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RESEARCH

Acoustic monitoring and occupancy analysis: cost-effective tools in reintroduction programmes for roroa-great spotted kiwi

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Abstract: Monitoring the response of wildlife populations to conservation management, such as translocations, is crucially important for assessing its effectiveness. Passive acoustic monitoring (PAM) is an emerging tool for monitoring cryptic and elusive species and is increasingly used in the management of kiwi. Inferences from data collected by PAM can be largely improved by occupancy analysis. By modelling occupancy, we overcome the issue of incomplete detectability, which would otherwise lead to underestimating actual site occupancy. Here we demonstrate the utility of occupancy analysis in a reintroduction programme for roroa-great spotted kiwi (*Apteryx maxima,* formerly known as *A. haastii*) in the Nina Valley, Lake Sumner Forest Park. We analysed PAM data from two survey years, 2012–2013 and 2017–2018 from the Nina Valley and the Hawdon Valley, Arthur's Pass National Park, which was the source population of the translocated birds. Occupancy estimates increased significantly between the two survey years at both study areas, despite the translocation of approximately 20% of known territorial adults (four pairs) from the Hawdon Valley to the Nina Valley in 2015. Moreover, at least three out of four territories, where adult birds were removed, were re-occupied by new pairs within three years. Site occupancy increased in the Nina Valley from 0.20 (SE 0.10) to 0.72 (0.10), and in the Hawdon Valley from 0.63 (0.10) to 0.95 (0.04). Detectability varied significantly between study areas and was influenced by the length of survey night, breeding/non-breeding season, and also wind speed. The differences between the naïve and estimated occupancy values underscore the benefits of occupancy modelling for measuring population response to conservation management. This study highlights the utility of using PAM in monitoring translocation outcomes: to track changes in occupancy and local distribution, as well as assessing impacts on the source population following the birds' removal for translocation.

Keywords: *Apteryx haastii*, *Apteryx maxima*, bioacoustics, occupancy analysis, occupancy modelling, passive acoustic monitoring, reintroduction, translocation outcome

Introduction

Conservation translocations, together with *in situ* management interventions, are important tools to safeguard threatened species and avert the risk of their extinction. For these efforts to be successful, it is crucial to understand how individuals of the target species are spatially distributed and how their populations respond to applied management measures (Nichols & Armstrong 2012; Robinson et al. 2018; Metcalf et al. 2019). Monitoring programmes generally attempt to estimate population trends and identify factors that lead to changes in abundance and distribution (Marsh & Trenham 2008). However, monitoring rare and cryptic species can be technically challenging and labour-intensive (MacKenzie et al. 2005; MacKenzie et al. 2018). So, there is a need to develop sensitive cost-efficient methods for effective monitoring.

One of the emerging tools to monitor animals is passive acoustic monitoring (PAM) (Teixeira et al. 2019), which is increasingly used for monitoring cryptic species, such as kiwi (*Apteryx* spp.), and has been widely used in avian studies (Furnas & McGrann 2018; Metcalf et al. 2019; Franklin et al. 2020). Passive acoustic monitoring enables more extended survey periods by leaving automated recorders at study sites and is less demanding on personnel than traditional call counts by human surveyors, given that a single person can deploy multiple recorders within a day (Digby et al. 2013a; Shonfield & Bayne 2017). Acoustic monitoring in kiwi management tends to focus either on call counts or presence/absence solely based on detection/non-detection (Robertson & Colbourne 2017), which implies an assumption of complete or near-complete detection of target individuals. However, in most survey regimes, the detection probability (detectability) is < 1 (Gu & Swihart 2004). The consequences of imperfect detectability tend to result in underestimation of occupancy in the studied area and thus biases in estimates of rates in population change (Seddon et al. 2011). Therefore, it is essential to account for

imperfect detection probability when using PAM to eliminate occupancy estimate bias.

Occupancy modelling addresses the differences in species detectability at a given study site by incorporating the probability of detection to estimate the site's true occupancy (MacKenzie et al. 2002). Occupancy is defined as the proportion of a study area where the species occurs or a fraction of landscape units occupied by the species (MacKenzie et al. 2005; MacKenzie et al. 2018). By assigning a probability that the species occurs in the sample unit, despite the non-detection, we estimate true occupancy. This process is usually more straightforward than estimating abundance for cryptic species, and it can be considered as a surrogate for abundance (MacKenzie et al. 2018) following appropriate calibration (Royle & Nichols 2003). The utility of occupancy modelling for site-faithful territorial species has been demonstrated in estimating abundance (Tingley et al. 2016) and thus is promising for kiwi studies.

Kiwi species are iconic New Zealand birds. All kiwi taxa are classified either at risk or threatened (Robertson et al. 2017) and are the target of conservation management across the country. Populations of all taxa are managed to various degrees, either *in situ* or by translocations (Innes et al. 2015). However, the population response to management is challenging to measure because of the kiwi's elusive behaviour and the often remote and rugged areas that they inhabit. Monitoring of kiwi translocations mainly focuses on translocated populations, but is also useful for understanding the impacts of the birds' removal on source populations, understanding whether and how quickly the populations recover and informing further translocation planning.

Outcomes of kiwi translocations are often monitored by radio-tracking of released birds (Robertson & Colbourne 2017), which typically takes place over several months to a few years post-release (Jahn et al. 2022). Due to the cost of radio-transmitters and labour intensiveness of this method, only a subsample of the released birds is usually monitored. Long-term outcomes of some kiwi translocations are evaluated by the mark-recapture method (Robertson et al. 2019a, 2019b), which is also labour intensive, intrusive to the monitored birds, and with limited practicality over large areas with low-density populations (Robertson & Colbourne 2017). In contrast to these methods, occupancy analysis based on acoustic data allows inferences on population status and change through time without the need for intrusive capture and handling, is easily scaled up over large areas, and is better suited for long term population studies (Noon et al. 2012). Therefore, occupancy modelling displays great promise for evaluating management outcomes for kiwi species.

Great spotted kiwi or roroa (*Apteryx maxima*, previously known as *A. haastii*, Shepherd et al. 2021) were reintroduced to the Nina Valley in Lake Sumner Forest Park between 2011–2015 in the course of a local ecosystem restoration project. Eighteen birds were released to date: eight wild-caught adults and ten subadults hatched in captivity from wild-sourced eggs as part of head-starting efforts under the Operation Nest Egg programme (Colbourne et al. 2005). This translocation was the first, and to date only, reintroduction of the Arthur's Pass–Hurunui population of roroa. It is vital to assess the outcome of this reintroduction and the impacts of the removal on the source population. In the Nina Valley, we monitored translocated birds by radio telemetry for two years after their release to track post-release dispersal and establishment of territories. However, even though this period likely captures

the population establishment phase post-translocation, the radio telemetry provided only a limited insight into the development of the distribution and abundance of kiwi in the Nina Valley. The source population in the Hawdon Valley, Arthur's Pass National Park, was not monitored using radio telemetry following the birds' removal, so it did not allow us to determine whether the vacated territories were re-occupied or any other changes occurred in the population that would bar future population harvest. Hence, we used data from acoustic surveys in 2012–2013 from both areas and carried out follow-up surveys in 2017–2018 to examine occupancy. The occupancy analysis based on acoustic data allowed us to answer the following questions:

(1) How did the distribution of roroa develop in the Nina Valley following their reintroduction?

(2) What is the site occupancy of roroa in the Nina Valley post-translocation?

(3) How was the site occupancy of roroa in the Hawdon Valley affected by removing the adult territorial individuals for translocation?

Methods

Study areas

Kiwi acoustic surveys were undertaken in the Nina Valley (42°28' S, 172°19' E) in the Lake Sumner Forest Park, and the Hawdon Valley (42°57' S, 171°45' E), Arthur's Pass National Park. Both areas are located on the eastern side of the main divide near the Lewis Pass and the Arthur's Pass, respectively, suggesting similar climatic conditions. The Nina Valley floor is at an altitude between 610–860 m a.s.l. and is surrounded by mountain peaks between 1500–1780 m high. The Hawdon Valley floor is at an altitude between 570–780 m and is surrounded by mountains 1400–1930 m high. Native montane beech forest covers steep slopes and lower terraces in both valleys until reaching the bush line at approximately 1300 m. The dominant tree species are mountain beech (*Fuscospora cliffortioides*), red beech (*F. fusca*), and silver beech (*Lophozonia menziesii*) (Read & O'Donnell 1987; Blakely et al. 2008). Both study areas are managed for invasive predators such as stoats (*Mustela erminea*) and possums (*Trichosurus vulpecula*), which are the main predators of juvenile kiwi and eggs (McLennan et al. 1996). However, while limited trapping for these predators occurs in the Nina Valley, the Hawdon Valley receives much more intensive pest management in terms of trapping effort and aerial applications of 1080 (sodium fluoroacetate) poison.

Species description

Great spotted kiwi or roroa is an endemic species to the South Island of New Zealand, inhabiting mainly montane beech and podocarp forests. They are ecologically similar to other kiwi species: cryptic, nocturnal, ground feeders, and habitat generalists (McLennan & McCann 2002). The present range of roroa is restricted to the northwest of the South Island, separated into four main populations: northwest Nelson, Westport, Paparoa Range, and the Arthur's Pass–Hurunui region (Germano et al. 2018). Both males and females produce sexually dimorphic whistle calls (Dent & Molles 2015), which are often recorded and used for monitoring populations and distribution surveys (Robertson & Colbourne 2017). The calling behaviour of roroa likely serves to maintain territories

and the pair bond, and aid communication between males and females that co-operatively incubate eggs and take turns between feeding and tending the egg, similarly to other kiwi species (Digby et al. 2013b; Colbourne & Digby 2016).

Acoustic surveys

Our main objective was to compare occupancy before-and-after the 2015 translocation event and between the study areas. The acoustic surveys in the Nina and Hawdon Valleys took place between August 2017 and June 2018, which allowed time for the translocated birds in April 2015 (eight wild-caught adults/ four pairs) to settle in and establish new territories. Additionally, it provided sufficient time for ten subadults released between 2011–2013 (two subadults were released after the 2012–2013 surveys) to mature and establish territories. Because we wanted surveys to be directly comparable, the survey followed the same design as the acoustic surveys in 2012–2013 in the Nina and Hawdon Valleys carried out by the Department of Conservation (DOC). All sites were within the same habitat type: Montane beech forest usually at the mid- or lower-half of the forested valley slopes. DOC Electronics acoustic recorders (Department of Conservation 2019) were placed on trees at the same sites in the same month of the year to replicate similar detection probabilities between surveys at each site. The acoustic sampling rate was set at Low-8 kHz, creating 16-bit resolution WAV files. The same type of recorders (AR3) was used in both surveys to minimise systematic variability in the ability to capture kiwi calls.

In the Hawdon Valley, recorders' positions were based on the previous radio telemetry monitoring of kiwi done by the DOC staff; individual recorder units were placed approximately in the centre of presumed kiwi territories to maximise the detection probability. Topography features were also considered and steep gullies with streams were avoided due to high volumes of noise and the assumption that kiwi use these features as territorial boundaries. The recorder locations generally followed a transect sampling scheme, however, there were gaps caused by logistical issues during the 2012–2013 survey year. In the Nina Valley, the recorders were spatially distributed similarly to the Hawdon Valley, based on the assumption of equivalent territory size and ranging behaviour to roroa in other studies (Keye et al. 2011; Jahn et al. 2013). The mean distance between neighbouring recorders in the Nina and Hawdon Valleys were 909 and 1174 m, respectively. Such distances are similar to the currently recommended guidance to position recorders at least 1 km apart to minimise detection of the same individuals by multiple recorders (Robertson & Colbourne 2017). Only the area adjacent to the recorder was effectively surveyed, which was likely only a part of the kiwi home range, even though the exact detection radius was unknown. However, we made inferences about the occupancy within the whole sample unit (MacKenzie et al. 2002), which aims to encompass the target animals' home range boundaries (Noon et al. 2012).

In both survey years, 2012–2013 and 2017–2018, 23 and 21 recorder units were placed in the Nina and Hawdon Valleys, respectively (Figs 1, 2). The recorders were activated approximately 30 min after sunset and stayed on until 30 min before sunrise (8.5–14 hours), according to best practice guidance (Robertson & Colbourne 2017). In both survey years, the recorders ran for up to three weeks to maximise the number of survey nights. If it was evident upon retrieval that a recorder had failed to record data, we immediately replaced it and attempted another recording period. Given the limited
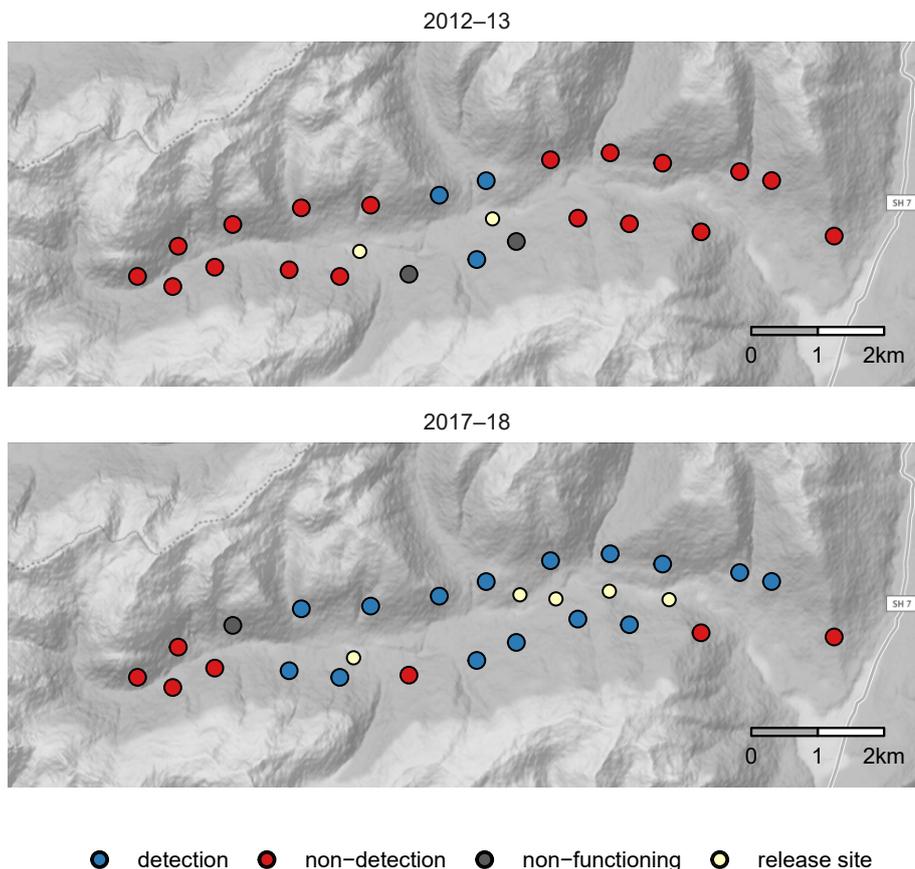

2012–13

2017–18

detection non−detection non−functioning release site

Figure 1. Site occupancy of roroa in the Nina Valley increased between 2012–2013 and 2017–2018. Sites detecting kiwi calls are in blue, non-detecting sites in red, and non-functioning recorders in grey. Release sites of reintroduced kiwi are displayed in yellow. Birds were released prior to the 2012–2013 survey year at two sites shown on the top map. Five more release sites from between 2012–2013 and 2017–2018 survey years are displayed on the bottom map.
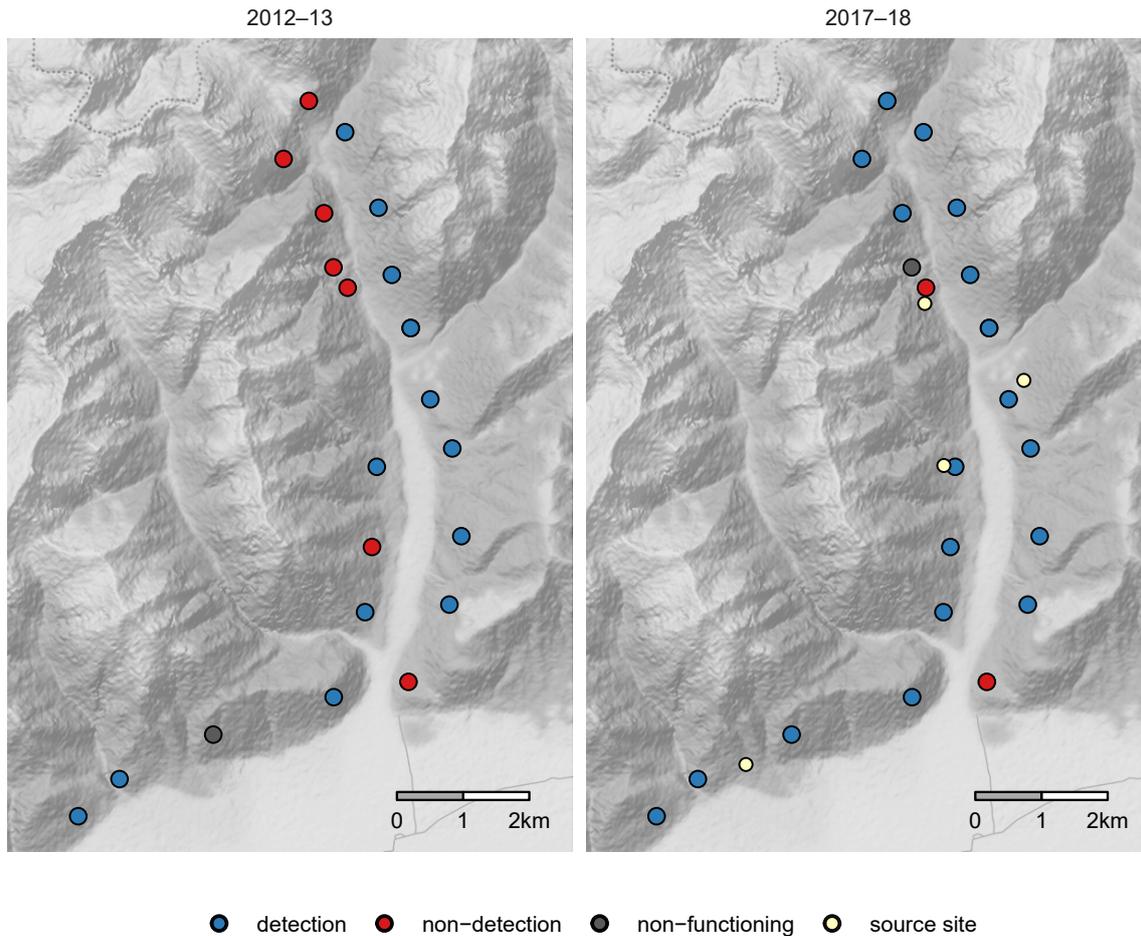
Figure 2. Site occupancy of roroa in the Hawdon Valley. The occupancy increased between 2012–2013 and 2017–2018 despite removing eight adults from four sites (displayed in yellow) and translocating them to the Nina Valley in 2015. Sites detecting kiwi calls are in blue, non-detecting sites in red, and non-functioning recorders in grey.

number of recorders available, we placed them at survey sites in stages, which meant that nearly a year was needed to survey all sites. Specifically, in the Nina Valley, recorders were deployed between August–December and May–June. In the Hawdon Valley, the recording periods were August–October and February–April. The first recording period at both study areas fell into the breeding season of roroa, whereas the second period fell into the non-breeding season (Heather & Robertson 2015). Despite this relatively long period to complete the surveys, it was likely that it would not affect the results of occupancy analysis due to the high stability of territories and longevity of roroa exceeding 25 years, even at sites without predator control (Robertson et al. 2005).

Kiwi call count

To model occupancy, we first searched for kiwi calls captured by the acoustic recorders. We reviewed raw acoustic data using Kaleidoscope Pro v.4.5 analysis software (Wildlife Acoustics 2019). We first trained Kaleidoscope to scan for roroa vocalisations using a sample of 7250 15-minute recordings collected from automated recorders placed within the territories (and in many cases near known nests) of kiwi pairs in the Hawdon Valley between 2013–2015. Our initial scan searched for target sounds with the following characteristics: frequency range of 650–3000 Hz, with a total duration of 6–40 s and

a maximum between-syllable gap of 1.5 s. The fast Fourier transform (FFT) window size was set to 10.67 ms. Kaleidoscope uses discrete cosine transform coefficients of spectra from sequential FFT frames to build feature vectors representing each target sound. K-means clustering and hidden Markov models are then used to determine initial clusters among these feature vectors. Following the initial scan, we manually labelled vocalisations identified as male or female roroa and re-scanned the same recordings. In this step, Kaleidoscope uses human-supervised labelling to refine clusters and better separate target sounds from other kinds of recorded animal vocalisation (such as calls of ruru *Ninox novaeseelandiae*).

We used the resulting classification algorithm from the training process to auto-detect roroa vocalisations in all recordings collected during the 2012–2013 and 2017–2018 survey years. Following Kaleidoscope's auto-detection, we manually confirmed the auto-detection results by visually inspecting the spectrograms and, where necessary because of unclear spectrograms, listening to the identified calls, including those marked as other species. We removed any false positives and captured false negatives (calls initially labelled as other species) through this approach and minimised the need for more complex models adjusting for misclassification of the calls (Miller et al. 2011). We classified all calls as either male or female, and we considered male and female calls as duets if

they likely occurred in the same territory (i.e. were captured by the same recorder) within a minute of one another (Robertson & Colbourne 2017). The visual inspection and confirmation process took approximately one hour of manual work per 1000 hours of raw acoustic data. Each detected kiwi call was accompanied by information on the date, time, and recorder site. For each survey night, we recorded the survey's duration and environmental variables such as the local daily amount of rain and daily average wind speed obtained from the NIWA virtual climate station network (https://data.niwa.co.nz).

Occupancy analysis

To analyse the occupancy at listening sites, we used the detection of at least one call versus zero calls as presence/absence data for every night that a recorder was active at each site. This approach allowed us to construct a detection history of kiwi calls for up to 21 consecutive survey nights, provided that the batteries lasted this whole period. Visualisation of naïve site occupancy was done with the package ggmap in R (Kahle & Wickham 2013; R Core Team 2020). Subsequently, we estimated site occupancy ψ (the probability of species presence) and the detection probability p (MacKenzie et al. 2002) using the R package unmarked 1.0.1 (Fiske & Chandler 2011). We analysed occupancy using single-season models (MacKenzie et al. 2002) based on kiwi presence/absence regardless of sex. The low number of detected female calls did not allow for more advanced co-occurrence analyses of sexes. However, we reported the detected presence of sexes and possible pair status of birds separately to understand better the breeding potential and population structure in each study area.

The single-season models allowed a comparison of the differences between the site occupancy when the study area (Nina and Hawdon Valleys) and survey year (2012–2013 and 2017–2018) were treated as covariates for occupancy ψ. We did not use a dynamic multi-season occupancy model (MacKenzie et al. 2003), because we had data only from two survey years and the focus of the analysis was not to model long-term population dynamics, but the differences between the two survey years, for which the single-season model provided sufficient tools.

Our analysis assumed that site occupancy was constant within each survey year, which implies static home ranges and no colonisation or local extinction during the survey year. The intensity of the pest management regime, potentially affecting occupancy, differed between study areas, but within study areas occupancy was assumed to be constant with respect to habitat type and pest control intensity. In addition, we considered the habitat type identical at all listening sites across both study areas. To account for the variable detectability of kiwi calls, we included four covariates possibly affecting detectability: length of survey night, breeding/non-breeding season, precipitation

(mm day^{-1}), and wind speed (m s^{-1}, daily average). We included the breeding/non-breeding season because of an observed call rate variability between the seasons, and the environmental factors because it was shown that kiwi calls, notably lower-frequency female calls, are often masked by strong wind and heavy rain (Colbourne & Digby 2016). To account for different survey durations at each site caused by the different length of night throughout the year and varying battery capacity, we included this metric as another covariate affecting detection probability. It has been proposed that moonlight illumination might affect kiwi call rates, affecting detectability (Colbourne & Kleinpaste 1984). However, we did not include moon illumination as it was shown not to have a significant effect on roroa male calls and it correlates with a reduction in female vocalisations only at the brightest moon period (Colbourne & Digby 2016).

Finally, we analysed occupancy in the Nina and the Hawdon Valleys and the difference in occupancy between 2012–2013 and 2017–2018 by fitting a set of 16 candidate models to the data. We assumed that detection probability would be affected by the survey night length and interaction between the study area and the survey year in each model. The models varied based on the inclusion or absence of breeding/non-breeding season, wind speed, and rainfall covariates affecting the detection probability. All models assumed that occupancy is specific to the study area and survey year (by including the interaction between these two factors). We also tested models assuming that the survey year had the same effect in both study areas. Subsequently, we evaluated the covariates' impact by selecting the model with the most parsimonious Akaike's Information Criterion (AIC) (Burnham & Anderson 2002).

Results

Detection of kiwi calls

Acoustic data was successfully recorded from most recording sites during both survey years (Table 1). The number of detected kiwi calls at each study area substantially varied as there were nearly 12 times the number of calls detected in the Hawdon Valley than in the Nina Valley, in total. The numbers of male kiwi calls were substantially higher than female calls across both survey years and study areas.

In the Nina Valley, only three sites recorded kiwi calls in 2012–2013, in the vicinity of the release site where five subadult birds were translocated to in early 2011 (Fig. 1). Three more subadults were released in the valley in early 2012, but no recorder site detected kiwi calls near their release site. The number of recorder sites detecting kiwi calls increased to 15 in 2017–2018, following the release of two more subadults in 2013 and eight adults in 2015. Most of the sites detecting kiwi

Table 1. Numbers of recorders and kiwi calls detected during 2012–13 and 2017–18 roroa acoustic surveys. Duet calls consist of both male and female calls and are counted separately in the total call count.

Study area	Survey year	Recorder sites	Active recorders	Kiwi calls			
				Total	Male	Female	Duet
Nina Valley	2012–2013	23	21	14	13	1	0
	2017–2018	23	22	91	84	7	0
Hawdon Valley	2012–2013	21	20	578	403	95	40
	2017–2018	21	20	636	510	66	30

calls were near the release areas from 2011–2015 translocations and no recorders detected kiwi in the top of the valley. In 2012–2013, only one site in the Nina Valley detected male and female calls indicating the presence of a potential pair, the remaining two sites with detections recorded males only. In 2017–2018, the only pair detected was at the same site as in 2012–2013. In contrast, eleven sites recorded males only and three sites recorded female calls only, despite both males and females being detected by radio telemetry and recapture in 2017 near several of the recorder sites (PJ, unpubl. data).

In the Hawdon Valley, 13 sites recorded kiwi calls in 2012–2013 (Fig. 2). All but one of these recorded both male and female calls indicating the presence of at least 12 potential pairs. The remaining site detected only male calls. In 2017–2018, the number of sites detecting kiwi increased to 18, and all of these recorded both male and female calls, which indicates the presence of at least 18 potential pairs. These included three recording sites within known territories of adult birds that were translocated to the Nina Valley in 2015. Detection of both male and female calls during both survey years suggests that these territories were re-occupied by new pair within three years following the original pairs' removal. The recording site nearest to (but not in the centre of) the fourth pairs territory did not detect any kiwi calls at either of the survey years.

Occupancy analysis

We fitted a set of 16 candidate models to the data (Table 2). The most parsimonious model suggests the influence of survey night length, breeding/non-breeding season, wind speed, and the interaction between the study area and survey year on the detection probability (summary of the data in Table 3). The evidence to include the rain accumulation in the model is weaker, however not negligible. We fitted models both with and without the interaction between the study area and survey year as a covariate affecting occupancy. Without this interaction, the models showed a smaller AIC as both study areas, Nina and Hawdon Valleys, displayed a similar pattern in occupancy change between the survey years.

Detection probability p was higher during the roroa breeding season (August–December), as opposed to the non-breeding season. Also, as expected, detectability increased with longer survey nights at both study areas and survey years given that longer recording times raise the chance of recording a calling roroa moving through its territory within the acoustic range of the recorder (Fig. 3). The length of the survey night varied throughout the year due to changing daylight duration (programmed between 8.5–14 hours) and decreasing battery charge after several consecutive survey nights. The differences in detection probability between the study areas vary with the overall numbers of kiwi calls and the time until the first call

Table 2. Models of roroa site occupancy in the Nina and Hawdon Valleys. K denotes the number of parameters. The model structure includes covariates affecting occupancy ψ and detection probability p: study area, survey year, length of survey night, breeding/non-breeding season, wind speed, and amount of rain.

model	ΔAIC	K	−2LogLike	weight
ψ(area + year), p(area * year + length + season + wind)	0.00	10	985.55	0.35
ψ(area + year), p(area * year + length + season + wind + rain)	1.62	11	985.17	0.16
ψ(area * year), p(area * year + length + season + wind)	1.77	11	985.33	0.15
ψ(area + year), p(area * year + length + wind)	2.57	9	990.13	0.10
ψ(area * year), p(area * year + length + season + wind + rain)	3.39	12	984.94	0.06
ψ(area + year), p(area * year + length + wind + rain)	3.84	10	989.40	0.05
ψ(area * year), p(area * year + length + wind)	4.21	10	989.77	0.04
ψ(area + year), p(area * year + length + season)	5.17	9	992.73	0.03
ψ(area * year), p(area * year + length + wind + rain)	5.48	11	989.03	0.02
ψ(area * year), p(area * year + length + season)	6.99	10	992.54	0.01
ψ(area + year), p(area * year + length + season + rain)	7.17	10	992.73	0.01
ψ(area + year), p(area * year + length)	7.57	8	997.12	0.01
ψ(area * year), p(area * year + length + season + rain)	8.99	11	992.54	0.00
ψ(area * year), p(area * year + length)	9.29	9	996.84	0.00
ψ(area + year), p(area * year + length + rain)	9.50	9	997.06	0.00
ψ(area * year), p(area * year + length + rain)	11.23	10	996.78	0.00

Table 3. Summary data for the occupancy model covariates. Values for survey night length, wind speed, and rain accumulation display their mean and value ranges.

Study area	Survey year	Breeding / non-breeding nights	Survey night length (hrs)	Average wind speed (m s^{-1})	Rain accumulation (mm day^{-1})
Nina Valley	2012–2013	168 / 87	11.1 (0.5–14.0)	2.7 (1.2–4.8)	9.5 (0–61.8)
	2017–2018	259 / 111	10.0 (0.3–13.8)	2.9 (1.3–5.3)	5.2 (0–49.4)
Hawdon Valley	2012–2013	142 / 122	9.0 (0.4–12.0)	3.3 (1.7–6.4)	2.9 (0–28.0)
	2017–2018	157 / 181	9.7 (0.2–12.5)	3.4 (1.8–6.7)	5.2 (0–78.8)

Table 4. Occupancy estimates increase between the survey years and the mean time to the first detection of roroa calls differ substantially between the study areas. Only sites detecting calls were included in the calculation of the mean.

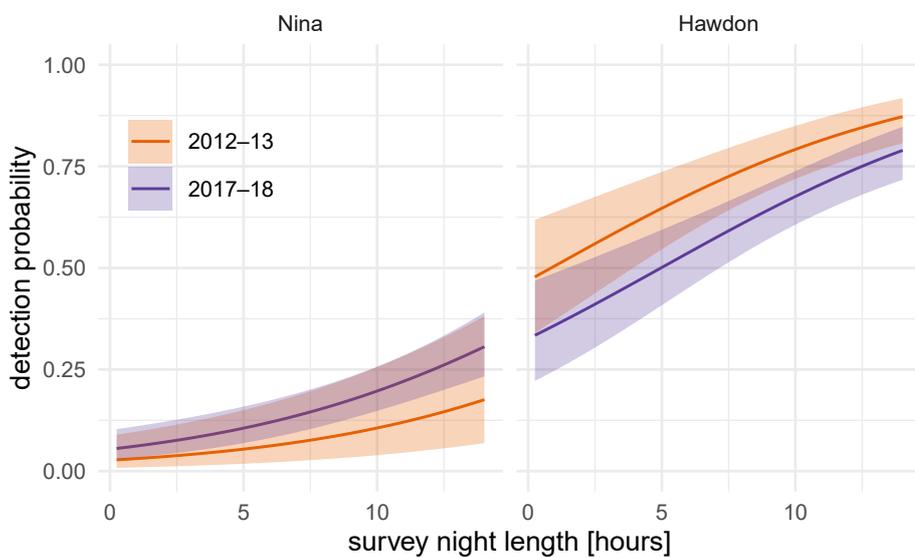| Study area	Survey year	Naïve occupancy	Occupancy estimate ψ	Standard error	Survey nights	First detection night
Nina Valley	2012–2013	0.14	0.20	0.097	255	3.3 (2–4)
	2017–2018	0.68	0.72	0.098	370	4.5 (1–10)
Hawdon Valley	2012–2013	0.65	0.63	0.103	264	1.3 (1–3)
	2017–2018	0.90	0.95	0.037	338	1.9 (1–6)

Figure 3. Detection probability in the Nina and Hawdon Valleys increases with the length of the survey night. Shaded areas represent one standard error around detection probability estimates projected for the breeding season with wind speed at its mean observed values. The detection probability is projected for the survey night length ranging between the observed 15 min–14 hours. The recorders were set to record between 8.5–14 hours, however low battery charge at the end of the recording cycle sometimes resulted in substantially shorter survey nights.

was detected (Table 4). While in the Nina Valley it took on average 3.3 and 4.5 nights to detect a kiwi call for the first time in 2012–13 and 2017–18, respectively, in the Hawdon Valley it was in less than two nights on average during both survey years.

Occupancy estimates ψ based on the top-ranked model were higher or similar to the naïve occupancy: the proportion of sites where kiwi calls were detected (Table 4). Despite substantial uncertainty around the estimates due to statistically small sample sizes in each survey year at each study area, there was a significant difference in overall site occupancy in the Nina Valley between the survey years (Fig. 4; Table 5). As expected, the increase in occupancy took place after releasing additional birds into the valley following the first survey year and after sufficient time had passed for all released subadults to reach maturity and develop the calling behaviour typical of adults.

A similar pattern in the occupancy change appeared in the Hawdon Valley. Both naïve and estimated occupancy increased in the Hawdon Valley between the survey years, contrary to the expectation that site occupancy may be negatively affected by removing the eight adult birds from four territories. The significant increase in site occupancy (Table 5) suggests no adverse impact on the extant roroa population in the Hawdon Valley by the removal of territorial adults for reintroduction elsewhere.
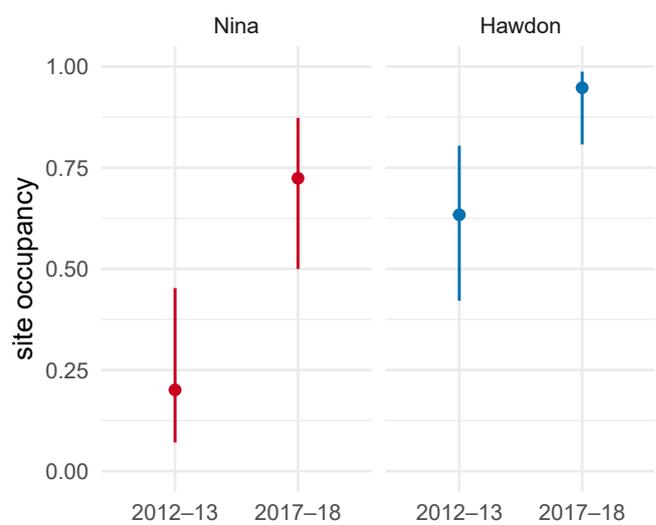

Figure 4. Estimated site occupancy in the Nina and Hawdon Valleys show a significant increase between 2012–2013 and 2017–2018 survey years. Error bars display one standard error of the occupancy estimates.

Table 5. Occupancy and detection probability estimates relative to their covariates based on the most parsimonious model.

occupancy ψ (logit-scale):	estimate	SE	z	P(>|z|)
(Intercept)	0.55	0.44	1.24	0.21
area Nina Valley	−1.93	0.69	−2.80	<0.01
year 2017–2018	2.35	0.71	3.32	<0.01
detection probability p (logit-scale):	**estimate**	**SE**	**z**	**P(>|z|)**
(Intercept)	1.32	0.20	6.57	<0.01
area Nina Valley	−3.47	0.59	−5.87	<0.01
year 2017–2018	−0.60	0.21	−2.84	<0.01
survey night length	0.50	0.09	5.40	<0.01
wind speed	−0.22	0.08	−2.65	0.01
season breeding/non-breeding	−0.36	0.17	−2.13	0.03
area Nina Valley: year 2017–2018	1.33	0.60	2.20	0.03

Discussion

The results from the acoustic surveys suggest that site occupancy by roroa increased in both the Nina and Hawdon Valleys between the survey years 2012–2013 and 2017–2018 (Fig. 4). The naïve occupancy was generally lower than the estimated site occupancy, which highlights the need to address incomplete detectability during analysis to avoid occupancy underestimation (MacKenzie et al. 2002; Seddon et al. 2011). The significant increase in site occupancy in the Hawdon Valley was surprising given that the 2017–2018 survey year took place only a few years after approximately 20% of the known territorial adults in the surveyed area were removed to establish the population in the Nina Valley as part of the roroa reintroduction project. Even though the exact roroa population size in the entire Hawdon Valley was unknown, it was estimated to be at least 20 territorial pairs based on the previous radio telemetry and acoustic monitoring by the DOC staff (S Yong, DOC, unpubl. data).

The increase in site occupancy in the Nina Valley was largely expected because of the translocations of adult and subadult birds from the Hawdon Valley. Additionally, the observed distribution of roroa in the Nina Valley was consistent with the post-translocation radio telemetry monitoring (PJ, unpubl. data). Detecting kiwi at recording sites near the translocation release sites indicates the establishment of a territorial structure of adjacent territories in the central part of the valley, the retention of most of the released birds, and possible recruitment of subadults.

The detectability of roroa calls differed between the study areas (Fig. 3). In the Nina Valley, the detection probability was markedly lower than in the Hawdon Valley during both survey years. The lower detectability corresponds to the overall lower number of calls detected in the Nina Valley despite a similar survey effort, which may indicate a lower population density (Colbourne & Digby 2016). Consistently lower numbers of detected female calls suggest substantially lower acoustic detectability of females, even though we did not have enough data to formally analyse the difference between sexes across study areas and survey years. The higher detectability during the breeding season was consistent with expected higher call rates during mating and the beginning of the incubation period (Robertson & Colbourne 2017). In contrast, another study found lower call rates for roroa during the breeding season, which could potentially decrease detectability; however, this study also identified large interannual variability in roroa calling patterns (Colbourne & Digby 2016).

We also found evidence that detectability was influenced by wind speed and, to a smaller degree, by rain accumulation, which is consistent with other studies (Buxton & Jones 2012; Willacy et al. 2015; Colbourne & Digby 2016). Presumably, the evidence for the influence of rain would likely be stronger in our models if more detailed data on rain accumulation throughout the day was available. Finally, the detection probability could have also been affected by recorder sensitivity. Although all the recorders were of the same model, microphone sensitivity can be variable and possibly degrade over time (Turgeon et al. 2017). Unfortunately, the information on the age and previous use of all recorders was not available, and therefore we could not include it as a covariate in the occupancy modelling. We did not consider within-season microphone degradation substantial enough to have a dramatic effect on the results based on the testing of a sample of recorder units used in this study in a subsequent project (LM, unpubl. data).

Following our modelling, we assumed that most of the recorded birds were territorial individuals that would be detected only at one recording site. Nonetheless, wide-ranging non-territorial subadults could have been potentially detected at multiple sites. Post-translocation radio telemetry monitoring from the Nina Valley (PJ, unpubl. data) suggests that several adult birds were roaming widely in the first year post-release (until mid-2016) and likely settled into stable home ranges before the 2017–2018 surveys took place. However, the likely lower density in the Nina Valley led to the establishment of larger territories than in the Hawdon Valley, as indicated by radio telemetry data from translocated adult birds from two years post-release monitoring. If some birds were detected at more than one recording site, model assumptions would be violated, and it would potentially lead to an over estimation of occupancy (Berigan et al. 2019). Therefore, occupancy estimates in the Nina Valley should rather be interpreted as location use rather than site occupancy (MacKenzie et al. 2004).

Conservation implications

Passive acoustic monitoring has proven to be a useful tool for monitoring and informing conservation management for cryptic and rare species (Teixeira et al. 2019), such as roroa in this study. Acoustic recorders have been shown to be able to

detect comparable numbers of kiwi calls as human observers during listening surveys, and therefore can be highly efficient in monitoring kiwi populations (Digby et al. 2013a; Stewart & Hasenbank 2018). Passive acoustic monitoring techniques can generate extremely large volumes of raw recordings to process, but there is a rapidly expanding set of tools for automated processing and analysis, providing training data is available. For example, training Kaleidoscope software to identify roroa calls required dozens of examples of target calls as well as calls of non-target species that could be potentially confused with roroa. Occupancy models based on bioacoustics can be particularly useful in monitoring kiwi species and evaluating population response to conservation management, as shown in this study. Changes in site occupancy estimates displayed a positive response to the continuation of the roroa reintroduction programme in the Nina Valley. In the Hawdon Valley, the occupancy increase likely displayed a positive response to ongoing intensive pest mammal control by trapping and regular applications of 1080 (sodium fluoroacetate) poison, which presumably outweighed the negative impact of the birds' removal for the Nina translocation. Moreover, reliability of occupancy analysis has been demonstrated in other territorial bird species, such as California spotted owl (*Strix occidentalis occidentalis*), where changes in occupancy were shown to match population changes based on mark-recapture data (Tempel & Gutiérrez 2013). Additionally, the utility of bioacoustics-based occupancy analysis has been shown in several common and rare bird species, together with the potential to inform their conservation management (Campos-Cerqueira & Aide 2016; Furnas & McGrann 2018; Stiffler et al. 2018; Metcalf et al. 2019; Abrahams & Geary 2020). If expanded, large scale studies have the capability to detect even small changes in territorial occupancy with high confidence (Furnas & Callas 2015; Wood et al. 2019), which may be useful in monitoring populous and sparsely distributed kiwi species, such as roroa or tokoeka (*A. australis*).

Occupancy modelling is particularly promising in monitoring translocation outcomes alongside other types of data such as vital rates (Armstrong & Reynolds 2012). A specified site occupancy can be expressed as a target objective for a particular reintroduction project as an alternative to a population growth rate (Nichols & Armstrong 2012). Moreover, the benefits of occupancy modelling using PAM data include the ability to estimate differences in detectability caused by the use of various recorder models, animal behaviour, weather conditions, or differing survey effort over multiple survey years (Shonfield & Bayne 2017). As shown, this method is likewise useful for assessing impacts of the birds' removal on the source population and informing when further harvests are suitable. Since it also tracks distribution changes over time, it is an effective tool for monitoring reintroduced populations and their spread within and beyond designated project areas (Nichols & Armstrong 2012; Noon et al. 2012).

Advances in identifying individual birds by their calls, as demonstrated in roroa (Dent & Molles 2016), little spotted kiwi (*A. owenii*) (Digby et al. 2014), and other territorial bird species (Odom et al. 2013; Wood et al. 2021), have the potential to further improve inferences from PAM data (Juodakis et al. 2021). By identifying individual birds during territorial occupancy analysis, we should be able to account for wide-ranging individuals and assign them to a single site (Berigan et al. 2019). This approach avoids double counting of individuals at multiple recording sites and therefore ensures key model assumptions are not violated when estimating

occupancy. In our case, it would allow us to determine if any bird was detected at more than one recording site in the Nina Valley and whether these sites were truly occupied or transitionally used. Additionally, it will allow non-intrusive mark-recapture studies of population dynamics and estimating abundance based on territorial occupancy (Tingley et al. 2016). Therefore, PAM and associated occupancy analysis with individual identification could provide tools for cost-effective and long-term monitoring in kiwi reintroduction programmes, both at the translocated and source populations. Occupancy analysis—potentially coupled with individual identification—can also be used to demonstrate and measure the effectiveness of *in situ* conservation programmes and so to improve kiwi recovery management.

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Author contributions

PJ, JR, and LM all contributed to the conceptualising of the study; PJ, DM, and LM designed the methodology. PJ and LM curated the data. LM acquired funding and processed the data in Kaleidoscope. PJ undertook data collection, data analysis, and visualisation. PJ wrote the manuscript and all other authors reviewed and contributed text.

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