimates for 10 of 13 species compared to models that included the C statistical offset from the human observer data only (Figure 1.3). Three species, the Kereru, Silvereye, and Tui, had negatively biased density estimates (95% confidence intervals around bias estimates did not overlap zero) when δ offsets were not incorporated and one species, the Chaffinch, had a positively biased density estimate without δ offsets. Density estimates for all species were unbiased (95% confidence intervals overlapped zero) when δ offsets were incorporated (Figure 1.3).

Models with the 'Survey Type' effect were supported over null models for seven of thirteen species, but both null models and models with the 'Survey Type' effect had ΔAICc < 2.0 for all but the Bellbird, Kereru, Silvereye, and Tui (Table 1.2), suggesting that ARU data may produce biased estimates relative to human observer data for these species.

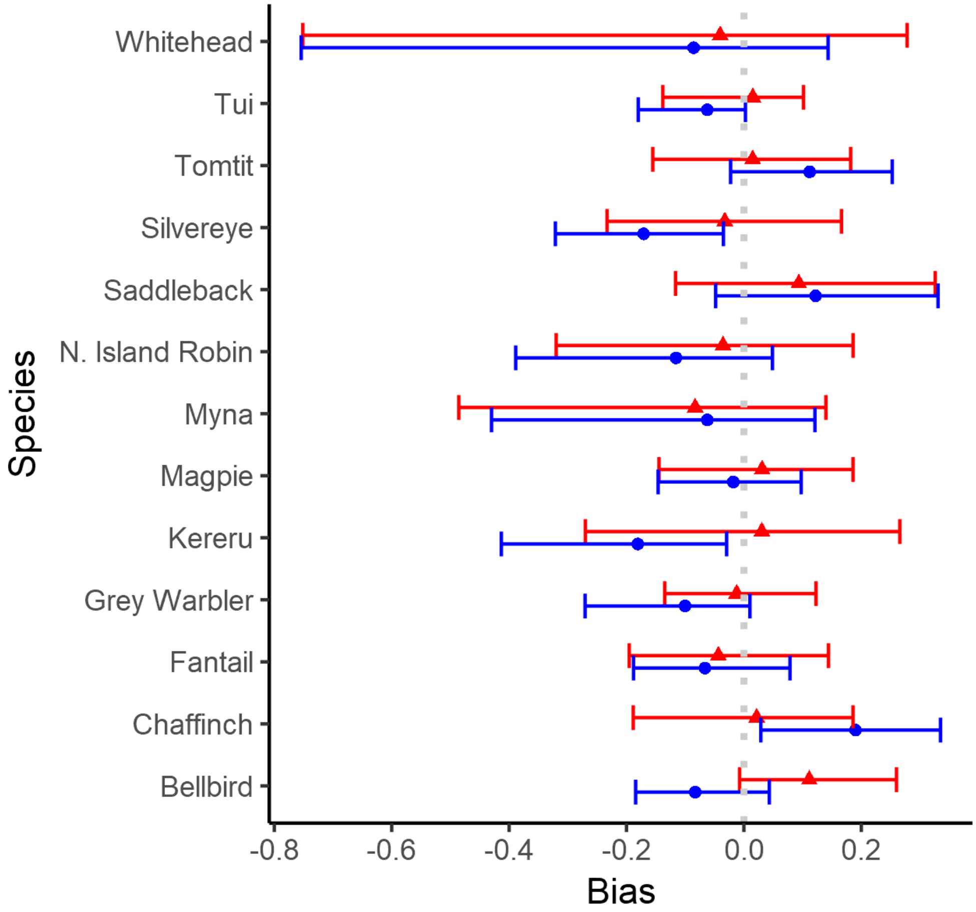

Figure 1.3. Bias in density estimates (birds/ha +/- 95% confidence intervals) from ARUs relative to estimates from human point counts for models with the offset for C only (blue circles) compared to models with an offset for C and δ (red triangles), where $C = \pi\hat{\tau}_H^2 p_H$ or area sampled $(\pi\hat{\tau}_H^2)$*probability of availability (p_H) from human observer data, and $\delta = \sqrt{\exp(\beta)}$ from GLMM models fit to 70% of the data over 50 iterations. The C constant is a correction for two components of detection probability, i.e. the probability that a bird sings or is available for detection, and the probability a bird was detected if available. The δ constant corrects for differences in the area sampled between ARUs and human observers. Bias was calculated by subtracting predicted mean densities from human observer models from ARU model mean densities $(\widehat{D}_A - \widehat{D}_H)$ for both offset strategies using the withheld 30% validation data.

Table 1.2. Model selection results (ΔAICc values of model rank relative to the model with the lowest AICc value) for Poisson generalised linear mixed effects model comparisons between null models (random effect for point transect only) and models with both a point transect random effect and a 'Survey Type' fixed effect to account for differences between bird surveys conducted by autonomous recording units (ARUs) and human observers.

Species	**Null**	**Survey Type**
Bellbird	7.575	0.000
Chaffinch	1.808	0.000
Fantail	0.000	1.701
Grey Warbler	1.000	0.000
Kereru	3.253	0.000
Magpie	0.000	1.656
Myna	0.000	1.975
N. Island Robin	0.000	0.532
N. Island Saddleback	0.000	1.713
Silvereye	11.579	0.000
Tomtit	1.411	0.000
Tui	2.599	0.000
Whitehead	0.000	1.902

Discussion

ARUs may offer a promising tool for increasing the efficiency of forest bird population monitoring in New Zealand. Densities produced by ARU counts and human observer counts were generally equivalent for most species, and when present, ARU bias can be corrected for using the paired acoustic sampling method (Van Wilgenburg et al. 2017). Results partially supported our hypothesis that ARU bird counts would be lower relative to human observer counts, as the δ estimate (representing the ratio of ARU counts to human observer counts) from both maximum likelihood and empirical approaches was slightly below 1.0 (Figure 1.2, Appendix 1.4), and the bias in density estimates between ARU and human observer counts was negative for most species (Figure 1.3). However, 95% confidence intervals around δ overlapped 1.0 for 9 of 13 species (Figure 1.2, Appendix 1.4), 95% confidence intervals around density bias estimates overlapped zero for 9 of 13 species (Figure 1.3), and null models were supported by the data (ΔAICc < 2.0) for 9 of 13 species, suggesting that the bias in ARU bird count data is negligible for most species. This finding that ARUs and human counts produce similar results is consistent with several other studies that found comparable bird abundance, occupancy, or community composition between ARU and human observer counts (Hobson et al. 2002, Celis-Murillo et al. 2009, Blumstein et al. 2011, Digby et al. 2013, Van Wilgenburg et al. 2017).

Although ARU and human observer data were comparable for most species, ARUs may underrepresent densities for the Bellbird, Kereru, Silvereye, and Tui. Upper confidence limits for δ were < 1.0 and δ values ranged from 0.80 to 0.91 for these species (Figure 1.2, Appendix 1.4). Density estimates were negatively biased for all but the Bellbird (Figure 1.3), and null models were not supported in AIC model selection comparisons for all four species (Table 1.2). These lines of evidence suggest that ARU data may underestimate population densities of these species by approximately 10-20% if the bias is not accounted for. Yet, the upper confidence limit for the Tui δ estimate was just below 1.0 (UCL = 0.99), so bias in ARU counts for the Tui may be minimal.

Based on our knowledge of bird behaviour and our experience conducting field surveys, we can speculate why some species were detected less in ARU recordings than in human point counts. First, the Bellbird and Tui often produced short single-note calls from distances over 70m away. These distant calls were easily detected by the observer but were likely missed by the audio recorder. Second, the Kereru was generally detected by the observer upon hearing its strong wingbeats while flying, or by its low frequency (2-3kHz) coos, but these sounds were easily drowned out by even low background noise during point counts. The observer was able to see birds when flying, which seemed to compensate for missed sound cues. Without the added visual cues, sound cues from Kereru may be missed in acoustic recordings in all but the quietist situations, resulting in under-estimated densities, if uncorrected. The Silvereye also produces relatively low-frequency calls and songs (< 10kHz), but they call or sing with regularity which generally made them easy for the observer to detect in our study and in the audio recordings. However, they also frequently occurred in large flocks that were easy to count by visual observation but would be impossible to accurately count in an audio recording. Thus, we likely undercounted Silvereyes during the audio transcription process. Distance sampling can be adapted to accommodate species that frequently occur in clusters by including an estimate of cluster size (Buckland et al. 2001); however, we did not collect data to estimate cluster size and could not apply this technique. We recommend that observers collect data to estimate cluster size when Silvereye populations are being monitored with ARUs. Based on our findings and field observations, we speculate that ARUs may underestimate bird counts in the following conditions: 1) when species are frequently detected from far distances by single-note calls, 2) when species only produce low-frequency sounds, or 3) when species occur in clusters if information on cluster size is not included during distance sampling analysis.

Two species, the Tomtit and Chaffinch, had δ estimates above 1.0, suggesting that they were slightly more detectable in ARU recordings than in counts by human observers, but confidence intervals around δ slightly overlapped 1.0. We speculate that these species were more detectable in ARU recordings because transcribers can pause and rewind recordings, which may facilitate detection of species that are easily missed, e.g. those with short duration calls. Although the Tomtit and Chaffinch both have long duration songs, their calls are relatively short, and some calls may have been missed during human observer counts that were detected in audio recordings. Celis-Murillo et al. (2009) also found higher detection probability for some birds when comparing ARU data to field survey data, which suggests that paired acoustic sampling may improve detection in some cases. Another explanation for the positive bias in ARU recordings may relate to the consistency of bird calls – Steer (2010) indicated that species that call regularly could be overrepresented in audio recordings. The Chaffinch and Tomtit sometimes call repeatedly, but other species that call regularly (e.g. Silvereyes) were not overrepresented in the audio recordings during our study, so calling regularity may not explain the positive bias for these species. Furthermore, we carefully viewed spectrograms when listening to audio recordings to reduce the chance of double-counting an individual that calls regularly during the recording.

Inclusion of δ statistical offsets reduced bias in density point estimates from ARU recordings relative to human point counts for most species, including the Kereru, Silvereye, and Tui, which had δ estimates below 1.0 and negatively biased density estimates when models did not include δ. Importantly, confidence intervals around the density bias estimate overlapped zero when the δ offset was incorporated into GLMMs, which suggests that the paired acoustic sampling approach (Van Wilgenburg et al. 2017) can be used to produce unbiased density estimates relative to human point counts for many New Zealand forest birds. This strategy uses common Poisson GLM or GLMM models with ‘Survey Type’ effects to generate offsets that correct for potential biases from ARU-derived data. Given the relative ease of adding an audio recorder to existing bird count schemes, and the familiarity of the GLMM modeling procedure, this approach provides a promising opportunity for researchers and scientists to advance population monitoring nation-wide.

We emphasize, however, that ARUs should be considered a supplemental monitoring strategy to field-based data collection. If reliable population monitoring estimates are to be produced, researchers will need to regularly conduct paired counts to test the assumption of equal availability and validate the performance of these models over time and in different contexts. In particular, since we tested this approach in indigenous forest habitat, caution should be used when extrapolating our findings to different habitat types, as the acoustic environment may change in other habitats and impact the relationship between ARU counts and human observer counts for some species (Van Wilgenburg et al. 2017, Yip et al. 2017). We suggest, however, that this method warrants exploration and field testing in other habitat types and encourage inclusion of 'habitat' fixed effects into the GLMMs to account for habitat variation if multiple habitats are surveyed for a species, and the inclusion of 'observer' fixed effects when surveys are conducted by multiple observers.

It is also important to note that although the data collection component of this method requires minimal investment relative to regular point counts, transcription of audio recordings post-data collection requires an added time investment by skilled observers. However, advancements in machine learning technology may soon make automated detection of bird calls from acoustic datasets a cost-effective and reliable solution (Brandes et al. 2008, Acevedo et al. 2009, Digby et al. 2013, Stowell and Plumbley 2014).

We tested the paired acoustic sampling method with a relatively low-cost acoustic recording setup. We chose to use a basic, low-cost voice recorder without an added microphone as opposed to a professional bioacoustic monitoring setup (e.g. Song Meter SM4, Wildlife Acoustics, Inc., Maynard, MA, USA) because we wanted to test the application of the paired sampling method under a high cost efficiency scenario. There is a compromise in using our low-cost approach in terms of battery life and storage capacity, however. More expensive recorders have greater storage capacity and can record high-quality audio for longer time periods before internal batteries need to be replaced (Wildlife Acoustics 2018). Thus, our low-cost setup will require more frequent visitation by field workers to download data and change batteries than with professional setups, and these added costs need to be considered when selecting an appropriate acoustic monitoring scheme. Although biases may exist for different acoustic recording setups (Yip et al. 2017), paired acoustic sampling can remove these biases because it corrects for differences in detection probabilities between a given ARU and human observers (Van Wilgenburg et al. 2017).

Other methods are available to estimate bird densities from acoustic data, e.g. acoustic arrays (Dawson and Efford 2009, Mennill et al. 2012) and acoustic localisation (Collier et al. 2010), or to estimate the bias in density between ARU and human observers with experimental playbacks (Yip et al. 2017). Yet, these methods are logistically more challenging, costlier, and in the case of the playbacks, require extra assumptions to be made about a species' singing amplitude (Van Wilgenburg et al. 2017). Thus, the paired acoustic sampling approach can provide a cost-effective, relatively easy to implement alternative to other sampling strategies that correct biases in ARU data when estimating bird abundance or population densities. Our study and others have shown that ARUs can produce unbiased abundance and presence-absence data for many bird species in New Zealand and globally (Hobson et al. 2002, Celis-Murillo et al. 2009, Blumstein et al. 2011, Digby et al. 2013), and our study provides additional support that the paired sampling approach can be used to correct for ARU bias when present (Van Wilgenburg et al. 2017). Thus, we recommend increased use of ARUs for bird population monitoring programs in New Zealand and additional testing to refine our estimates and asses our findings in a variety of habitats and contexts.

ARUs offer promising new opportunities to expand research on bird conservation and ecology in New Zealand. Increased efficiency may allow bird surveys to be conducted at greater spatial and temporal scales, which could lead to, e.g., advances in our understanding of forest bird population responses to invasive mammal eradications, habitat fragmentation or loss, or changes in metapopulation dynamics. Paired acoustic sampling can also be used in a meta-analysis of historic point count data (Van Wilgenburg et al. 2017), which further highlights the potential for this method to be used to expand research opportunities and generate new insights for bird conservation and ecology in New Zealand.

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CHAPTER TWO

FENCED MAINLAND ISLAND SANCTUARIES: AN EFFECTIVE TOOL FOR BIRD CONSERVATION IN NEW ZEALAND

Introduction

Reversing biodiversity loss on islands is a priority for conservation science and practice (Jones et al. 2016, McCreless et al. 2016, Spatz et al. 2017). Islands are biodiversity hotspots - they contain over 20% of earth's terrestrial species but occupy only five percent of the earth's terrestrial surface (Kier et al. 2009, Spatz et al. 2017). Yet island species are also disproportionately susceptible to extinction. Over half of all extinct species and more than one-third of critically endangered species occur on islands (Tershy et al. 2015). Species are at risk due to greater specialization, smaller populations, and few defenses against invasive species, the principal driver of biodiversity loss and decline on islands (Holdaway 1989, Craig et al. 2000, Tershy et al. 2015, Innes et al. 2010, Spatz et al. 2017). Mammals have been deliberately and accidentally introduced to islands worldwide over the last millennium. These introductions began with global exploration and settlement in 1000-1200 AD, accelerated with European exploration in the 1700s, and have continued into the present with rapid growth in global trade and travel (Holdaway 1989, Craig et al. 2000). Because native species generally lack a shared evolutionary past with invaders, mammals can spread quickly, preying on ecologically naïve animals and degrading their habitats (Holdaway 1989, Craig et al. 2000, Innes et al. 2010).

More recently, invasive mammals have been successfully eradicated from many islands globally, leading to the recovery of several threatened populations (Jones et al. 2016). For example, 110 species (234 populations) of land birds have benefitted from invasive mammal eradications on islands, with potentially widespread but undocumented co-benefits for many other native biota (Jones et al. 2016, McCreless et al. 2016). Most successful eradications occurred on small islands (median island size = 0.63 km^2; DIISE 2015). Eradications on small islands are often successful because they occur at a manageable scale, the ocean limits reinvasion, and small islands frequently lack human populations, which minimizes accidental reintroductions (Craig et al. 2000, Glen et al. 2013). However, the number of small islands that are good candidates for invasive mammal eradication is finite, and these islands do not provide suitable habitat for all species susceptible to invasive mammals (Elliott et al. 2010a). Transferring the small island eradication model to large islands or mainland habitat islands has potential to magnify conservation impact. However, eradicating invasive species from such areas is costly and challenging, as mammal populations often rebound or reinvade (Glen et al. 2013).

Conservation organizations in New Zealand have developed a creative solution to this problem – a nation-wide network of fenced ‘mainland island’ sanctuaries (hereafter sanctuaries). These sanctuaries replicate the small island eradication model by excluding invasive mammals with predator-proof fencing. This approach allows ‘mainland islands’ to be established on large islands or continents inhabited by people with the aim of recovering threatened native bird populations (Day and MacGibbon 2007, Campbell-Hunt and Campbell-Hunt 2013, Scofield et al. 2011, Innes et al. 2012). Many of New Zealand’s native birds are absent from mainland forests, despite vast areas of native forest habitat remaining (Craig et al. 2000, Elliott et al. 2010b, Innes et al. 2010). Even common widespread native bird species occur at lower densities due to impacts from invasive mammals (Elliott et al. 2010b, Innes et al. 2010). Due to this loss and decline of common and threatened native bird populations, New Zealand’s forests are occupied by avian communities quite different from historic ones (Craig et al. 2000, Elliott et al. 2010b, Innes et al. 2010). Sanctuaries offer a promising tool for recovery and have become priority sites for bird reintroductions

Yet, sanctuaries have been subject to critique. They are extremely costly and labor-intensive to maintain, and it is unclear if they are a strategic conservation investment given the lack of empirical evidence on whether they effectively recover and sustain bird populations (Scofield et al. 2011). Although much evidence suggests that mammal eradication on small offshore or oceanic islands benefits native bird populations (Jones et al. 2016), few studies evaluate the effectiveness of sanctuaries for restoring entire bird communities to mainland areas (Scofield et al. 2011; but see Tanentzap and Lloyd 2017 and Miskelly 2018). Sanctuaries could fail to provide the same level of protection as small isolated islands. Most birds can fly outside the sanctuary boundaries into the surrounding habitats, where they may experience high predation. Furthermore, not all island bird populations are predicted to benefit from mammal eradication (Innes et al. 2002). Introduced species and biogeographically recent species (native birds that more recently diverged from Australian congeners, i.e. Grey Warbler *Gerygone igata* and New Zealand Fantail *Rhipidura fuliginosa*, or were recently self-introduced, i.e. Silvereye *Zosterops lateralis*'; Fleming,1979, Worthy et al. 2017) may decline after mammal eradications due to increased competition with native species (Innes et al. 2002, Innes et al. 2010, Miskelly 2018).

Because New Zealand is already serving as a model for fenced sanctuaries in other island and mainland systems (Burns et al. 2012), identifying whether sanctuaries are meeting conservation objectives, and characterizing which species benefit, is a priority for advancing conservation globally. To this aim, we compared bird densities in fenced 'mainland island' sanctuaries to paired unfenced sites with similar habitat on the North Island of New Zealand. We expected to find substantially higher densities of native species, especially globally threatened species, and lower densities of introduced and biogeographically recent native species in sanctuaries relative to reference sites (Innes et al. 2002).

Materials and Methods

Study Design

We selected three fenced sanctuary sites on the North Island, New Zealand. All invasive mammals (rats *Rattus* spp., possums *Trichosurus vulpecula*, mustelids *Mustela* spp., and domestic cats *Felis catus*), except for mice, have been eradicated from these sanctuaries. We paired each sanctuary site with a nearby reference site with similar flora but minimal mammal control (i.e. no mammal control at two sites and low-density possum control at one site every 2-4 years; Figure 2.1, Table 2.1). We compared bird densities in sanctuaries to reference sites instead of historic baselines because bird population data in sanctuaries prior to establishment are not available. We note that several bird species that have low tolerance to invasive mammal predation and are rare in most mainland forests have been translocated into sanctuaries, but most bird species are common to both sanctuary and reference sites without human intervention (Table 2.1). Sanctuaries were not disproportionally established in pristine forest habitat; Maungatautari is considered floristically poor (MacGibbon 2001), Rotokare encloses regenerating forest, and Tawharnui has a long history of timber harvesting (Murdoch 2008). Rather, these sanctuaries and paired sites encompass forests typical of their broader regions (MacGibbon 2001, Murdoch 2008).

Paired sanctuary and reference sites were within 25-40km of each other and reference sites were selected to be similar in dominant forest cover, area, elevation range, mean temperature, mean precipitation, land use history, and landscape context (Figure 2.1, Table 2.1). Landscape context was quantified at all sanctuary and reference sites by three metrics that described the landscape spatial pattern in a 20km buffer around each study site, including Patch Area (proportion covered by native forest), Shape Index (native forest fragmentation), and Euclidean Nearest Neighbor (distance to the nearest native forest patch) (Table 2.1, McGarigal et al. 2012). Using a geographic information system, we measured the size of each site as the area covered by indigenous forest, excluding pasture, water bodies, and other non-forest habitat.

Across all six study areas, we established 297 unique sampling points > 200m apart (MacLeod et al. 2012) along randomly-selected mammal monitoring lines (sanctuary sites) or along randomly-placed transects (reference sites). More sampling points were placed in the larger sites (Maungatautari and Te Tapui), but we increased the number of visits to small sites to balance the number of samples among sites (Table 2.1). We placed the maximum number of points possible in smaller sites given the 200m minimum spacing, but not in the two large sites, as their size made this untenable. Some points were placed along tracks in sanctuary and reference sites to increase survey efficiency, and we assessed whether this placement affected the detection process by modeling variation in detection probability as a function of whether the point was on or off a track in our analysis (see *Bird Population Density Analysis* section).

Bird surveys

Bird surveys were conducted from February-April in 2016 and 2017 as part of a larger study assessing bird-mediated seed dispersal, which peaks during these months. Each set of paired sites (sanctuary and reference) were surveyed every ten days such that all six sites were surveyed every month. We surveyed birds using distance sampling (Buckland et al. 2001) at 297 sampling points. We revisited each sampling point an average of 2.99 (+/- 0.17 SE; range 2-11) times on average across the four-month sampling period for a total of 761 surveys in 2016 and 823 surveys in 2017 (Table 2.1). Surveys were conducted between 30 minutes and five hours after sunrise by three trained observers. The observers collected distance data following point transect distance sampling protocol (Buckland et al. 2001) and time-of-detection data following time removal sampling protocol (Farnsworth et al. 2002, Sólymos et al. 2013). Specifically, the observer recorded horizontal distances to the point where each bird was first detected using a laser rangefinder and recorded the minute interval of initial detection for each individual bird observation. For birds that were not clearly seen but were heard, we measured the horizontal distance to the plant or tree in which the bird was first detected vocalizing. We did not conduct surveys during precipitation above a light drizzle or when winds were greater than 20kph. We recorded whether birds were detected by sight or sound and several covariates associated with the surveys including the observer, date of survey, visibility (percent sky visible at sampling point), track (0= off track, 1 = on track), percent cloud cover, precipitation (0 = none, 1= light drizzle), wind (0 < 1kph, 1 = 1-6kph, 2 = 6-12kph, 3 = 12-20kph), and survey time. We ignored flyovers unless we observed a bird taking flight from a sedentary position within close proximity of the sampling point.

Bird Population Density Analysis

We used distance sampling to estimate the probability of detecting an individual bird as a function of distance from the sampling point and used this detection probability to estimate bird population density, corrected for detection bias (Buckland et al. 2001), for fifteen different bird species (Appendix 2.1). We fit distance sampling models (Buckland et al. 2001) to ungrouped distance data for detected birds using program Distance (Thomas et al. 2010) with the following key detection functions and series expansions: half normal function with a hermite expansion, hazard rate function with a simple polynomial expansion, and uniform function with a cosine expansion. We included a sampling effort correction in the density calculation as the number of repeated visits to each sampling point (Buckland et al. 2001). We constructed models as described above for each species that met the minimum 40-60 detection threshold recommended by Buckland et al. (2001) (Appendix 2.1). Prior to analysis, we viewed detection function histograms and truncated data to visually identified distances when truncation improved model fit (higher p-value in Kolmogorov–Smirnov goodness-of-fit tests) over untruncated models (Buckland et al. 2001). We used Akaike's Information Criterion with small sample size correction (AICc), goodness of fit tests (Kolmogorov–Smirnov), and Q-Q plots to identify best-fit models among the three different detection function structures (ΔAICc < 2, Burnham and Anderson 2002). We then used the detection function structure from the most parsimonious model (ΔAICc = 0) to build main effects models that evaluated heterogeneity in detectability as a function of observer, date of survey, visibility, track, percent cloud cover, precipitation, wind, and survey time. Covariate models were run for all species except those with low detection probabilities (< 0.20). Models that included a precipitation effect or wind effect sometimes failed to converge due to sparse data in the precipitation = 1 level or any of the wind levels, and thus were removed from the model set in these cases. Program distance does not allow fitting of models with covariate effects with a uniform function, thus if the most parsimonious model was the uniform function with a cosine expansion, we chose the next best supported model structure (if ΔAICc < 2) to fit covariate effects. After fitting all the covariate models with the best-fit model structure, we used AICc to select models across the full model set.

If the final model set showed model selection uncertainty (> 1 one model with ΔAICc < 2), we used a bootstrapping procedure to obtain model-averaged estimates of density across all such models. In the bootstrap procedure, an equal number of point transects as in the original data were randomly resampled (with replacement) 10000 times from the original data. Each of the original data samples had an equal probability of being resampled. AICc model selection was used to choose the best model, and the associated density estimate for each iteration. The density point estimate was the mean over all bootstrap replicates of all supported models and the confidence intervals were the 0.025 and 0.975 percentiles of the bootstrap estimates across all supported models, and thus included model selection uncertainty.

During the distance sampling process, we stratified the data by treatment (sanctuary or reference) to estimate mean population densities across all sanctuary sites and reference sites and compared these estimates for all fifteen forest bird species in both 2016 and 2017. We also estimated densities at each paired sanctuary and reference site for all fifteen species in both years. We compared mean densities by treatment and between each paired site, and considered non-overlapping 95% confidence intervals between sanctuary and reference site density estimates to indicate significant differences. If a species was not known to occupy or was rarely detected (< 10 observations across all surveys in a year) in any of the sites in a treatment level, we assumed a population density of zero for that species in that treatment level and compared the confidence intervals in the other treatment level to zero.

Two species (North Island Robin *Petroica longipes* and New Zealand Fantail) were observed moving towards the observers during our study, and thus violated the distance sampling assumption of no movement in response to observers. Since all observers were trained to monitor animal movement as they approached the point count location, and to note the initial location of any animals that moved in response to the observer, this issue should have been minimized by our field methods. However, some individuals may have been missed upon entry, so we also used a grouping analysis method outlined in Buckland et al. (2015) to address this potential issue. When animals that are attracted to observers are already close to the point count location, the distances can be grouped where the width of the first group is chosen to encompass the distance over which animals will respond and where animals in the second group are unlikely to respond. From field trials, we identified these distances to be 12m for the Fantail and 20m for the Robin and we grouped all detections between 0-12m and 0-20m for these species, respectively, during the model fitting process. All other model fitting analyses were conducted as described previously.

One of our sites, Tarata Conservation Area, was difficult to navigate due to dense vegetation and steep and unsafe terrain, and we were unable to obtain sufficient data for distance sampling analyses using traditional point count techniques. At this site, we estimated population densities for each species using the paired acoustic sampling approach of Van Wilgenburg et al. (2017). This method employs the use of autonomous recording units (ARUs) to increase the quantity of data collected at poorly sampled sites, and thus facilitates density estimation. We calculated population densities and quantified precision for all species present at the site as described in section 6.3.2 in Buckland et al. (2015), except we replaced $\hat{\nu}$ in the denominator with the correction factor ($C = \pi\hat{\tau}^2 p\sigma$) from Sólymos et al. (2013) and Van Wilgenburg et al. (2017), which corrects for the bias introduced by using ARUs for bird surveys relative to human point counts. See Chapter One for a complete description of our analysis.

We used AIC model selection and generalized linear mixed effects models (GLMMs) to assess whether variation in bird densities was explained by the sanctuary effect alone (factor with two levels: sanctuary or reference, reference as intercept), or by site area (in hectares), given that area varied substantially among all three paired sites (Table 2.1) and that forest bird abundance can vary by forest fragment size in New Zealand (Tanentzap and Lloyd 2017). Our final model set included a model with a sanctuary fixed effect, a model with an area fixed effect, an additive model with both sanctuary and area fixed effects, and a null model that lacked these effects. All four models included a random effect for repeated visits to sampling points. For Kaka *Nestor meridionalis*, Kakariki *Cyanoramphus novaezelandiae*, Saddleback *Philesturnus rufusater*, and Whitehead *Mohoua albicilla*, we did not include any sanctuary fixed effect models because these species were only found in sanctuaries, so comparisons between sanctuary and reference sites could not be made. We compared two models only for these species, an area model and a null model, both with a random effect for sampling points. We compared all models using AIC model selection and interpreted regression coefficients from all equally likely best-fit models to the data (ΔAIC < 2, Burnham and Anderson 2002). Finally, when estimating model coefficients, we used a two-stage bootstrap approach (Buckland et al. 2009) that inflates standard errors to account for uncertainty arising in the density estimating process. The distance data for each sampling point were randomly resampled 1000 times (with replacement), and in each iteration, coefficient values were stored. Coefficients and confidence intervals were produced using a bootstrap procedure in which the slope of the estimated probability detection function and the effective area sampled (Buckland et al. 2001) were re-estimated in each resample and incorporated as statistical offsets in generalized linear mixed effects models that modeled count data as a function of covariates using a Poisson distribution. The resulting coefficient point estimates are the mean over all bootstrap replicates and the confidence intervals are the 0.025 and 0.975 percentiles of the bootstrap estimates.

Results

We detected 29 bird species across all years and sites, of which we had sufficient data to estimate population densities for 15 species (Appendix 2.1). Most of the species for which we did not estimate densities were introduced species that tend to prefer forest edges over interior (e.g., European Goldfinch *Carduelis carduelis* and European Greenfinch *Chloris chloris*, IUCN 2016a, IUCN 2016b), but some were native forest birds that were extremely rare at our study sites, e.g. Stitchbirds *Notiomystis cincta* and Fernbirds *Bowdleria punctata*, or were nocturnal species only occasionally observed during the day, e.g. Morepork *Ninox novaeseelandiae* (Appendix 2.1).

Most native bird species (including reintroduced species and those already present when sanctuaries were established) had significantly higher population densities in fenced sanctuaries than in reference sites in both 2016 and 2017. This held true when the mean effect of sanctuaries across all sites was evaluated (Figure 2.2), and when comparisons were made between each paired set of sites separately (Table 2.2). For six of twelve native species, including two globally threatened species (Kaka and North Island Saddleback) and four uncommon species (Bellbird *Anthornis melanura*, Kakariki, North Island Robin, and Whitehead), densities were significantly higher in sanctuaries across all sites and years (Figure 2.2, Table 2.2). These species had 0.27 to 9.00 more birds/ha in sanctuaries than in reference sites (Figure 2.2). Three other common native species, the Tui *Prosthemadera novaeseelandiae*, Kereru *Hemiphaga novaeseelandiae*, and Tomtit *Petroica macrocephala*, had significantly higher densities in sanctuary sites when the mean across all sites was considered (Figure 2.2) and in all but one set of sites when sites were compared independently (Table 2.2). These species had 0.90 to 4.10 more birds/ha in sanctuaries than in reference sites (Figure 2.2). Only two native species' population densities were not higher in sanctuary sites than in reference sites when sites were compared independently (Table 2.2) or when the mean response across all sites was assessed (Figure 2.2). These are both biogeographically recent native species - the Grey Warbler and the Silvereye. Another biogeographically recent native species, the New Zealand Fantail, had significantly higher densities in one of the sanctuary sites than in its paired reference site in 2017 only, and did not differ between sanctuary and reference sites in 2016 (Table 2.2), or when the mean response across all sites was assessed (Figure 2.2).

There was no significant difference in mean population densities between sanctuary and reference sites for all three introduced species (Figure 2.2) and there were significantly higher densities of the introduced Eurasian Blackbird *Turdus merula* at only one sanctuary site in 2016 when sites were compared independently (Table 2.2). The effect of sanctuaries on mean population densities was the same in both 2016 and 2017 for all native and introduced species, and the estimated densities were similar between years for most species (Figure 2.2). Site-level estimates varied between years, but site-level effects of sanctuaries on bird densities were consistent between years for most species (Table 2.2).

In our analysis of whether bird densities were related to sanctuary or area effects, both covariates were supported by models for all species, although the strength and direction of the effect of each covariate varied by species (Appendix 2.2). The sanctuary effect was in one or more supported models and positively related to densities for all native species that could be analyzed with a sanctuary effect (Bellbird, Blackbird, Kereru, Tomtit, and Tui), and the area effect was in one or more supported models and negatively related to densities for all native species (Appendix 2.2). There was no significant effect of sanctuary or area covariates on Grey Warbler densities, and mixed effects of sanctuary and area covariates on densities of Chaffinches

Fringilla coelebs, Fantails, Silvereyes, and North Island Robins; coefficients for either covariate were negative, non-significant, or positive, depending on year (Appendix 2.2).

There was little evidence that detection probability varied by the covariates we measured. The observer covariate was included in supported models for four of fifteen species in 2016 and for one species in 2017, and the track covariate was included in supported models for one species each in 2016 and 2017 (Appendix 2.3).

Discussion

Native birds, including globally threatened species, were the 'winners' of mammal eradication in fenced sanctuaries (Innes et al. 2002). In contrast, we did not find significant differences in mean population densities between sanctuary and reference sites for three biogeographically recent native species and three introduced species (Figure 2.2). Introduced birds and biogeographically recent native species shared an evolutionary past with mammals more recently (Starling-Windhof et al. 2011); thus, these species may possess life history strategies that help them evade mammal predation more effectively than native island species (Starling-Windhof et al. 2011, Parlato et al. 2015).

Our results generally aligned with previous studies measuring bird responses to mammal control in fenced sanctuaries, unfenced sites and offshore islands. Tanentzap and Lloyd (2017) found higher abundance of native frugivorous species within and immediately outside Orokonui Sanctuary but found little effect on introduced species' abundances. Mikselly (2018) also found that native species, particularly Tui and translocated species, responded positively to mammal exclusion in Zealandia, New Zealand's first fenced sanctuary, while biogeographically recent native and introduced species responded neutrally to mammal exclusion and negatively to competition. All native species that were more abundant in fenced sanctuaries in this study (Fig.

2) also benefitted from mammal control in unfenced forests or offshore islands (Innes et al. 2004, Smith and Westbrooke 2004, Taylor et al. 2006, Baber et al. 2009, O'Donnell and Hoare 2012, Graham et al. 2013, Ruffell and Didham 2017). However, neutral or negative responses to mammal control have been documented for Tomtit (Innes et al. 2004, O'Donnell and Hoare 2012, Ruffell and Didham 2017) and Tui (Smith and Westbrooke 2004). Our site-level comparisons showed mixed results for these two species (Table 2.2). Thus, other site-specific factors that were not measured in this study (e.g. forest structure, resource availability) may also regulate native bird population size (Innes et al. 2010). Although densities of some native species (e.g., Bellbird, Tui, Whitehead) were higher at one sanctuary site (Table 2.2), we found significant differences in the abundance of these species inside and outside sanctuaries across all paired sites, suggesting that our inferences would remain the same if these sites were not included.

Several mechanisms may explain the increased density of most native birds in fenced sanctuaries. In areas with invasive mammal control, lower predation rates often result in higher nesting success, particularly for native bird species (Clout et al. 1995**,** Dilks et al. 2003, Innes et al. 2004, Moorhouse et al. 2003, Kelly et al. 2005, Innes et al. 2010, Starling-Windhof et al. 2011**).** Adult mortality may also be reduced; females sitting on nests commonly experience high mortality, although little is known about predation rates on adults away from nests (Innes et al. 2010). Populations may also increase because of increased habitat quality or food availability (Innes et al. 2010). Browsing by invasive mammalian herbivores outside fenced sanctuaries may change forest structure and reduce plant biomass, affecting habitat quality for native birds (Diamond and Veitch 1981). Some mammal species consume native plants, fruits, flowers, and invertebrates, and may directly compete with native birds for these resources. Although it can be difficult to separate the relative importance of these mechanisms, predation by pest mammals is generally considered to be the primary factor affecting bird populations in New Zealand's forests, and food availability is likely to be secondary (Innes et al. 2010). Finally, although several native species were actively reintroduced to sanctuaries because they have low tolerance to invasive mammal predation (Table 2.1), these species responded less strongly to sanctuaries than other native species (Figure 2.2). Thus, reintroduced species are part of, but not driving, the overall conclusion that sanctuaries benefit native birds.

We found no effect of sanctuaries on the abundance of introduced and biogeographically recent native species. Introduced species abundance also did not differ in Orokonui Sanctuary (Tanentzap and Lloyd 2017), and twenty years of bird counts at Zealandia show that native species, including many introduced by translocation, now dominate the avifauna, while introduced and biogeographically recent native species significantly declined (Miskelly 2018). Changes in relative abundance at Zealandia suggests a strong role for competition in determining structure of New Zealand forest bird communities (Miskelly 2018). Although predation is the primary driver of population declines for native forest birds, competition with native species may have a greater impact on introduced bird populations (Diamond & Veitch 1981, Innes et al. 2010, MacLeod et al. 2012, Miskelly 2018). Overall, past work has found neutral, positive, and negative responses to mammal control for introduced species in unfenced sites or on islands (Innes et al. 2004, Smith and Westbrooke 2004, Spurr and Anderson 2004, Baber et al. 2009, O'Donnell and Hoare 2012, Ruffell and Didham 2017). We also found inconsistent responses for these groups; mean responses and most site-by-site responses were neutral, but a few responded positively or negatively to fenced sanctuaries, providing only limited support for competition as a driver of introduced bird abundances (Table 2.2, Appendix 2.2). These inconsistencies suggest that responses of introduced and biogeographically recent native species may be mediated by multiple site-specific factors beyond the effects of mammal predation and competition alone (e.g. differences in forest structure, resource availability, or in the composition of the surrounding landscape; Diamond and Veitch 1981, Innes et al. 2010, Barnagaud et al. 2014).

The size of the study site (area effect) was included in top-ranked models and was often weakly and negatively associated with native bird densities, but was either negatively, positively, or neutrally associated with biogeographically recent native and introduced species densities (Appendix 2.2). This finding contrasted with that of Tanentzap and Lloyd (2017), who found a slight positive association between forest fragment size and native bird abundance. These differing results may be explained by variation in the amount of surrounding forest cover, since forest landscape composition can be an important predictor of bird densities (Ruffell and Didham 2017). However, we caution against interpreting our results to suggest that small sanctuaries support higher native bird densities than larger ones because we did not explicitly design our study to test the effect of area on bird abundance, and only included an area effect in the analysis to account for the high variation in sanctuary size.

This study is the first to assess the effects of fenced sanctuaries on multiple native and introduced birds in a replicated study design using paired ‘treatment’ and ‘reference’ sites that accounts for imperfect detection (MacLeod et al. 2012). Despite these strengths, our study has some limitations that warrant discussion. First, although paired sites were carefully selected to be as similar as possible (Table 2.1), we could not control all sources of variation. Our inferences would be stronger if we were able to assess differences in sanctuary and reference sites before and after eradication, but bird population data prior to fence installation were not available across all sites. We also assessed bird responses to fenced sanctuaries over a two-year period, approximately 10–14 years after mammal eradications in sanctuaries were completed. Thus, although our mean density estimates were very consistent across both years of our study (Figure 2.2), our findings do not capture possible long-term temporal variation in demographic responses to mammal eradication and conservation fencing (Miskelly 2018). Furthermore, we sampled birds during January through April to coincide with a study on seed dispersal, so densities may differ from those estimated from spring bird counts. However, our mean density values for most species in sanctuary and reference sites were within the range of previously reported estimates in sites with (Greene et al. 2010) or without (MacLeod et al. 2012) mammal control, respectively. Finally, we acknowledge that species abundance or population densities may not always be good indicators of habitat quality or population persistence, and inferences about the effects of management actions on populations should be based on additional demographic data (Van Horne 1983). However, previous New Zealand autecology studies generally indicate that higher bird densities in mammal-controlled areas correspond to higher nesting success and juvenile and adult survival (Innes et al. 2010). Future research that assesses multi-species demographic responses to fenced sanctuaries using multiple metrics, e.g. survival, abundance, reproduction, would be valuable.

We demonstrate that fenced sanctuaries, which require a substantial investment of conservation funds, are meeting conservation objectives. Although conservation fences alone cannot halt large-scale biodiversity loss (Hayward and Kerley 2009), by increasing population densities for common and threatened native forest birds, fenced sanctuaries are a promising tool for providing exemplar restoration sites on large islands or continents in close proximity to human communities. Until New Zealand's 'predator free by 2050' vision (Russell et al. 2015) is realized, fenced sanctuaries are the only viable pathway for restoring most critically endangered birds to mainland forests, and have tremendous potential to be exported to global biodiversity hotspots where invasive predators threaten native species.

Figure 2.1. A map of the six study areas on New Zealand's North Island in which we compared bird population densities in 2016 and 2017, including three fenced sanctuary sites shown with black triangles (1- Tawharanui Regional Park, 4- Maungatautari Ecological Reserve, 6- Rotokare Scenic Reserve) and three paired reference sites with minimal mammal control shown with white triangles (2- McElroy Scenic Reserve, 3- Te Tapui Scenic Reserve, and 5- Tarata Conservation Area).

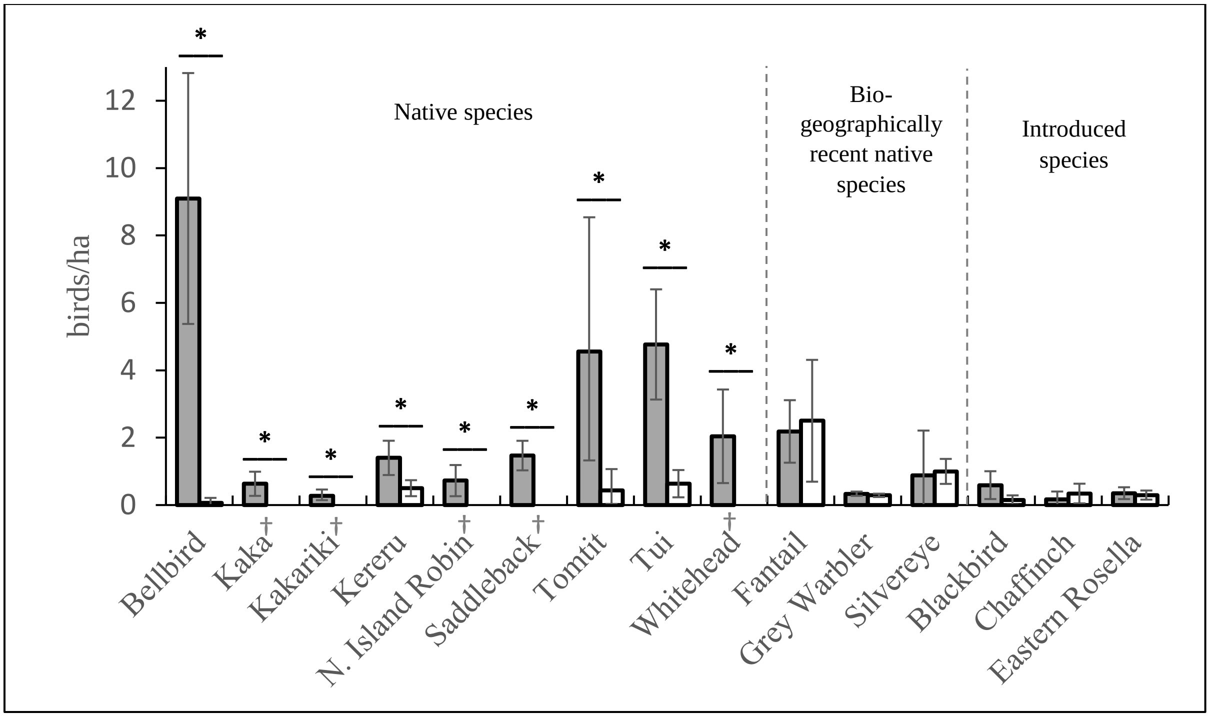

Figure 2.2. Mean density (number of birds/ha) of and 95% confidence intervals of birds in fenced ‘mainland island’ sanctuaries (grey bars) relative to reference sites (white bars) in 2016 (results for 2017, not shown, were very similar).

*Significant effect = confidence intervals around sanctuary site and reference means do not overlap. Confidence intervals were derived from 0.025 and 0.975 percentiles of the distribution of density estimates from the bootstrap resampling procedure across all models with ΔAIC < 2.0 (see methods).

†species translocated to sanctuaries

Table 2.1. Characteristics of the six study areas in which we compared bird densities in 2016 and 2017, including three fenced sanctuary sites and three paired reference sites.

	Tawharanui Regional Park ***Sanctuary***	**McElroy Scenic Reserve** ***Reference***	**Maungatautari Ecological Reserve** ***Sanctuary***	**Te Tapui Scenic Reserve** ***Reference***	**Rotokare Scenic Reserve** ***Sanctuary***	**Tarata Conservation Area** ***Reference***
No. sampling points	17	20	103	115	28	14
No. samples[1] 2016	118	144	133	152	109	105
No. samples[1] 2017	111	146	140	160	140	126
Total ann. precip. (mm)[2]	1200	1400	1200	1200	1400	1800
Mean ann. temp. (°C) [2]	16	16	13	13	13	13
Elev. range (m)	0-100	0-120	250-700	200-500	170-300	100-240
Area (ha)[3]	90	148	3210	2330	215	150
Fence completion year	2004	NA	2006	NA	2008	NA
Dominant forest cover	Manuka mixed native	Manuka mixed native	Rimu-Tawa mixed native	Rimu-Tawa mixed native	Tawa mixed native	Tawa mixed native
Latitude/ longitude	36°22’18” S, 174°50’33” E	36°27’32” S, 174°41’32” E	38°02’58” S, 175°33’36” E	37°48’38” S, 175°37’23” E	39°27’14” S, 174°24’35” E	39°10’05” S, 174°21’24” E
Mammal control	Eradication of all mammal predators, except mice	None	Eradication of all mammal predators, except mice	Low-density possum control every 2-4 years	Eradication	None
Forest birds translocated to sanctuary[4]	Kakariki, Kiwi, N. Island Robin, Kaka, Whitehead, N. Island Saddleback	NA	Kakariki, Kiwi, N. Island Robin, Hihi, Kaka, Whitehead, N. Island Kokako, N. Island Saddleback	NA	Kiwi, N. Island Robin, Hihi, Whitehead, N. Island Saddleback	NA
Land use[5]	Timber harvest (1800s) and grazing	Timber harvest (1800s) and grazing	Light timber harvest (through 1980)	Light timber harvest (dates unknown) and deer hunting	None documented	None documented
Patch Area (AWM) (ha)[6]	558	400	1422	1309	6222	3300
Shape Index (AWM)[6]	3.3	3.1	2.5	2.5	6.4	5.8
Nearest neighbor (m)[6]	85	101	170	168	124	108

[1] No. of samples = no. sampling points * number of visits

[2] Total annual precipitation and mean annual temperature data are from the National Institute of Water and Atmospheric Research 29-year average (1981-2010).

[3] Area indicates the total size of all forest patch(es) within a reserve, not the size of the entire reserve.

[4] See Appendix 2.1 for scientific names; Kiwi includes any of the five *Apteryx* species.

[5] based on data obtained from the New Zealand National Vegetation Survey Databank (https://nvs.landcareresearch.co.nz) or from site management plans.

[6] Patch Area, Shape Index, and Euclidean Nearest Neighbor are landscape metrics that were analyzed in a 20km buffer around each of the six study sites using Fragstats (McGarigal et al. 2012).

Table 2.2**.** Site-level estimates of population densities (number of birds/hectare) for observed bird species at fenced ‘mainland island’ sanctuary sites (Rotokare Scenic Reserve, Tawharanui Regional Park, and Maungatautari Ecological Reserve) and paired reference sites with minimal mammal control (Tarata Conservation Area, McElroy Scenic Reserve, and Te Tapui Scenic Reserve) in 2016 and 2017.

Species	**Sanctuary site**	**Density**	**LCL**	**UCL**	**Reference site**	**Density**	**LCL**	**UCL**
2016								
Bellbird *Anthornis melanura*	Maungatautari	1.471*	0.999	1.943	Te Tapui	0.214*	0.067	0.362
	Rotokare	3.406*	2.307	4.505	Tarata	0.650*	0.001	1.306
	Tawharanui	16.912*	9.578	24.246	McElroy	0.000[a]	NA	NA
Blackbird[I] *Turdus merula*	Maungatautari	1.280*	0.447	2.113	Te Tapui	0.152*	0.001	0.304
	Rotokare	3.005	1.065	4.945	Tarata	4.527	0.772	8.283
Fantail *Rhipidura fuliginosa*	Maungatautari	5.747	3.709	7.786	Te Tapui	4.765	1.846	7.685
	Rotokare	8.176	4.237	12.114	Tarata	4.109	0.506	7.712
	Tawharanui	3.234	1.867	4.600	McElroy	5.067	-1.189	11.323
Grey Warbler *Gerygone igata*	Maungatautari	1.219	0.750	1.688	Te Tapui	1.180	0.894	1.466
	Rotokare	1.237	0.690	1.784	Tarata	1.478	0.001	2.960
	Tawharanui	Rare [b]	NA	NA	McElroy	0.424	0.288	0.560
Kererū *Hemiphaga novaeseelandiae*	Maungatautari	1.938	1.150	2.725	Te Tapui	2.025	0.103	3.948
	Rotokare	3.955*	1.796	6.114	Tarata	0.585*	0.083	1.087
	Tawharanui	5.563*	4.229	6.897	McElroy	1.574*	1.093	2.055
Silvereye *Zosterops lateralis*	Maungatautari	3.108	0.630	5.586	Te Tapui	4.579	3.195	5.962
	Rotokare	3.420	1.399	5.441	Tarata	5.712	0.018	11.405
	Tawharanui	Rare[b]	NA	NA	McElroy	3.125	2.292	3.958
Tomtit *Petroica macrocephala*	Maungatautari	5.536*	3.364	7.709	Te Tapui*	2.209	1.124	3.294
	Rotokare	7.240	3.632	10.848	Tarata	6.868	0.079	13.657
Tūī *Prosthemadera novaeseelandiae*	Maungatautari	3.894*	2.865	4.924	Te Tapui	1.217*	0.919	1.515
	Rotokare	6.075*	3.673	8.477	Tarata	0.752*	0.002	1.508
	Tawharanui	7.860*	5.094	10.626	McElroy	1.244*	0.657	1.831
2017								
Bellbird *Anthornis melanura*	Maungatautari	1.014*	0.685	1.342	Te Tapui	0.139*	0.035	0.243
	Rotokare	0.747*	0.530	0.964	Tarata	0.142*	0.014	0.270
	Tawharanui	16.562*	12.238	20.886	McElroy	0.000 [a]	NA	NA

Blackbird[I] *Turdus merula*	Maungatautari	1.254	0.582	1.926	Te Tapui	0.528	0.247	0.810
	Rotokare	1.337	0.973	1.701	Tarata	1.811	0.378	3.244
	Tawharanui	0.782	0.385	1.179	McElroy	Rare[b]	NA	NA
Fantail *Rhipidura fuliginosa*	Maungatautari	3.038	2.348	3.727	Te Tapui	2.613	1.927	3.300
	Rotokare	5.511	4.563	6.460	Tarata	4.288	0.115	8.462
	Tawharanui	6.164*	4.115	8.212	McElroy	3.033*	2.431	3.635
Grey Warbler *Gerygone igata*	Maungatautari	1.748	1.267	2.230	Te Tapui	2.182	1.687	2.678
	Rotokare	2.104	1.776	2.432	Tarata	1.325	0.016	2.634
	Tawharanui	0.408	-0.010	0.919	McElroy	1.162	0.894	1.429
Kererū *Hemiphaga novaeseelandiae*	Maungatautari	2.182	1.350	3.015	Te Tapui	2.011	1.219	2.803
	Rotokare	4.443*	3.421	5.466	Tarata	0.956*	0.115	1.797
	Tawharanui	3.904*	2.995	4.814	McElroy	0.732*	0.347	1.117
Silvereye *Zosterops lateralis*	Maungatautari	3.403	2.142	4.663	Te Tapui	5.808	4.377	7.240
	Rotokare	5.795	4.815	6.775	Tarata	4.899	0.523	9.276
	Tawharanui	2.992*	1.080	4.905	McElroy	6.631*	5.424	7.838
Tomtit *Petroica macrocephala*	Maungatautari	6.731*	4.180	9.282	Te Tapui	2.837*	1.724	3.950
	Rotokare	6.697	5.481	7.913	Tarata	5.854	0.274	11.433
Tūī *Prosthemadera novaeseelandiae*	Maungatautari	3.491	2.674	4.308	Te Tapui	2.462	1.583	3.342
	Rotokare	6.192*	4.852	7.532	Tarata	0.453*	0.014	0.892
	Tawharanui	6.860*	4.548	9.172	McElroy	0.956*	0.684	1.228
Pooled 2016 and 2017 due to sparse site-level data in each year[c]								
Chaffinch[I] *Fringilla coelebs*	Maungatautari	0.628	0.166	1.090	Te Tapui	0.398	0.130	0.665
	Rotokare	0.745	0.240	1.249	Tarata	0.718	0.080	1.348
	Tawharanui	Rare[b]	NA	NA	McElroy	0.561	0.283	0.839
Kākā[†] *Nestor meridionalis*	Maungatautari	0.205*	0.105	0.304	Te Tapui	0.000[a]	NA	NA
	Tawharanui	0.899*	0.440	1.359	McElroy	0.000[a]	NA	NA
Kākāriki[†] *Cyanoramphus novaezelandiae*	Tawharanui	1.206*	0.750	1.662	McElroy	0.000[a]	NA	NA
N. Island Robin[†] *Petroica longipes*	Maungatautari	2.650*	1.871	3.429	Te Tapui	0.000[a]	NA	NA
	Rotokare	1.410*	0.920	1.901	Tarata	Rare[b]	NA	NA
	Tawharanui	3.319*	-3.451	10.088	McElroy	0.000[a]	NA	NA
	Tawharanui	0.966	0.305	1.626	McElroy	0.444	0.231	0.658

Rosella[I] *Platycercus eximius*								
Saddleback[†] *Philesturnus rufusater*	Maungatautari	0.252*	0.114	0.389	Te Tapui	0.000 [a]	NA	NA
	Rotokare	2.072*	1.707	2.437	Tarata	0.000[a]	NA	NA
	Tawharanui	3.779*	2.587	4.971	McElroy	0.000 [a]	NA	NA
Whitehead[†] *Mohoua albicilla*	Maungatautari	1.874*	1.035	2.712	Te Tapui	0.000 [a]	NA	NA
	Rotokare	1.028*	0.339	1.717	Tarata	0.000 [a]	NA	NA
	Tawharanui	4.849*	3.581	6.116	McElroy	0.000 [a]	NA	NA

* significant difference in bird population density estimates between paired sanctuary site and reference sites based on non-overlapping 95% confidence intervals. Confidence intervals derived from 0.025 and 0.975 percentiles of the distribution of density estimates from bootstrap resampling procedure across all models with delta AICc < 2.0 (see methods).

[I] introduced species

†species translocated to sanctuaries

[a] Densities were set to zero for species that were not known to occur at a site.

[b] Species marked as rare were detected too infrequently at a site to estimate population densities.

[c] Site-level data were pooled across 2016 and 2017 for some species to provide sufficient data for analysis and a ‘year’ covariate was included in the distance sampling detection function model comparisons to account for yearly variation in detection probability.

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CHAPTER THREE

MORE BIRDS AND SEEDS DISPERSED IN A NOVEL NETWORK OF FENCED 'MAINLAND ISLAND' SANCTUARIES

Islands suffer greater species loss and decline than any other ecosystem globally (Tershy et al. 2015, Spatz et al. 2017), disrupting ecological processes such as seed dispersal and pollination (Traveset and Richardson 2006, Robertson et al. 2008, Anderson et al. 2011). Extinction and decline of island animals is primarily driven by predation and habitat degradation by invasive mammals (Holdaway 1989, Craig et al. 2000, Innes et al. 2010, Spatz et al. 2017). Island-wide invasive mammal eradications have increased exponentially over the last several decades (DIISE 2015) and have been successful in reversing population declines for many island species (Jones et al. 2016). Yet whether invasive mammal eradications have cascading effects on plant-animal interactions is virtually unknown (Byrom et al. 2016, Jones et al. 2016).

One such interaction, biotic seed dispersal, plays a crucial role in structuring and maintaining plant communities by moving seeds away from parent plants to suitable microsites (Terborgh et al. 2008, Terborgh 2013), allowing seedlings to escape competition and density-dependent mortality (Janzen 1970, Connell 1971, Wotton & Kelly 2011). Long-distance seed dispersal by birds can also play a critical role in facilitating the colonization of new sites, in spreading genetic material, and in maintaining metapopulations (Cain et al. 2000). Thus, the decline and recovery of frugivorous birds could have profound effects on plant density and diversity, and plant community composition (Terborgh et al. 2008, Sharam et al. 2009, Kurten 2013).

The potential for invasive mammal eradications to affect dispersal interactions may be particularly revealing in New Zealand. In the absence of native apex mammalian predators, species interactions such as seed dispersal, pollination, and herbivory play a disproportionate role in regulating communities (Clout and Hay 1989, Innes et al. 2010). Over 70% of New Zealand's woody plants produce fruit and birds are the primary frugivores and dispersers (Clout and Hay 1989, Thorsen et al. 2009). Although some frugivorous birds in New Zealand are common and widespread, most bird populations are declining (Craig et al. 2000, Elliot et al. 2010, Innes et al. 2010) and many species occupy highly restricted ranges (Robertson et al. 2007, Parlato et al. 2015). Several globally rare species (e.g. North Island Saddleback *Philesturnus rufusater*) consume fruit, and may have been important seed dispersers historically, but cannot coexist with invasive mammals and are functionally extinct in mainland forests (Kelly et al 2006).

After successfully eradicating mammals and recovering bird populations on dozens of small off-shore islands, New Zealand pioneered the establishment of a large network of fenced mammal-free 'mainland island' sanctuaries (Burns et al. 2012); hereafter 'sanctuaries'. This large-scale replicated experiment creates a unique opportunity to assess the consequences of mammal eradication for restoring seed dispersal interactions. We used sanctuaries and paired reference sites with minimal mammal control to test hypotheses that frugivorous bird densities, foraging rates, and dispersed seed densities would be higher in the absence of invasive mammals, and to identify factors explaining seed dispersal dynamics.

We selected three fenced sanctuaries and three paired patches of indigenous forests within 25-40km that were similar in canopy composition, area, elevation range, mean temperature and precipitation, land use history, and landscape context (Appendix 3.1, Appendix 3.2). In each study area, we established sampling points > 200m apart (MacLeod et al. 2012) at random locations along transects. During the two-year study (2016-2017), we estimated bird densities and measured two components of seed dispersal quantity - foraging rates and number of dispersed-seeds at each sampling point. We measured bird foraging rates on common canopy or subcanopy fruiting plants, and we collected seeds in 0.5m x 0.5m seed traps and along 1.0m x 100m transects and counted and identified all bird-dispersed seeds to species. We compared bird densities, foraging rates, and seed counts (mean number of seeds collected in nets or on transects) between fenced sanctuaries and paired reference sites for bird and plant species with sufficient data for analysis.

Mean population densities for all seven native frugivorous bird species were significantly higher in sanctuaries (see Chapter Two, Figure 2.2). In contrast, there were no differences in density between sanctuaries and reference sites for all three recently introduced frugivorous species (including the recently self-introduced Silvereye *Zosterops lateralis*, McLintock and Williams 1966, Chapter Two, Figure 2.2). Mean foraging rates were significantly higher in sanctuary sites; 0.03 to 0.52 more fruits were consumed on average per 5-minute survey in sanctuary sites for all six fruiting species observed in 2017 and patterns were similar in 2016 (Figure 3.1, Appendix 3.3). Native frugivore density and fruit abundance were significant positive predictors of foraging rates for most plant species (Table 3.1, Appendix 3.4). The relationship between foraging rates and recently introduced frugivore densities was mixed; there were significant positive correlations for two plant species and significant negative correlations for two other plant species in one or both years (Table 3.1). Dispersed seed counts were also significantly higher in sanctuary sites for all four plant species evaluated (Figure 3.2), and native frugivore density was a significant positive predictor of dispersed seed counts for two of four species (Table 3.2, Appendix 3.5). We did not find correlations between dispersed seed counts and recently introduced frugivore densities, except for one negative relationship (Table 3.2).

Studies on the effects of invasive species removal on plant-animal interactions are rare (Robertson et al. 2008, Jones et al. 2016), and our findings provide some of the first evidence that seed dispersal of multiple native plant species is positively associated with eradication of invasive mammals in fenced sanctuaries. Although they did not measure the interaction between birds and plant recruitment directly, Tanentzap and Lloyd (2017) also found higher abundance of native frugivores and higher sapling regeneration of mammal-sensitive plants within and near Orokonui Sanctuary than at forest sites 20km away. These patterns could be attributed to the direct effect of removing potential seed predators and herbivores, or the indirect effects of mammal eradication on frugivorous birds. Most invasive mammals are ineffective dispersers and impact seed dispersal through seed predation (Williams et al. 2001, Duron et al. 2017). For example, possums *Trichosurus vulpecula* may serve as dispersers of several native and non-native fruiting plants (Williams et al. 2001), but possums frequently destroy seeds and consume unripe fruits (Cowan 1990, Campbell and Atkinson 2002), and plants typically experience lower germination success when dispersed by possums (Williams et al. 2001). Thus, invasive mammal browsing on fruits and seeds may reduce seed dispersal and recruitment for native plants (Campbell and Atkinson 2002), and mammal eradication may release plants from these direct impacts.

Yet our study also suggests that invasive mammal eradication has strong indirect effects on seed dispersal. More fruits were consumed and seeds dispersed by birds in the absence of invasive mammals, and the densities of native frugivorous birds were positively related to both metrics of seed dispersal for most plants, regardless of natural variation in fruit availability. An important factor that could influence the strength of the relationship between frugivore densities and seed dispersal is the degree of ecological redundancy among dispersing animals (Walker 1992, Loiselle and Blake 2002). Plants that are dispersed by multiple species may be less sensitive to changes in individual frugivore abundance (Loiselle & Blake 2002). Large-seeded species are generally more susceptible to dispersal failure due to a lack of ecological redundancy in dispersers (Wheelwright 1985, Clout & Hay 1989, Kitamura et al. 2002), and thus may benefit most if mammal eradication leads to increased bird richness and abundance. For example, Kereru *Hemiphaga novaeseelandiae*, a large-bodied native pigeon, is the only extant species capable of swallowing Puriri *Vitex lucens* fruits (Clout and Hay 1989). Thus, Puriri may benefit most from increased Kereru densities following mammal eradication. Indeed, dispersed seed abundance for Puriri was much higher in sanctuary sites where Kereru densities were higher (Figure 3.2), and there was a stronger correlation between native frugivore densities and dispersed seed counts for Puriri than for any other species (Table 3.2).

Whether birds are native or introduced, and their degree of frugivory, may also influence the relationship between frugivore densities and seed dispersal. Introduced birds were largely unassociated with higher foraging and seed dispersal in sanctuaries. New Zealand’s introduced frugivores are generalists that only occasionally visit fruit, whereas native species are responsible for most fruit visitation (Kelly et al. 2006). Thus, the contribution of introduced birds to seed dispersal of native plants appears to be minimal (Kelly et al. 2006).

Several native bird species (e.g. Kereru, Tui *Prosthemadera novaeseelandiae*) that benefited from fenced sanctuaries in our study and dispersed much of the fruit have been identified as key dispersers and fruit visitors by several investigators (Clout & Hay 1989, Kelly et al. 2006, Kelly et al. 2010). Yet we also found that the North Island Saddleback was a potentially important disperser, as this species was responsible for approximately 15% of the foraging observations in both years. Fenced sanctuaries enable the reintroduction of birds like the North Island Saddleback that cannot coexist with even very low densities of mammalian predators (Burns et al. 2012). Thus, the value of such bird species for seed dispersal and other ecological processes may be hidden, with their functional role only fully apparent and restored when mammal eradication occurs at large, ecologically relevant scales.

Mammals may also indirectly affect seed dispersal by reducing the abundance and activities of avian pollinators, which may reduce seed production in sites where birds are unprotected from invasive mammals (Anderson et al. 2011). Future studies should consider how fenced sanctuaries affect pollination and seed dispersal simultaneously, to deepen our understanding of the mechanisms driving higher seed dispersal in sanctuaries. Invasive mammal predators also impact native lizards, which are important short-range dispersers of some low-stature plants, especially in open shrubland and subalpine ecosystems (Kelly et al. 2006, Young and Kelly 2016, Wotton et al. 2016). Although our study occurred in forested habitat, fenced sanctuaries may also indirectly benefit seed dispersal when they occur in open habitats by increasing lizard abundance. Furthermore, higher seed dispersal in sanctuaries may also be associated with other indirect effects unrelated to mammal presence that were not measured or controlled in our study, e.g. differences in soil properties and nutrient availability. Future studies should prioritize data collection across these gradients to determine whether they add to or interact with avian frugivore densities to influence rates of seed dispersal.

Although measuring seedling survival was beyond the scope of our study, past work has demonstrated that animal-mediated movement of seeds away from parent plants can increase germination, survival, and growth of seedlings, and decrease seed predation in New Zealand

(Wotton and Kelly 2011) and in many other systems globally (Howe and Smallwood 1982, Clark and Clark 1984, Terborgh 2013). Thus, invasive mammal eradication may drive rapid changes in forest regeneration patterns. Saplings of mammal-sensitive fruiting trees have been shown to increase in a fenced sanctuary in less than ten years as a result of increased seed dispersal and reduced mammal browsing, which suggests that sanctuaries have potential to shift successional pathways in short time-scales (Tanentzap and Lloyd 2017). Yet, other studies suggest that recovery rates may take much longer after mammal removal (Tanentzap et al. 2012). Frugivore-mediated dispersal may also reduce density dependent mortality across multiple life stages for plants, driving long-term changes in forest regeneration and population persistence (Caughlin et al. 2015). Furthermore, higher disperser densities and diversity, especially of large-bodied dispersers, may result in more frequent long-distance dispersal events (Jordano et al. 2007), facilitating increased gene flow among disparate populations (Garcia et al. 2007).

Our findings suggest that eradicating invasive mammals may increase bird populations to ‘ecologically effective densities’ needed to maintain seed dispersal (Soulé et al. 2003). The persistence of plant-animal interactions is an indicator of restoration success and is increasingly recognized as a priority for conserving resilient communities (Kaiser-Bunbury et al. 2010). We demonstrate that fenced mainland island sanctuaries support bird populations and their ecological roles at much higher levels than in similar forests without mammal eradication, a strong indication that New Zealand’s ambitious ‘predator-free by 2050’ goal will pay dividends for this global biodiversity hotspot. For the many other island and continental systems under threat from invasive mammals, New Zealand’s fenced mainland island model offers a promising tool for restoring biodiversity and important ecological processes.

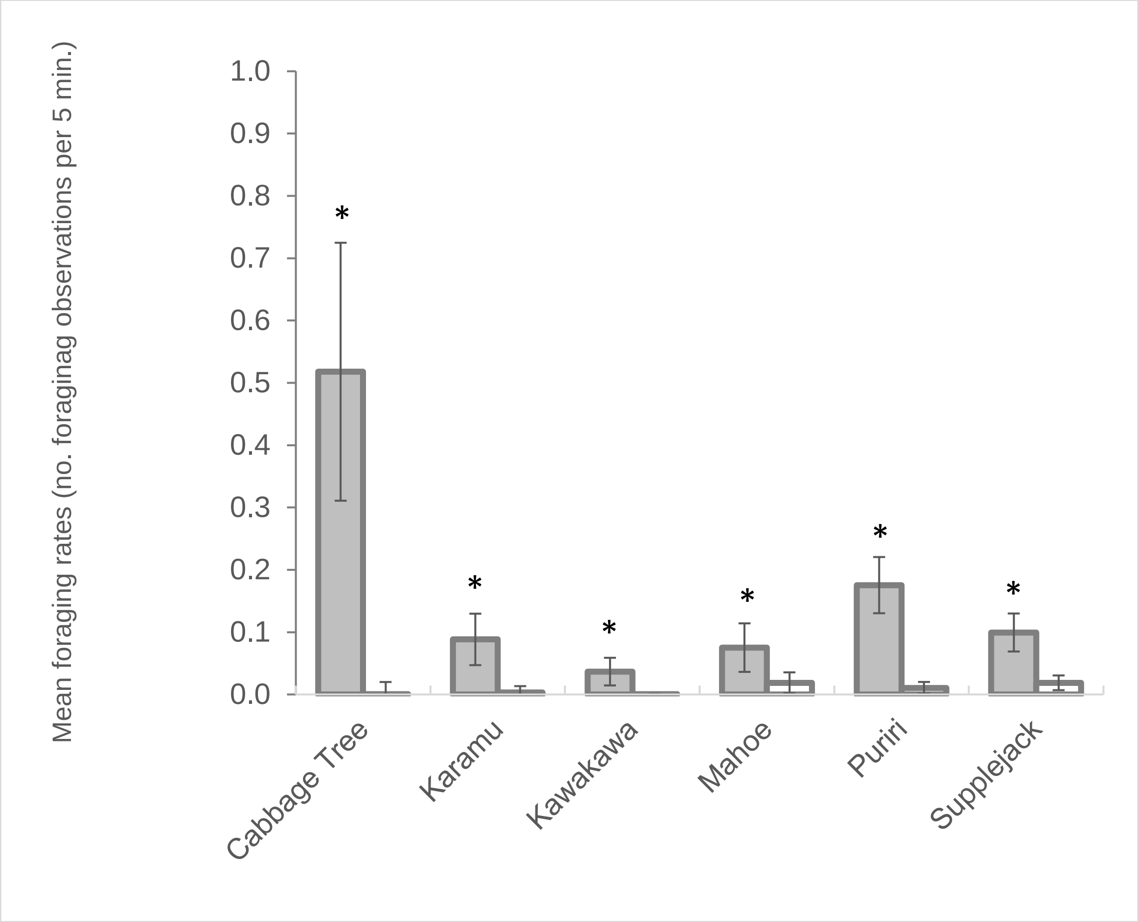

Figure 3.1. Comparison of mean foraging rates (mean number of birds observed foraging on fruit per five-minute observation period) and 95% confidence intervals for six different plant species in fenced mainland island sanctuaries (grey bars) relative to reference sites with minimal mammal control (white bars) in 2017. Species names: Cabbage tree *Cordyline australis*, Karamu *Coprosma lucida* and *Coprosma robusta* combined, Kawakawa *Piper excelsum*, Mahoe *Melicytus ramiflorus*, Puriri *Vitex lucens*, and Supplejack *Ripogonum scandens.* Results were similar in 2016 (Appendix 3.3) except for no significant difference found for Karamu in 2016 and no results presented for Supplejack due to a lack of fruiting Supplejack at study sites in 2016. Puriri only occurs at the two northern sites (Tawharanui Regional Park and McElroy Scenic Reserve), therefore mean foraging rates for Puriri are from this pair of sites only. Asterisk indicates a significant difference in mean foraging rates between paired eradication and reference sites (Wilcoxon Rank Sum Test, α < 0.05).

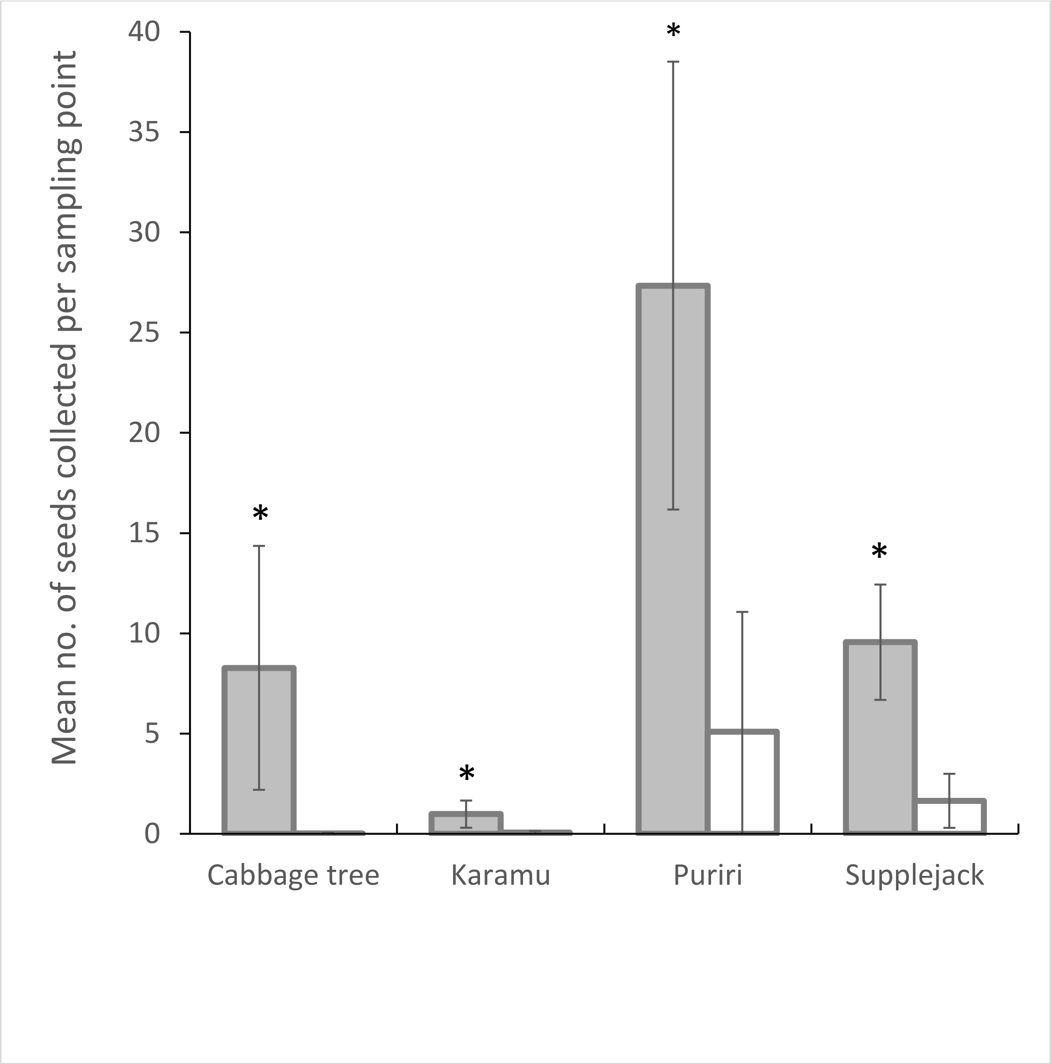

Figure 3.2. Comparison of mean dispersed-seed counts (mean number of seeds collected in seed traps or on 1m x 100m transects, n=416 total) and 95% confidence intervals for four different plant species in fenced mainland island sanctuaries (grey bars) relative to reference sites with minimal mammal control (white bars). Data from 2016 and 2017 were pooled for the analysis to increase sample size. Puriri only occurs at the northern sites (Tawharanui Regional Park and McElroy Scenic Reserve), so mean dispersed-seed counts for Puriri are from this pair of sites only. Asterisk indicates a significant difference in dispersed-seed counts between paired eradication and reference sites (Wilcoxon Rank Sum Test, $\alpha < 0.05$). Species names: Cabbage tree *Cordyline australis*, Karamu *Coprosma lucida* and *Coprosma robusta* combined, Puriri *Vitex lucens*, and Supplejack *Ripogonum scandens*.

Table 3.1. Kendall's (tau) rank correlation results for tests of significant correlations between foraging rates and mean plot-level density of native frugivores, recently introduced frugivores, and all frugivores combined (n = 761 sampling points in 2016 and 823 in 2017). Significant correlations ($p < 0.05$) are bolded. Species names: Cabbage tree *Cordyline australis,* Karamu *Coprosma lucida* and *Coprosma robusta* combined, Kawakawa *Piper excelsum*, Mahoe *Melicytus ramiflorus*, Puriri *Vitex lucens*, and Supplejack *Ripogonum scandens.*

Plant species	**Native frugivores**	**p**	**Introduced frugivores**	**p**	**All frugivores**	**p**
2016						
Cabbage tree	0.210	**0.000**	0.012	0.523	0.202	**0.000**
Karamu	0.202	**0.000**	0.150	**0.001**	0.192	**0.000**
Kawakawa	0.052	0.062	-0.044	0.060	0.045	0.071
Mahoe	0.190	**0.000**	0.095	**0.032**	0.175	**0.000**
Puriri	0.246	**0.000**	-0.087	**0.028**	0.249	**0.000**
2017						
Cabbage tree	0.228	**0.017**	-0.244	0.**011**	0.227	**0.018**
Karamu	0.098	**0.044**	0.011	0.830	0.066	0.177
Kawakawa	0.104	**0.006**	-0.010	0.795	0.072	0.057
Mahoe	0.080	**0.045**	0.061	0.129	0.104	**0.009**
Puriri	0.206	**0.000**	-0.140	0.**000**	0.199	**0.000**
Supplejack	0.143	**0.000**	0.045	0.200	0.145	**0.000**

Table 3.2. Kendall's (tau) rank correlation results for tests of significant correlations between mean dispersed-seed counts (from 199 seed traps and 216 fecal transects) and mean plot-level density of native frugivores, recently introduced frugivores, and all frugivores combined. Data from 2016 and 2017 were pooled to increase sample size. Significant correlations ($p < 0.05$) are bolded. Species names: Cabbage tree *Cordyline australis*, Karamu *Coprosma lucida* and *Coprosma robusta* combined, Puriri *Vitex lucens*, and Supplejack *Ripogonum scandens.*

Plant Species	**Native Frugivores**	**p**	**Introduced Frugivores**	**p**	**All frugivores**	**p**
Cabbage tree	0.144	**0.000**	-0.041	0.315	0.143	**0.000**
Karamu	0.058	0.145	0.040	0.324	0.059	0.137
Puriri	0.292	**0.000**	-0.294	**0.000**	0.341	**0.000**
Supplejack	0.094	**0.013**	0.067	0.081	0.079	**0.036**

Materials and Methods

Study locations

Our study was conducted at six forested sites on the North Island, New Zealand, including two sites each in Auckland, Waikato, and Taranaki Regions (Appendix 3.1). We selected three fenced sanctuary sites on the North Island, New Zealand, and identified three nearby forest sites with minimal mammal control (i.e. no mammal control at two sites and low-density possum control at one site every 2-4 years) to serve as reference sites (Appendix 3.2). Paired sanctuary and reference sites were within 25-40km of each other and reference sites were selected to be similar in dominant forest cover, area, elevation range, mean temperature, mean precipitation, landscape context, and land use history (Appendix 3.1, Appendix 3.2). Sanctuary sites might not represent pristine New Zealand forest habitat; Maungatautari is considered floristically poor (MacGibbon 2001), Rotokare encloses regenerating forest, and Tawharnui has a long history of timber harvesting (Murdoch 2008). However, these sanctuaries encompass forests that are typical of their broader regions (MacGibbon 2001, Murdoch 2008). Landscape context was quantified at all sanctuary and reference sites by three metrics that described the landscape spatial pattern in a 20km buffer around each study site, including Patch Area (proportion covered by native forest), Shape Index (native forest fragmentation), and Euclidean Nearest Neighbor (distance to the nearest native forest patch) (Table 3.1, McGarigal et al. 2012). Using a geographic information system, we measured the size of each site as the area covered by indigenous forest habitat only, and did not include area covered by pastures, lakes, or other non-forest habitat. Forest cover was dominated by manuka (*Leptospermum scoparium*) mixed with other indigenous trees in Tawharanui Regional Park and McElroy Scenic Reserve, and Tawa (*Beilschmiedia tawa*) mixed indigenous forest in Maungatautari Ecological Reserve, Te Tapui

Scenic Reserve, Tarata Conservation Area, and Rotokare Scenic Reserve. Median annual total rainfall ranged from 1200 mm to 1800 mm, median annual mean temperature ranged from 13°C to 16°C (both rainfall and temperature data from National Institute of Water and Atmospheric Research 1981-2010 data), and site elevation ranged from sea level to 700m (Appendix 3.2).

Study design

Sampling was conducted at 297 unique sampling stations that were repeatedly visited in 2016 and 2017 (for a total of 761 samples in 2016 and 823 samples in 2017) from January through April, which coincides with the peak fruit production period for native fruiting plants in New Zealand (Wotton and McAlpine 2015). Points were established > 200m apart (MacLeod et al. 2012) along randomly-selected mammal monitoring lines (fenced eradication sites) or along randomly-placed transects (reference sites). More sampling points were placed in the larger sites, but we increased the number of visits to small sites to approximately balance the number of samples per site among all six sites in each year (Appendix 3.2). We placed the maximum number of points possible in smaller sites given the 200m minimum spacing requirement, but the size of the two largest sites (Maungatautari and Te Tapui) made establishing the maximum number of sampling points in these areas prohibitive.

Bird surveys and analysis

See Chapter 2 for a complete description of our bird survey and analysis methodology. We used frugivorous bird density data in our foraging rate and dispersed seed analysis, described below.

Foraging Surveys

Foraging surveys were conducted using focal plant foraging observations (Snow and Snow 1971) to determine the mean number of times a species was observed foraging on fruit of a select plant per five-minute period. We randomly selected focal plants that were clearly visible from the sampling point and observed bird activity in the plant for a 5-min observation period. We conducted foraging surveys on one or more plants during all 761 visits to sampling points in 2016 and 823 visits in 2017. The foraging surveys were started at the end of the bird surveys. All birds observed consuming fruit were identified to species and recorded. We did not record foraging observations if there was any uncertainty as to whether a bird consumed fruit from the focal plant. Separate foraging observations were conducted at all sampling points for six plant species commonly found in one or more paired sites (Cabbage Tree *Cordyline australis*, Karamu *Coprosma* spp., Kawakawa *Piper excelsum*, Mahoe *Melicytus ramiflorus*, Puriri *Vitex lucens*, and Supplejack *Ripogonum scandens*) unless they were not present at the sampling point. We did not conduct foraging surveys for Supplejack in 2016 due to a lack of fruit for this species in this year. Other New Zealand fruiting plants/trees were either uncommon at most of our study sites (e.g. Kotukutuku *Fuchsia excorticata*), did not produce fruit crops during our sampling period (e.g. Rimu *Dacrydium cupressinum*), or were difficult to observe birds foraging in due to their large size (Tawa *Beilschmiedia tawa*). Puriri only occurs at the northern sites (Tawharanui Regional Park and McElroy Scenic Reserve), so foraging surveys were conducted for Puriri at this pair of sites only. At the end of the focal plant observation period, we estimated fruit abundance for each fruiting plant present using an index of fruit crop for each observed plant (0-9 fruits, 10-99 fruits, 100-999 fruits, 1000-9999 fruits, 10000-99999 fruits, 100000+ fruits). We later viewed data distributions for each category and combined categories with few observations with the next higher or lower category before analysis.

Foraging Rate Analysis

We used Wilcoxon Rank Sum tests to compare mean foraging rates (total counts of foraging events detected per 5-min. survey periods) across all eradication sites to mean foraging rates across all reference sites for all six plant species separately. We also used zero-inflated Poisson generalized linear mixed effects models (GLMMs) to evaluate whether frugivorous bird densities (predictor of interest) or other variables were associated with foraging rates. We modeled foraging rates as a function of frugivorous bird densities, fruit abundance, and additive or interactive effects between the two. We expected that foraging rates would be influenced by sampling date and time of survey, but sampling date was correlated with fruit abundance and survey time was correlated with frugivore density, so we did not run models with date or time fixed effects. All models included a random effect to account for repeated visits to sampling points. We also fit a null model that considers an absence of effects except the random effect for repeated sampling. We fit models using the glmmTMB package in R (R development Core Team 2008, Brooks et al. 2017) for all six plant species. The five models were compared using AIC model selection and regression coefficients from all plausible best-fit models to the data ($\Delta AIC < 2$ Burnham and Anderson 2002) were used to interpret relationships between foraging activity and the predictor variables when they were significant ($p < 0.05$). Finally, to assess whether native or non-native bird species were contributing more to foraging activity, we used Kendall correlation tests to assess relationships between foraging rates and total frugivorous bird density, native frugivorous bird density, and recently introduced frugivorous bird density. We chose to evaluate relationships between foraging rates and various bird densities separately using Kendall correlation tests instead of including them in the GLMM analysis because total frugivorous bird density was correlated with native and recently introduced bird densities, so we did not choose to compete models with these correlated covariates in the AIC model selection analysis.

Dispersed Seed Sampling

To estimate dispersed-seed counts, bird-dispersed seeds were collected in the three eradication sites and three reference sites using two different sampling methods. We set 199 0.5m x 0.5m nets (seed traps) at a subset of the 297 sampling points to catch bird droppings and collected bird-dispersed seeds (seeds with fleshy pulp fully removed) from the nets approximately every 2-3 weeks. Twenty-six percent of the traps were set approximately 50m from tracks to allow easier access when revisiting nets and collecting seeds while the remaining 74% were randomly located. We also collected seeds from fresh bird droppings found on the forest floor along 1m x 100m strip transects (n = 216) that were established in a random direction near a randomly-selected subset of sampling points. We used these two different methods to sample seed rain because each method has strengths and weaknesses that are offset by the other method. The transects allowed us to collect seed rain over a large area, thus increasing our sample size, but we were concerned that smaller seeds would be missed during transect searches. Seed traps are made of fine mesh that captures even the smallest seeds in bird droppings, but seed traps only sample a small area and thus capture fewer dispersed seeds. All dispersed seeds found in nets and on transects were collected and identified using a reference seed library collected from fresh fruit at each site, a dichotomous key (Webb and Simpson 2001), and a dissecting scope. Puriri only occurs at the northern sites (Tawharanui Regional Park and McElroy Scenic Reserve), so dispersed seeds were collected for Puriri at this pair of sites only.

Dispersed Seed Analysis

Analyses were only run on plant species with sufficient data for analysis, including Cabbage Tree, Karamu (combination of *Coprosma robusta* and *Coprosma lucida*), Puriri, and Supplejack. Dispersed seed data from seed traps and transects for both 2016 and 2017 were pooled to increase the sample size in the analysis. We conducted a similar analysis of dispersed seed counts (total counts of bird-dispersed seeds caught in traps or collected on transects) as we did for foraging rates. We used AIC model selection (Burnham and Anderson 2002) and zero-inflated negative binomial generalized linear mixed models to assess whether frugivore densities, fruit abundance, or both frugivore densities and fruit abundance, influenced dispersed seed counts by comparing models with these effects to each other and to null models with only a random effect for repeated visits to sampling points. We also included a fixed effect to account for heterogeneity in the sampling method (seed trap or transect) used to collect dispersed seeds. Including the fixed effect added four models where sampling method was an additive fixed effect to frugivore densities, fruit abundance, or additive or interactive effects of both, and one model where sampling method was the sole predictor. We fit models using the glmmTMB package in R (R development Core Team 2008, Brooks et al. 2017). These ten models were compared using AIC model selection and regression coefficients from all plausible best-fit models to the data (ΔAIC < 2 Burnham and Anderson 2002) were used to interpret relationships between dispersed seed counts and the predictor variables when they were significant ($p < 0.05$). We used Kendall correlation tests to assess relationships between dispersed seed counts and total frugivorous bird density, native frugivorous bird density, and recently introduced frugivorous bird density. As before, we chose to evaluate relationships between dispersed seed counts and native or recently introduced bird densities separately using Kendall correlation tests instead of including them in the GLMM analysis because total frugivorous bird density was correlated with native and introduced bird densities, so we did not want to compete models with these correlated covariates in the AIC model selection analysis.

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CONCLUDING REMARKS

My research demonstrates that fenced mainland island sanctuaries effectively conserve native bird populations and seed dispersal in New Zealand forests. Furthermore, I show that paired acoustic sampling can correct biases in acoustic data relative to human observers when estimating bird population densities for multiple New Zealand forest birds. These findings provide some of the first evidence that successful population recovery outcomes observed following mammal eradication on small islands can be replicated on large islands or continents using fenced sanctuaries, and that these benefits may extend to important ecosystem processes. This work also suggests a promising pathway to expand bird population monitoring in New Zealand using acoustic sampling. My dissertation provides a foundation for several important future research avenues. Some potential research priorities on bird and seed dispersal recovery in fenced sanctuaries include:

1) How do the benefits of fenced ‘mainland island’ sanctuaries for birds and seed dispersal compare to other approaches, such as mammal eradication on offshore islands and suppression within unfenced mainland sanctuaries?
2) Do the benefits of fenced sanctuaries for birds and seed dispersal spillover into nearby forests, i.e. what is the spatial footprint of fenced sanctuaries for bird and seed dispersal recovery and restoration?
3) How does mammal eradication in fenced sanctuaries affect other ecological processes such as pollination and seed predation, and how do these in turn affect plant recruitment and survival?

4) Does higher seed dispersal quantity in sanctuaries provide a fitness benefit to plants, e.g. higher germination and seedling survival?
5) What other taxonomic groups benefit from fenced sanctuaries and what are their contributions to seed dispersal and other ecological processes?

Some potential research priorities on paired acoustic monitoring of New Zealand birds include:

1) Does the bias in acoustic data relative to human survey data, and the ability to correct this bias with paired acoustic sampling, differ in non-forest habitats, e.g. shrubland, farmland, and alpine ecosystems? If so, for which groups of species?
2) Can the bias in acoustic data be corrected when using different acoustic recording units in the same monitoring program by including a covariate to account for recorder variation?
3) How will the ability to correct bias in acoustic data relative to human survey data be affected if using automated identification algorithms to transcribe audio recordings instead of using human transcribers?
4) How feasible is it to incorporate acoustic sampling into existing bird monitoring programs? What are the relative costs and benefits of adding acoustic sampling?

These are among a few of many potential future questions that have emerged from my study. My dissertation, together with this research agenda, has the potential to advance avian ecology and conservation in New Zealand and beyond. Specifically, my research offers new insights into fenced ‘mainland island’ sanctuaries as a model for restoring biodiversity and ecosystem processes in the many places under threat from invasive species.

APPENDICES

Appendix 1.1. Characteristics of the six study areas in which we conducted bird point counts using both human observers and autonomous recording units (ARUs). Total annual precipitation and mean annual temperature data are from the National Institute of Water and Atmospheric Research 29-year average (1981-2010). Area indicates the total size of all forest patch(es) within a reserve, not the size of the entire reserve. The sanctuary column indicates whether the site is a fenced sanctuary or not.

Study area	**Latitude/ Longitude**	**Total Annual Precip. (mm)**	**Mean Annual Temp. (°C)**	**Mean Elev. (m)**	**Area (ha)**	**Sanctuary?**
Maungatautari Ecological Reserve	38°02’58” S, 175°33’36” E	1200	13	442	3210	Yes
McElroy Scenic Reserve	36°27’32” S, 174°41’32” E	1400	16	88	150	No
Rotokare Scenic Reserve	39°27’14” S, 174°24’35” E	1400	13	221	215	Yes
Tarata Conservation Area	39°10’05” S, 174°21’24” E	1800	13	147	149	No
Tawharanui Regional Park	36°22’18” S, 174°50’33” E	1200	16	44	90	Yes
Te Tapui Scenic Reserve	37°48’38” S, 175°37’23” E	1200	13	269	2330	No

Appendix 1.2. Species detected across all study sites in 2017, indigenous status, and whether density was estimated or not for the species and the reason.

English name	**Māori name**	**Scientific name**	**Indigenous Status**	**Density estimated**	**Reason**
Australian magpie	Makipae	*Gymnorhina tibicen* (Latham, 1802)	Introduced	Yes	
Bellbird	Korimako	***Anthornis melanura*** (Sparrman, 1786)	Native	Yes	
Bush parrot	Kākā	*Nestor meridionalis* (Gmelin, 1788)	Native	No	< 20 detections, species often detected as flyovers
Chaffinch	Pahirini	*Fringilla coelebs* Linnaeus, 1758	Introduced	Yes	
Common myna	NA	*Acridotheres tristis* (Linnaeus, 1766)	Introduced	Yes	
Common starling	NA	*Sturnus vulgaris* Linnaeus, 1758	Introduced	No	< 20 detections
Eastern Rosella	NA	*Platycercus eximius* (Shaw, 1792)	Introduced	No	< 20 detections
Eurasian Blackbird	Manu pango	*Turdus merula* Linnaeus, 1758	Introduced	No	< 20 detections
European goldfinch	NA	*Carduelis* (Linnaeus, 1758)	Introduced	No	< 20 detections
European greenfinch	NA	*Carduelis chloris* (Linnaeus, 1758)	Introduced	No	< 20 detections
Fernbird	Mātātā	*Bowdleria punctata* Quoy & Gaimard, 1830	Native	No	< 20 detections
Grey warbler	Riroriro	*Gerygone igata* (Quoy & Gaimard, 1830)	Native	Yes	
House sparrow	Tiu	*Passer domesticus* (Linnaeus, 1758)	Introduced	No	< 20 detections, uses mainly edge habitat not forest interior
Morepork	Ruru	*Ninox novaeseelandiae* (Gmelin, 1788)	Native	No	Study not designed to observe nocturnal species
New Zealand falcon	Kārearea	*Falco novaeseelandiae* Gmelin, 1788	Native	No	< 20 detections, species often detected as flyovers
New Zealand Fantail	Pīwakawaka	*Rhipidura fuliginosa* (Sparrman, 1787)	Native	Yes	

New Zealand pigeon	Kererū	*Hemiphaga novaeseelandiae* (Gmelin, 1789)	Native	Yes	
North Island Robin	Toutouwai	*Petroica longipes* (Garnot, 1827)	Native	Yes	
North Island Saddleback	Tīeke	*Philesturnus rufusater* (Lesson, 1828)	Native	Yes	
Parson bird	Tūī	*Prosthemadera novaeseelandiae* (Gmelin, 1788)	Native	Yes	
Red-crowned parakeet	Kākāriki	*Cyanoramphus novaezelandiae* (Sparrman, 1787)	Native	No	< 20 detections
Rifleman	Tītipounamu	*Acanthisitta chloris* (Sparrman, 1787)	Native	No	< 20 detections
Sacred kingfisher	Kōtare	*Todiramphus sanctus* Vigors & Horsfield, 1827	Native	No	< 20 detections
Shining cuckoo	Pīpīwharauroa	*Chrysococcyx lucidus* (Gmelin, 1788)	Native	No	< 20 detections
Silvereye	Tauhou	*Zosterops lateralis* (Latham, 1802)	Introduced/ Naturalised	Yes	
Song thrush	NA	*Turdus philomelos* Brehm, 1831	Introduced	No	< 20 detections
Stitchbird	Hihi	*Notiomystis cincta* (du Bus de Gisignies, 1839)	Native	No	< 20 detections
Tomtit	Miromiro	*Petroica macrocephala* (Gmelin, 1789)	Native	Yes	
Whitehead	Pōpokatea	*Mohoua albicilla* (Lesson, 1830)	Native	Yes	

Appendix 1.3. Estimates of effective detection radius, τ, in meters, and 95% confidence intervals for 13 bird species detected across six indigenous forest sites in 2017 on the North Island of New Zealand, estimated by fitting distance sampling models (Buckland et al. 2001) to data from point counts conducted by human observers.

Species	$\boldsymbol{\tau}$	**LCL**	**UCL**
Bellbird	46.300	45.018	47.254
Chaffinch	33.174	30.880	36.601
Fantail	22.793	18.111	24.989
Grey Warbler	50.962	47.807	51.976
Kereru	29.551	27.341	30.873
Magpie	85.173	82.551	88.923
Myna	41.967	38.962	44.495
North Island Robin	32.657	30.795	33.617
North Island Saddleback	54.129	52.610	56.192
Silvereye	24.168	21.953	28.734
Tomtit	16.345	15.345	16.569
Tui	53.313	51.827	54.787
Whitehead	16.345	11.485	20.281

Appendix 1.4. Estimates of the scaling constant δ (a measure of the ratio of the effective detection radius between bird count data derived from ARU and human survey methods) and 95% confidence intervals produced using 1) the maximum likelihood approach (MLE δ) of Van Wilgenburg et al. (2017) where $\delta = \sqrt{\exp(\beta)}$ in generalised linear mixed effects models, 2) using the MLE approach over 50 repeated subsamples of 70% of the data (calibration δ), and 3) by estimating empirical ratios of mean bird count totals from ARU surveys to mean count totals from human surveys over 50 repeated subsamples of 30% of the data. A δ value of 1.0 indicates that ARU count data and human count data are the same.

Species	**LCL**	**MLE δ**	**UCL**	**LCL**	**Calibration δ**	**UCL**	**LCL**	**Empirical Ratio δ**	**UCL**
Bellbird	0.744	0.835	0.936	0.730	0.833	0.949	0.712	0.827	0.943
Chaffinch	0.999	1.247	1.573	0.957	1.239	1.628	1.004	1.142	1.279
Fantail	0.859	0.967	1.091	0.838	0.962	1.105	0.926	0.998	1.071
Grey Warbler	0.832	0.917	1.011	0.819	0.916	1.025	1.020	1.048	1.076
Kereru	0.682	0.814	0.971	0.644	0.793	0.975	0.876	1.031	1.186
Magpie	0.814	0.954	1.118	0.780	0.943	1.140	0.948	1.020	1.093
Myna	0.788	1.021	1.324	0.751	1.018	1.383	0.990	1.205	1.419
N. Island Robin	0.724	0.884	1.079	0.712	0.897	1.131	0.964	1.015	1.065
N. Island Saddleback	0.889	1.045	1.231	0.872	1.052	1.275	0.801	0.902	1.003
Silvereye	0.781	0.851	0.927	0.767	0.846	0.933	1.010	1.080	1.150
Tomtit	0.993	1.121	1.269	0.967	1.113	1.285	0.892	0.961	1.030
Tui	0.851	0.919	0.993	0.841	0.919	1.004	0.929	0.975	1.021
Whitehead	0.784	0.967	1.193	0.755	0.963	1.230	0.942	1.029	1.115

Appendix 2.1. Species detected across all study sites in 2016 and 2017, associated indigenous status, and whether density was estimated or not for the species and the reason.

English name	**Maori name**	**Scientific name**	**Indigenous Status**	**Density estimated**	**Reason**
Bellbird	Korimako	*Anthornis melanura* (Sparrman, 1786)	Native	Yes	
Eurasian Blackbird	Manu pango	*Turdus merula* Linnaeus, 1758	Introduced	Yes	
Chaffinch	Pahirini	*Fringilla coelebs* Linnaeus, 1758	Introduced	Yes	
New Zealand falcon	Kārearea	*Falco novaeseelandiae* Gmelin, 1788	Native	No	Few detections, home range extends beyond distances between sampling points
New Zealand Fantail	Pīwakawaka	*Rhipidura fuliginosa* (Sparrman, 1787)	Biogeographically recent native	Yes	
Fernbird	Mātātā	*Bowdleria punctata* Quoy & Gaimard, 1830	Native	No	Few detections
European goldfinch	NA	*Carduelis carduelis* (Linnaeus, 1758)	Introduced	No	Few detections
European greenfinch	NA	*Chloris chloris* (Christidis and Boles, 2008)	Introduced	No	Few detections
Grey warbler	Riroriro	*Gerygone igata* (Quoy & Gaimard, 1830)	Biogeographically recent native	Yes	
Stitchbird	Hihi	*Notiomystis cincta* (du Bus de Gisignies, 1839)	Native	No	Few detections
House sparrow	Tiu	*Passer domesticus* (Linnaeus, 1758)	Introduced	No	Few detections, uses mainly edge habitat not forest interior
Kākā	Kākā	*Nestor meridionalis* (Gmelin, 1788)	Native	Yes	
Red-crowned parakeet	Kākāriki	*Cyanoramphus novaezelandiae* (Sparrman, 1787)	Native	Yes	
New Zealand pigeon	Kererū	*Hemiphaga novaeseelandiae* (Gmelin, 1789)	Native	Yes	
Sacred kingfisher	Kōtare	*Todiramphus sanctus* Vigors & Horsfield, 1827	Native	No	Few detections
Australian magpie	Makipae	*Gymnorhina tibicen* (Latham, 1802)	Introduced	No	Home range extends beyond distances between sampling points
Common myna	NA	*Acridotheres tristis* (Linnaeus, 1766)	Introduced	No	Uses mainly edge habitat not forest interior
N. Island Robin	Toutouwai	*Petroica longipes* (Garnot, 1827)	Native	Yes	
Rifleman	Tītipounamu	*Acanthisitta chloris* (Sparrman, 1787)	Native	No	Few detections
Eastern Rosella	NA	*Platycercus eximius* (Shaw, 1792)	Introduced	Yes	
Morepork	Ruru	*Ninox novaeseelandiae* (Gmelin, 1788)	Native	No	Study not designed to observe nocturnal species
N. Island Saddleback	Tīeke	*Philesturnus rufusater* (Lesson, 1828)	Native	Yes	
Shining cuckoo	Pīpīwharauroa	*Chrysococcyx lucidus* (Gmelin, 1788)	Native	No	Few detections

Silvereye	Tauhou	*Zosterops lateralis* (Latham, 1802)	Biogeographically recent native	Yes	
Song thrush	NA	*Turdus philomelos* Brehm, 1831	Introduced	No	Few detections
Common starling	NA	*Sturnus vulgaris* Linnaeus, 1758	Introduced	No	Few detections
Tomtit	Miromiro	*Petroica macrocephala* (Gmelin, 1789)	Native	Yes	
Tūī	Tūī	*Prosthemadera novaeseelandiae* (Gmelin, 1788)	Native	Yes	
Whitehead	Pōpokatea	*Mohoua albicilla* (Lesson, 1830)	Native	Yes	

Appendix 2.2. Model selection results, regression coefficient values, and lower and upper confidence limits (LCL and UCL) from all equally-likely best-fit models (ΔAIC < 2, Burnham and Anderson 2002). AIC = Akaike's Information Criterion, ΔAIC = difference in AIC between current model and model with the lowest AIC, Rel. LL = relative log-likelihood, w = Akaike model weight, see Burnham and Anderson 2002). We compared four models for all species except those marked with an asterisk. Sanctuary + Area (model with a 'sanctuary' fixed effect for sanctuary vs. reference sites and an 'area' fixed effect for the size in ha of each site); Sanctuary only, Area only, and a null model without either fixed effect. All four models included a random effect for repeated visits to sampling points. For species marked with an asterisk, we did not include any sanctuary fixed effect models because these species were only found in sanctuaries so comparisons between sanctuary and reference sites could not be made. We ran two models only for these species, an Area model and a null model, both with a random effect for sampling points. Coefficients and confidence intervals were estimated using a bootstrapping procedure (see methods).

Species	model	AIC	ΔAIC	Rel. LL	*w*	Intercept	LCL	UCL	Sanctuary Coeff.	LCL	UCL	Area Coeff.	LCL	UCL
2016														
Bellbird	Sanctuary + Area	854.11	0.00	1.00	1.00	-2.25	-2.70	-1.93	3.01	2.69	3.45	-0.98	-1.14	-0.75
Blackbird	Sanctuary	339.34	0.00	1.00	0.71	-2.41	-3.30	-1.85	1.23	0.81	1.82			
Blackbird	Sanctuary + Area	341.16	1.82	0.40	0.29	-2.39	-3.07	-1.80	1.21	0.78	1.73	-0.03	-0.25	0.17
Chaffinch	Sanctuary	153.50	0.00	1.00	0.36	-6.89	-7.78	-5.99	1.61	0.70	2.42			
Chaffinch	Sanctuary + Area	153.71	0.21	0.90	0.33	-6.81	-7.81	-5.79	1.83	1.21	2.68	-0.47	-0.75	-0.15
Chaffinch	null	154.59	1.09	0.58	0.21	-6.38	-6.99	-5.73						
Fantail	Sanctuary	625.24	0.00	1.00	0.43	1.59	1.43	1.76	0.20	-0.02	0.40			
Fantail	null	626.00	0.76	0.68	0.29	1.68	1.54	1.80						
Fantail	Sanctuary + Area	627.04	1.80	0.41	0.17	1.57	1.45	1.74	0.22	0.03	0.41	-0.04	-0.12	0.06
Grey Warbler	null	693.20	0.00	1.00	0.50	0.11	0.02	0.17						
Grey Warbler	Area	694.88	1.68	0.43	0.22	0.11	0.06	0.18				0.03	-0.04	0.09
Grey Warbler	Sanctuary	695.08	1.88	0.39	0.20	0.09	-0.01	0.19	0.04	-0.10	0.18			
Kaka	null	56.57	0.00	1.00	1.00	-7.27	-8.59	-3.75	*	*	*			
Kaka	Area	model failed to converge				NA	NA	NA	NA	NA	NA	NA	NA	NA
Kakariki	null	25.63	0.00	1.00	1.00	-0.20	-1.36	0.71	*	*	*			
Kakariki	Area	model failed to converge				NA	NA	NA	NA	NA	NA	NA	NA	NA
Kereru	Sanctuary + Area	512.20	0.00	1.00	0.99	-0.03	-0.30	0.23	0.65	0.37	0.92	-0.32	-0.46	-0.22
N. Isl. Robin	null	203.98	0.00	1.00	0.55	-1.02	-1.68	-0.54	*	*	*			
N. Isl. Robin	Area	204.35	0.37	0.83	0.45	-1.06	-1.63	-0.46	*	*	*	0.17	-0.08	0.50

Rosella	null	26.09	0.00	1.00	1.00	-3.21	-7.76	-1.29	*	*	*			
Rosella	Area	model failed to converge				NA	NA	NA	NA	NA	NA	NA	NA	NA
Saddleback	Area	203.82	0.00	1.00	1.00	-1.03	-1.48	-0.76	*	*	*	-1.08	-1.37	-0.91
Silvereye	Sanctuary	889.22	0.00	1.00	0.63	1.16	1.00	1.29	-0.63	-0.85	-0.47			
Silvereye	Sanctuary + Area	890.37	1.15	0.56	0.35	1.15	1.01	1.34	-0.59	-0.81	-0.41	-0.11	-0.24	-0.01
Tomtit	Sanctuary + Area	560.01	0.00	1.00	0.69	0.82	0.58	1.15	1.45	1.11	1.70	-0.14	-0.21	-0.05
Tomtit	Sanctuary	561.66	1.65	0.44	0.31	0.85	0.66	1.05	1.37	1.14	1.50			
Tui	Sanctuary + Area	924.38	0.00	1.00	1.00	0.08	-0.06	0.20	1.76	1.63	1.89	-0.50	-0.57	-0.44
Whitehead	Area	226.94	0.00	1.00	0.63	-3.75	-5.34	-2.03	*	*	*	-0.55	-0.94	-0.20
Whitehead	null	228.05	1.11	0.58	0.37	-4.48	-5.68	-3.01	*	*	*			
2017														
Bellbird	Sanctuary + Area	663.25	0.00	1.00	1.00	-3.60	-4.13	-3.08	3.56	3.11	4.07	-0.83	-1.02	-0.65
Blackbird	Sanctuary	339.53	0.00	1.00	0.71	-2.37	-2.98	-1.75	1.21	0.73	1.75			
Blackbird	Sanctuary + Area	341.32	1.79	0.41	0.29	-2.37	-3.21	-1.79	1.22	0.68	1.82	0.00	-0.17	0.16
Chaffinch	null	189.41	0.00	1.00	0.37	-5.49	-6.29	-4.57						
Chaffinch	Sanctuary	190.05	0.63	0.73	0.27	-5.70	-6.57	-4.72	0.62	-0.15	1.18			
Chaffinch	Area	190.47	1.06	0.59	0.22	-5.59	-6.50	-4.33				0.28	0.01	0.67
Fantail	Sanctuary + Area	804.57	0.00	1.00	1.00	1.66	1.53	1.76	0.55	0.43	0.68	-0.24	-0.29	-0.18
Grey Warbler	null	778.23	0.00	1.00	0.30	0.75	0.68	0.81						
Grey Warbler	Sanctuary + Area	778.57	0.34	0.84	0.25	0.82	0.74	0.89	-0.15	-0.31	0.00	0.07	-0.01	0.14
Grey Warbler	Sanctuary	778.59	0.36	0.84	0.25	0.80	0.73	0.89	-0.13	-0.23	0.00			
Grey Warbler	Area	778.98	0.75	0.69	0.20	0.75	0.66	0.81				0.04	-0.03	0.11
Kaka	null	116.95	0.00	1.00	0.52	-5.93	-7.30	-4.47	*	*	*			
Kaka	Area	117.08	0.13	0.94	0.48	-5.15	-5.97	-4.19	*	*	*	-0.62	-0.92	-0.32
Kakariki	null	11.67	0.00	1.00	1.00	-5.20	-5.20	-5.20	*	*	*			
Kakariki	Area	model failed to converge				NA	NA	NA	NA	NA	NA	NA	NA	NA
Kereru	Sanctuary + Area	529.01	0.00	1.00	1.00	-0.03	-0.34	0.23	0.78	0.52	0.98	-0.33	-0.46	-0.25
N. Isl. Robin	Area	313.94	0.00	1.00	0.53	0.71	0.38	0.95				0.56	0.34	0.79
N. Isl. Robin	Sanctuary + Area	314.15	0.21	0.90	0.47	-7.28	-17.97	0.75	8.04	0.04	18.72	0.51	0.25	0.79
Rosella	null	35.81	0.00	1.00	1.00	-3.59	-6.86	-1.24						
Rosella	Area	model failed to converge				NA	NA	NA	NA	NA	NA	NA	NA	NA

Saddleback	Area	218.40	0.00	1.00	1.00	-0.52	-0.77	-0.24	*	*	*	-0.92	-1.16	-0.75
Silvereye	Sanctuary	1023.11	0.00	1.00	0.71	2.00	1.90	2.10	-0.43	-0.57	-0.24			
Silvereye	Sanctuary + Area	1024.96	1.85	0.40	0.28	1.98	1.88	2.12	-0.41	-0.55	-0.23	-0.03	-0.12	0.05
Tomtit	Sanctuary + Area	564.58	0.00	1.00	0.99	0.95	0.71	1.19	1.17	0.92	1.40	-0.28	-0.37	-0.21
Tui	Sanctuary + Area	985.64	0.00	1.00	1.00	0.75	0.64	0.87	0.86	0.69	0.99	-0.26	-0.32	-0.19
Whitehead	null	260.95	0.00	1.00	0.71	-0.65	-1.20	-0.05	*	*	*			
Whitehead	Area	262.78	1.83	0.40	0.29	-0.62	-1.33	-0.04	*	*	*	0.08	-0.18	0.31

*Models with 'sanctuary' effect were not part of the model set because the species was only found in sanctuary sites, so sanctuary vs. reference comparisons could not be made

Appendix 2.3. Distance sampling (Buckland et al. 2001) estimates of detection probability (p), and effective detection radius (EDR) from all best-fit models (ΔAICc >2) for all fifteen bird species in 2016 and 2017. Key detection functions and series expansions fit to the distance data included: half normal function with a hermite polynomial expansion (HN-Herm-Poly), hazard rate function with a simple polynomial expansion (HR-Sim-Poly), and uniform function with a cosine expansion (Uni-Cos). Trunc. (m) is the truncation distance in meters that the distribution of distances was truncated to, if applicable. Covariate indicates whether the best-fit models included a covariate effect to explain heterogeneity in detection probabilities (models with observer, date of survey, visibility, track, percent cloud cover, precipitation, wind, and survey time covariates were all competed using model selection with Akaike's Information Criterion with small sample size correction (AICc)). ΔAICc indicates the difference in AICc values between the best-fit model and other models in the candidate model set, k is the number of parameters in the model, and Log Lik is the log-likelihood.

Year	Species	Function	Trunc (m)	Treatment	Covariate	AICc	ΔAICc	k	Log Lik	EDR	p
2016	Bellbird	HR-Sim-Poly	99	Sanctuary	None	13394.50	0.00	5	-6692.13	24.25	0.04
2016	Bellbird	HR-Sim-Poly	99	Reference	None	13394.50	0.00	5	-6692.13	56.03	0.32
2016	Blackbird	HR-Sim-Poly	65	Sanctuary	Observer	805.20	0.00	6	-396.05	20.70	0.10
2016	Blackbird	HR-Sim-Poly	65	Reference	Observer	805.20	0.00	6	-396.05	30.66	0.22
2016	Chaffinch	HR-Sim-Poly	80	Sanctuary	None	831.00	0.00	4	-411.24	31.48	0.15
2016	Chaffinch	HR-Sim-Poly	80	Reference	None	831.00	0.00	4	-411.24	32.90	0.17
2016	Fantail	HR-Sim-Poly	46	Sanctuary	None	1638.69	0.00	4	-815.30	22.13	0.23
2016	Fantail	HR-Sim-Poly	46	Reference	None	1638.69	0.00	4	-815.30	17.94	0.15
2016	Grey Warbler	HR-Sim-Poly	99	Sanctuary	Observer	5905.77	0.00	6	-2946.81	60.91	0.38
2016	Grey Warbler	Uni-Cos	99	Sanctuary	None	5907.25	1.48	3	-2950.60	57.39	0.34
2016	Grey Warbler	HR-Sim-Poly	99	Reference	Observer	5905.77	0.00	6	-2946.81	64.99	0.43
2016	Grey Warbler	Uni-Cos	99	Reference	None	5907.25	1.48	3	-2950.60	67.87	0.47
2016	Kaka	HR-Sim-Poly	86	Sanctuary	None	866.96	0.00	2	-431.42	37.93	0.19
2016	Kakariki	HR-Sim-Poly	58	Sanctuary	None	308.93	0.00	2	-152.30	38.04	0.43
2016	Kakariki	Uni-Cos	58	Sanctuary	None	308.98	0.05	1	-153.44	33.51	0.33
2016	Kakariki	HN-Herm-Poly	58	Sanctuary	None	309.80	0.87	1	-153.85	32.70	0.32
2016	Kereru	Uni-Cos	45	Sanctuary	None	2964.51	0.00	2	-1480.23	27.75	0.38

2016	Kereru	Uni-Cos	45	Reference	None	2964.51	0.00	2	-1480.23	29.34	0.43
2016	N.I. Robin	Uni-Cos	56	Sanctuary	None	276.03	0.00	3	-134.88	22.26	0.16
2016	Rosella	HN-Herm-Poly	55	Sanctuary	Track	1151.25	0.00	4	-571.43	22.69	0.17
2016	Rosella	HN-Herm-Poly	55	Reference	Track	1151.25	0.00	4	-571.43	36.11	0.43
2016	Saddleback	HR-Sim-Poly	94	Sanctuary	None	2480.47	0.00	3	-1237.19	40.81	0.19
2016	Silvereye	HR-Sim-Poly	60	Sanctuary	Observer	6068.89	0.00	6	-3028.38	35.21	0.34
2016	Silvereye	HR-Sim-Poly	60	Reference	Observer	6068.89	0.00	6	-3028.38	42.57	0.50
2016	Tomtit	HR-Sim-Poly	44	Sanctuary	None	2843.70	0.00	5	-1416.74	13.73	0.10
2016	Tomtit	Uni-Cos	44	Sanctuary	None	2844.78	1.08	4	-1418.33	19.67	0.20
2016	Tomtit	HR-Sim-Poly	44	Reference	None	2843.70	0.00	5	-1416.74	28.13	0.41
2016	Tomtit	Uni-Cos	44	Reference	None	2844.78	1.08	4	-1418.33	30.53	0.48
2016	Tui	HR-Sim-Poly	98	Sanctuary	None	11682.84	0.00	5	-5836.39	27.05	0.08
2016	Tui	HR-Sim-Poly	98	Reference	None	11682.84	0.00	5	-5836.39	47.96	0.24
2016	Whitehead	HR-Sim-Poly	45	Sanctuary	Observer	1087.57	0.00	3	-540.70	25.71	0.33
2017	Bellbird	HR-Sim-Poly	100	Sanctuary	None	14074.91	0.00	6	-7031.17	25.67	0.07
2017	Bellbird	HR-Sim-Poly	100	Reference	None	14074.91	0.00	6	-7031.17	69.39	0.48
2017	Blackbird	HR-Sim-Poly	64	Sanctuary	None	2145.85	0.00	4	-1068.81	37.89	0.35
2017	Blackbird	HR-Sim-Poly	64	Reference	None	2145.85	0.00	4	-1068.81	42.86	0.45
2017	Chaffinch	HR-Sim-Poly	55	Sanctuary	None	1173.90	0.00	4	-582.79	33.96	0.38
2017	Chaffinch	HR-Sim-Poly	55	Reference	None	1173.90	0.00	4	-582.79	33.21	0.36
2017	Fantail	Uni-Cos	36	Sanctuary	None	3452.72	0.00	6	-1720.32	20.30	0.32
2017	Fantail	Uni-Cos	36	Reference	None	3452.72	0.00	6	-1720.32	22.88	0.40
2017	Grey Warbler	HR-Sim-Poly	73	Sanctuary	None	4118.77	0.00	4	-2055.36	49.85	0.47
2017	Grey Warbler	HR-Sim-Poly	73	Reference	None	4118.77	0.00	4	-2055.36	49.10	0.45
2017	Kaka	HR-Sim-Poly	NA	Sanctuary	None	681.28	0.00	2	-338.56	42.48	0.18
2017	Kaka	Uni-Cos	NA	Sanctuary	None	683.01	1.74	3	-338.34	38.91	0.15
2017	Kaka	HN-Herm-Poly	NA	Sanctuary	None	683.14	1.86	1	-340.54	45.78	0.21

2017	Kakariki	HR-Sim-Poly	NA	Sanctuary	None	284.51	0.00	2	-140.07	28.63	0.16
2017	Kakariki	HN-Herm-Poly	NA	Sanctuary	None	284.93	0.41	1	-141.40	29.94	0.18
2017	Kakariki	Uni-Cos	NA	Sanctuary	None	285.25	0.74	2	-140.44	30.23	0.18
2017	Kereru	HR-Sim-Poly	63	Sanctuary	None	4765.56	0.00	5	-2377.72	29.05	0.21
2017	Kereru	HN-Herm-Poly	63	Sanctuary	None	4767.09	1.53	3	-2380.52	26.60	0.18
2017	Kereru	HR-Sim-Poly	63	Reference	None	4765.56	0.00	5	-2377.72	32.11	0.26
2017	Kereru	HN-Herm-Poly	63	Reference	None	4767.09	1.53	3	-2380.52	26.52	0.18
2017	N.I. Robin	Uni-Cos	56	Sanctuary	None	883.73	0.00	3	-438.82	23.61	0.18
2017	N.I. Robin	HR-Sim-Poly	56	Sanctuary	None	883.92	0.19	3	-438.92	24.09	0.19
2017	N.I. Robin	HN-Herm-Poly	56	Sanctuary	None	885.32	1.59	1	-441.65	27.11	0.23
2017	Rosella	HN-Herm-Poly	60	Sanctuary	None	756.47	0.00	2	-126.01	23.72	0.16
2017	Rosella	HN-Herm-Poly	60	Reference	None	756.47	0.00	2	-126.01	37.41	0.39
2017	Saddleback	HN-Herm-Poly	69	Sanctuary	None	4446.95	0.00	3	-2220.45	38.40	0.31
2017	Silvereye	HR-Sim-Poly	48	Sanctuary	None	4992.50	0.00	4	-2492.24	29.23	0.37
2017	Silvereye	HR-Sim-Poly	48	Reference	None	4992.50	0.00	4	-2492.24	31.51	0.43
2017	Tomtit	HN-Herm-Poly	32	Sanctuary	Observer	3671.94	0.00	4	-1831.90	17.02	0.28
2017	Tomtit	HN-Herm-Poly	32	Reference	Observer	3671.94	0.00	4	-1831.90	23.76	0.55
2017	Tui	HR-Sim-Poly	98	Sanctuary	None	20456.39	0.00	6	-10222.17	33.87	0.12
2017	Tui	Uni-Cos	98	Sanctuary	None	20457.95	1.56	8	-10220.94	34.69	0.13
2017	Tui	HR-Sim-Poly	98	Reference	None	20456.39	0.00	6	-10222.17	44.31	0.20
2017	Tui	Uni-Cos	98	Reference	None	20457.95	1.56	8	-10220.94	44.56	0.21
2017	Whitehead	HR-Sim-Poly	39	Sanctuary	None	1595.30	0.00	3	-794.60	26.18	0.45
2017	Whitehead	HR-Sim-Poly	39	Sanctuary	Track	1596.03	0.73	3	-794.96	26.78	0.47

Appendix 3.1. A map of the six study areas in the North Island of New Zealand in which we compared bird densities, foraging rates, and dispersed-seed counts in 2016 and 2017, including three fenced mainland island sanctuaries shown with black triangles (1- Tawharanui Regional Park, 4- Maungatautari Ecological Reserve, 6- Rotokare Scenic Reserve) and three paired reference sites with minimal mammal control shown with white triangles (2- McElroy Scenic Reserve, 3- Te Tapui Scenic Reserve, and 5- Tarata Conservation Area).

Appendix 3.2. Characteristics of the six study areas in which we compared bird densities, foraging rates, and dispersed seed counts in 2016 and 2017, including three fenced sanctuary sites and three paired reference sites.

	Tawharanui Regional Park ***Sanctuary***	**McElroy Scenic Reserve** ***Reference***	**Maungatautari Ecological Reserve** ***Sanctuary***	**Te Tapui Scenic Reserve** ***Reference***	**Rotokare Scenic Reserve** ***Sanctuary***	**Tarata Conservation Area** ***Reference***
No. sampling points	17	20	103	115	28	14
No. samples[1] 2016	118	144	133	152	109	105
No. samples[1] 2017	111	146	140	160	140	126
Total ann. precip. (mm)[2]	1200	1400	1200	1200	1400	1800
Mean ann. temp. (°C) [2]	16	16	13	13	13	13
Elev. range (m)	0-100	0-120	250-700	200-500	170-300	100-240
Area (ha)[3]	90	148	3210	2330	215	150
Fence completion year	2004	NA	2006	NA	2008	NA
Dominant forest cover	Manuka mixed native	Manuka mixed native	Rimu-Tawa mixed native	Rimu-Tawa mixed native	Tawa mixed native	Tawa mixed native
Latitude/ longitude	36°22’18” S, 174°50’33” E	36°27’32” S, 174°41’32” E	38°02’58” S, 175°33’36” E	37°48’38” S, 175°37’23” E	39°27’14” S, 174°24’35” E	39°10’05” S, 174°21’24” E
Mammal control	Eradication of all mammal predators, except mice	None	Eradication of all mammal predators, except mice	Low-density possum control every 2-4 years	Eradication	None
Forest birds translocated to sanctuary[4]	Kakariki, Kiwi, N. Island Robin, Kaka, Whitehead, N. Island Saddleback	NA	Kakariki, Kiwi, N. Island Robin, Hihi, Kaka, Whitehead, N. Island Kokako, N. Island Saddleback	NA	Kiwi, N. Island Robin, Hihi, Whitehead, N. Island Saddleback	NA
Land use[5]	Timber harvest (1800s) and grazing	Timber harvest (1800s) and grazing	Light timber harvest (through 1980)	Light timber harvest and Deer hunting	None	None
Patch Area (AWM) (ha)[6]	558	400	1422	1309	6222	3300
Shape Index (AWM)[6]	3.3	3.1	2.5	2.5	6.4	5.8

Nearest neighbor (m)[6]	85	101	170	168	124	108

[1] No. of samples = no. sampling points x number of visits (foraging observations only; dispersed seeds were collected at a random subset of sampling points in 199 seed traps and 216 fecal transects - see methods)

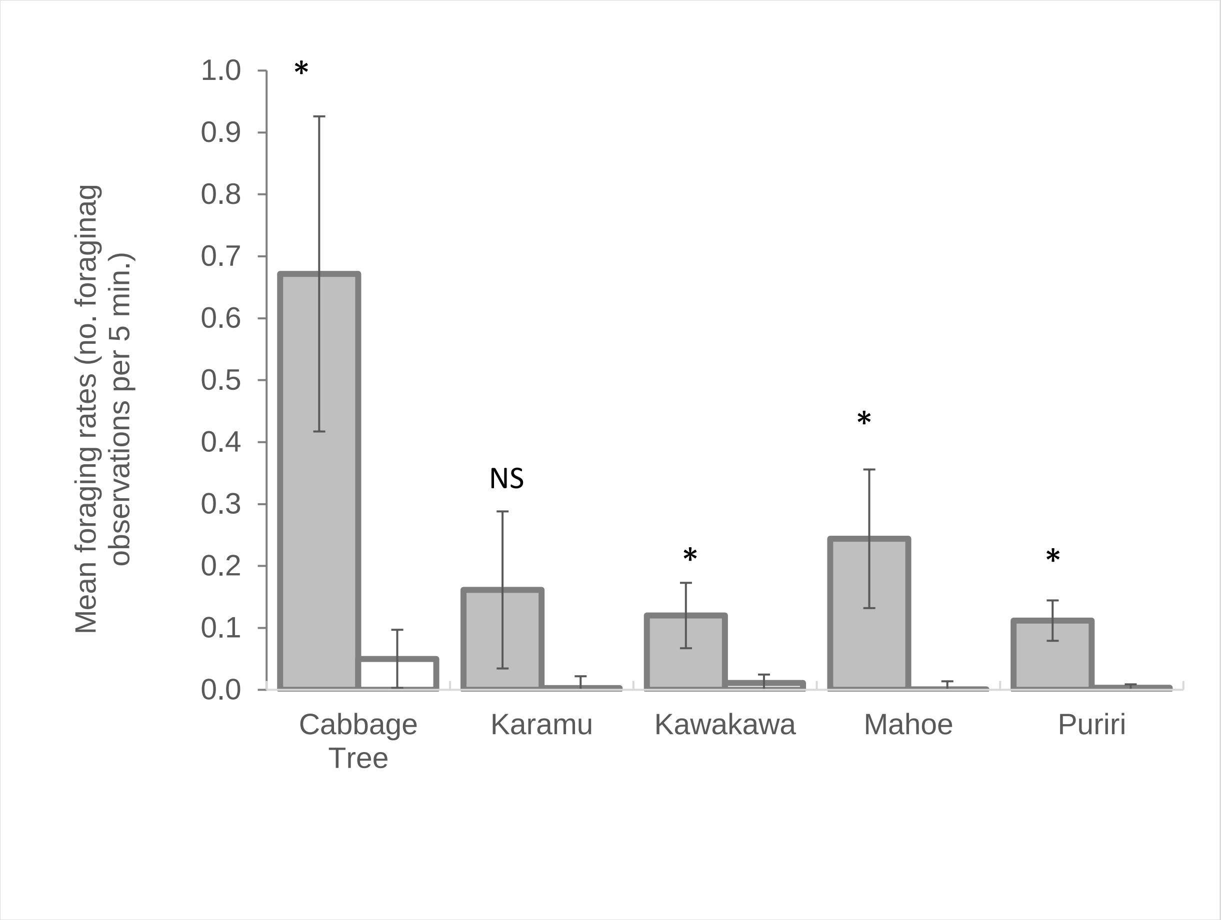
[2] Total annual precipitation and mean annual temperature data are from the National Institute of Water and Atmospheric Research 29-year average (1981-2010).

[3] Area indicates the total size of all forest patch(es) within a reserve, not the size of the entire reserve.

[4] See Appendix 1 for scientific names; Kiwi includes any of the five *Apteryx* species.

[5] based on data obtained from the New Zealand National Vegetation Survey Databank (https://nvs.landcareresearch.co.nz) or from site management plans.

[6] Patch Area, Shape Index, and Euclidean Nearest Neighbor are landscape metrics that were analyzed in a 20km buffer around each of the six study sites using Fragstats (McGarigal et al. 2012).



Appendix 3.3. Comparison of mean foraging rates (mean number of birds observed foraging on fruit per five-minute observation period) and 95% confidence intervals for five different plant species in fenced mainland island sanctuaries (grey bars) relative to reference sites with minimal mammal control (white bars) in 2016. Puriri only occurs at the two northern sites (Tawharanui Regional Park and McElroy Scenic Reserve), therefore mean foraging rates for Puriri are from this pair of sites only. Asterisk indicates significant difference in mean foraging rates between paired eradication and reference sites and NS indicates no significant difference (Wilcoxon Rank Sum Test, $\alpha < 0.05$). Species names: Cabbage tree *Cordyline australis*, Karamu *Coprosma lucida* and *Coprosma robusta* combined, Kawakawa *Piper excelsum*, Mahoe *Melicytus ramiflorus*, and Puriri *Vitex lucens*.

Appendix 3.4. Results of analysis of foraging rates from zero-inflated Poisson generalized linear mixed models for 2016 and 2017. All equally-likely best-fit models (delta AIC < 2.0; Burnham and Anderson 2002) are shown. Five models were run for each species (a null model with a random effect for sampling points only, a model with a fixed effect for point-level frugivore density, a model with a fixed effect for point-level fruit abundance, and models with additive and interactive effects of frugivore density and fruit abundance on foraging rates). Puriri only occurs at the northern sites (Tawharanui Regional Park and McElroy Scenic Reserve), so results for Puriri are from that pair of sites only. Species names: Cabbage tree *Cordyline australis*, Karamu *Coprosma lucida* and *Coprosma robusta* combined, Kawakawa *Piper excelsum*, Mahoe *Melicytus ramiflorus*, Puriri *Vitex lucens*, and Supplejack *Ripogonum scandens*.

Plant	**Model**	**Frugivore density**	**Std. error**	**p-value**	**Fruit Index**	**Std. error**	**p-value**
2016							
Cabbage tree	Frugivore density	0.244	0.080	0.002			
Karamu	Frugivore density	0.169	0.081	0.036			
Kawakawa	Frugivore density * Fruit Index	0.864	0.484	0.074	2.206	0.638	0.001
Kawakawa	Frugivore density + Fruit Index	0.501	0.284	0.078	1.936	0.545	0.000
Kawakawa	Fruit Index				1.928	0.549	0.000
Mahoe	Frugivore density + Fruit Index	0.827	0.367	0.024	1.739	0.825	0.035
Mahoe	Frugivore density	0.667	0.339	0.049			
Puriri	Frugivore density * Fruit Index	0.829	0.494	0.093	9.134	7.546	0.226
Puriri	Frugivore density + Fruit Index	0.312	0.101	0.002	0.794	0.525	0.130
Puriri	Frugivore density	0.316	0.106	0.003			
2017							
Cabbage tree	Frugivore density	0.187	0.076	0.014			
Karamu	Frugivore density * Fruit Index	0.097	0.187	0.603	3.338	2.504	0.183
Karamu	Frugivore density + Fruit Index	0.130	0.073	0.078	3.786	1.038	0.000
Karamu	Fruit Index				3.708	1.032	0.000
Kawakawa	Frugivore density * Fruit Index	0.586	0.525	0.265	3.236	0.820	0.000
Mahoe	Frugivore density	0.139	0.053	0.009			
Puriri	Frugivore density * Fruit Index	0.095	0.041	0.021	-0.360	0.891	0.686
Puriri	Frugivore density + Fruit Index	0.124	0.037	0.001	0.706	0.305	0.021
Supplejack	Frugivore density * Fruit Index	0.067	0.185	0.719	-0.071	2.242	0.975
Supplejack	Frugivore density + Fruit Index	0.216	0.088	0.014	2.043	0.783	0.009

Appendix 3.5. Results of analysis of dispersed-seed counts from zero-inflated Poisson generalized linear mixed models (data pooled across 2016 and 2017 to increase sample size). All equally-likely best-fit models (delta AIC < 2.0; Burnham and Anderson 2002) are shown. Ten models were run for each species (a null model with a random effect for sampling points only, a model with a fixed effect for point-level frugivore density, a model with a fixed effect for point-level fruit abundance, and models with additive and interactive effects of frugivore density and fruit abundance on foraging rates, and the five models listed above with an added effect for sampling method (transect or seed trap). Puriri only occurs at the northern sites (Tawharanui Regional Park and McElroy Scenic Reserve), so results for Puriri are from that pair of sites only. Species names: Cabbage tree *Cordyline australis*, Karamu *Coprosma lucida* and *Coprosma robusta* combined, Kawakawa *Piper excelsum*, Puriri *Vitex lucens*, and Supplejack *Ripogonum scandens.*

Plant	**Model**	**Frugivore density**	**Std. error**	**p-value**	**Fruit Index**	**Std. error**	**p-value**
Cabbage tree	Null						
Cabbage tree	Frugivore density + Sampling method	0.400	0.120	0.001			
Karamu	Fruit index + Sampling method				3.231	0.800	0.000
Karamu	Frugivore density + Fruit index + Sampling method	0.350	0.355	0.324	3.253	0.801	0.000
Kawakawa	Frugivore density + Sampling method	0.141	0.091	0.120			
Puriri	Frugivore density + Sampling method	0.108	0.022	0.000			
Supplejack	Null						