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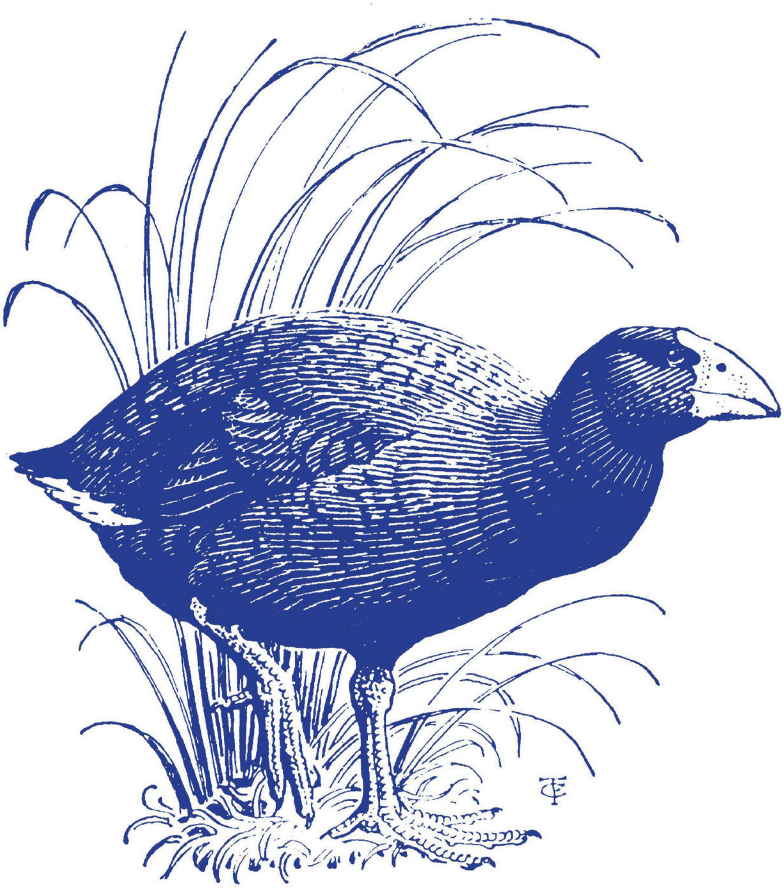

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NOTORNIS

Scope *Notornis* is published quarterly by the Ornithological Society of New Zealand Inc. The journal publishes original papers and short notes on all aspects of field or laboratory ornithology, and reviews of ornithological books and literature, student research, and reports of specialist ornithological events. *Notornis* concentrates on the birds of the ocean and lands of the Southern Pacific, with special emphasis on the New Zealand region. It seeks to serve professional, amateur and student ornithologists alike, and to foster the study, knowledge and enjoyment of birds.

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North Island brown kiwi (*Apteryx mantelli*) monitoring at Whenuakite: Trend comparison of observer and acoustic recorder collected call counts

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Abstract: Observer call count surveys are utilised throughout New Zealand to monitor kiwi populations. The development of affordable autonomous acoustic recorders by the Department of Conservation has enabled the collection of large quantities of digital data. Utilising call count data from the North Island brown kiwi (*Apteryx mantelli*) monitoring programme at Whenuakite from the 2010 and 2015 survey periods, a retrospective comparison between data collected by human observers and acoustic recorders was undertaken. Both survey methods indicated an increase in the number of kiwi calls per hour between the 2010 and 2015 surveys. The overall ratio of the number of calls per hour detected by acoustic recorders to those detected by human observers was 1:1.52. Results from the occupancy modelling indicated that the average detection probability for human observers was almost twice as high as that for acoustic recorders. Furthermore, increasing the number of sites for monitoring kiwi populations improved the associated level of precision of the derived occupancy probability estimates. Adjusting the survey design to the underlying characteristics of the kiwi population are therefore important to gain reliable estimates of their population trajectory.

Stewart, P.; Hasenbank, M. 2018. North Island brown kiwi (*Apteryx mantelli*) monitoring at Whenuakite: Trend comparison of observer and acoustic recorder collected call counts. *Notornis 65(4)*: 179–186.

Key words: acoustic recorders, call count survey, detection probability, sampling precision, applied monitoring

INTRODUCTION

The use of acoustic recorders in biodiversity surveys has created new opportunities for long-term studies of bird populations. Acoustic recorders have been shown to reduce observer bias (Rosenstock *et al*. 2002; Hutto & Stutzman 2009), and to avoid disturbance effects often associated with the presence of human observers (Alldredge *et al*. 2007). In addition, acoustic recorders are a cost-effective sampling method that can be deployed in difficult to access regions over long periods of time (Hutto & Stutzman 2009; Steer 2010). The latter also has the benefit of reducing sampling time-related bias by allowing data collection over a wider range of time periods (Diefenbach *et al*. 2007). However, acoustic recorders may not be as sensitive as human observers over larger distances (Hutto & Stutzman 2009). Surveys of North Island brown kiwi (*Apteryx mantelli*) and southern brown kiwi (*Apteryx australis*) populations using acoustic recorders have respectively been undertaken within Tongariro Forest Park in the Central North Island (Guillotel *et al*. 2015) and Sinbad Gully in Fiordland (Loe & Smart 2016). However, apart from a study on little spotted kiwi (*Apteryx owenii*) call counts by Digby *et al*. (2013), there are no published data regarding the outcome of human observer versus acoustic recorder efforts for monitoring kiwi populations. In their study, Digby *et al*. (2013) found that acoustic

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recorders could detect a similar proportion of the total number of calls compared to human observers (up to 80% compared to 94% respectively).

Our study utilised call count data from the Whenuakite North Island brown kiwi monitoring programme to compare the underlying linear trend in the number of calls detected in the data collected either by human observers or by acoustic recorders. In addition, the respective derived probabilities for a site being identified as being occupied by kiwi by either data collection method are compared. Furthermore, this study aims to provide guidance on selecting an appropriate number of sites and repeat surveys for kiwi monitoring based on different simulation scenarios.

MATERIALS & METHODS

Study area and field methods

The study area is situated within the Tairua Ecological District between Tairua and Whitianga (Fig. 1), on the east coast of the Coromandel Peninsula (36°56′ S, 175°50′ E), New Zealand. Historic land use practices have led to much of the indigenous vegetation becoming modified. A diverse range of secondary forest and induced scrublands cover steep hillsides. There are also some areas of farmed pasture where slope angles are gentler (Kessels *et al*. 2010). Remnant broadleaved associations on the coast grade to regenerating conifer forest on the landward side of the dividing coastal ridge, which reaches 311 metres a.s.l. Elements of primary lowland forest remain in the more inaccessible areas. As part of the 2,700 ha Whenuakite Kiwi Care project, distribution surveys have counted the number of calling kiwi from 24 permanently marked sites on 4 occasions between 2001 and 2015. These surveys have shown that kiwi densities increased fourfold between 2001 and 2015, with adult birds distributed evenly throughout the treatment area (Stewart *et al*. 2015).

This indirect comparison study was conducted retrospectively with the regular kiwi monitoring programme at Whenuakite during the 2010 and 2015 survey periods. Calls from 5 of the survey sites were chosen based on previous years presence of kiwi within the area, and to mirror population densities at sites where human observers were located. This allowed for a sufficiently high number of calls to be available for recording during the survey periods that were comparable between data collection methods. All survey sites chosen were located within indigenous forest habitat and at least 1 km apart. Autonomous acoustic recorders (ARs) developed by the Department of Conservation were used during this study (version B 2). ARs were deployed at the same sites as observers; however, they were programmed to operate at times when observers were absent to avoid creating an overlap between human observers and ARs. ARs were positioned on small tree branches approximately 1.5 m above ground level. Recordings were made in mono and were digitised at 16 kHz, 16-bit precision.

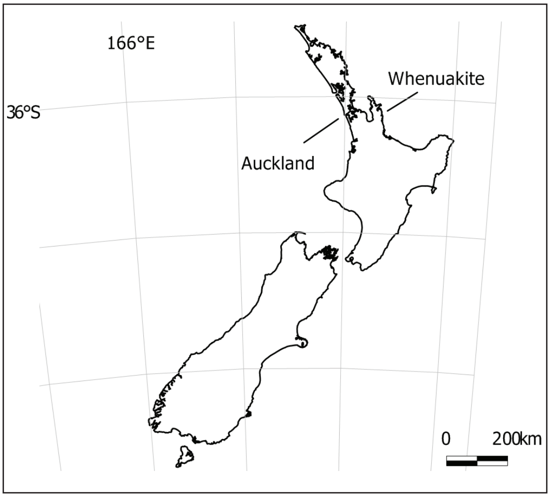

Figure 1. Map showing location of the Whenuakite study site. Graticule grid lines represent 4° latitude/longitude intervals.

Human observers collected call count data following methods outlined by Robertson & Colbourne (2003) over 3 nights from the periods 5–19 May 2010, and from 17 April to 28 May 2015. ARs were deployed for 20 consecutive nights from 14 June to 3 July 2010, and 18 consecutive nights from 16 April to 3 May 2015. Kiwi call count studies by Colbourne & Digby (2016) suggest that a small amount of variation in call rates can be attributed to differences in kiwi call activity during the different sampling months mentioned above. As these sampling months fell within the breeding season for brown kiwi, call activity was generally higher than during off-breeding season (Colbourne & Digby 2016). However, most of the variation is likely to stem from nightly fluctuations in call rates (Colbourne & Digby 2016). No human observer surveys were conducted during extreme weather, such as heavy rain or strong wind, or during full-moon periods. While extreme weather may affect a human observer's ability to detect kiwi call counts, kiwi are also known to be less likely to call during times of full moon (Colbourne & Digby 2016). In contrast, ARs continued data collection throughout their deployment period regardless of environmental conditions; hereby only the first 10 nights of readable data from each AR were subsequently inspected for kiwi calls using Raven

Pro 1.5© (Bioacoustics Research Program 2014) with a 512-sample Hann window and 15.6 Hz resolution. Limiting the data to 10 nights of readable recordings allowed for an equal number of good quality recordings to be used for each survey period. Call count data collection started 45 minutes after sunset, and human observers collected call count data for 1 hour during each survey night (3 hours/site/year). For the purpose of comparing the 2 data collection methods statistically, only AR data for the first hour post survey start (sunset plus 45 minutes) were used in the subsequent call count analysis (10 hours/site/year).

All data collected by human observers and ARs were completed during the same breeding season of the respective years.

Data analysis and simulation

Linear mixed-effects models (LMEs) were fitted to the call count data to test whether the average call count for human observer and AR data changed at a comparable magnitude between the 2 survey years. Inferences were made using an information theoretic approach, where multiple models were compared based on their relative AICc weights (Akaike 1974; Burnham & Anderson 2002). In contrast to the regular AIC value, the AICc value is corrected for sample size and the number of model parameters, therefore providing a better measure of model fit when comparing several similar models (Burnham & Anderson 2002). AICc weights are a relative measure used to compare similar models, whereby higher AICc weights indicate what combination of variables, of those tested, is better suited to explain the observed call count pattern (Burnham & Anderson 2002). The multi-model inference compared 5 different models (Table 1), all of which included the number of calls per hour, based on the first hour of the nightly sampling period, as response variable. In addition, all five models included a random effect for the survey year, which accounted for the repeated measures structure of the data. In comparison, model 1 included an interaction term between the sampling year and data collection method, as well as separate fixed effects for sampling site and month of year. The interaction term was included to compare the regression slopes predicted by the model for the change in call counts between survey years and data collection methods. Model 2 included all fixed effects of model 1 apart from month of year, while model 3 included the month of year parameter but not the fixed effect for sampling site. Furthermore, model 4 only included the interaction term between survey year and data collection method. In addition, a fifth intercept-only model was included as part of the multi-model inference.

The multi-model inference indicated model 2 to be the statistically best supported model. Based on that result, multiple comparisons between the different levels of the site fixed effect were performed using Tukey contrasts. To determine whether an effect was statistically significant, a bootstrap 95% confidence interval was computed for a given model parameter. An overlap of the 95% confidence interval with zero indicated that the model fit predicted the parameter to be statistically non-significant.

In a second step, the nightly call counts were converted into binary detection data (detection, non-detection) and fitted to a static, single-season occupancy model. This occupancy model was used to predict separate detection probabilities for both ARs and human observers for each survey season respectively. The occupancy model was fitted using Bayesian modelling approach as described by Kéry & Royle (2016). For this purpose, the sampled population of kiwi was assumed to be closed for the duration of the sampling period, which allowed for the simultaneous estimation of detection and occupancy probabilities for the respective survey periods and sampling methods (MacKenzie *et al*. 2002). The Bayesian modelling used (1) a state model to describe occupancy (z) at a particular site (i), and (2) an observation model to describe observations (y) made at a given site (i) and sampling night (j) based on the occupancy state at that particular site:

$z_i \sim \text{Bernoulli}(\psi)$

$y_{ij} \mid z_i \sim \text{Bernoulli}(z_i p)$

Both, the occupancy probability (ψ) and the probability of observation (p) were modelled as Bernoulli distributions using uninformative priors for the purpose of this study.

To provide some perspective on the number of sampling sites and number of survey nights required to achieve reliable estimates of occupancy probability, the above Bayesian modelling approach was used to simulate data assuming an average occupancy probability (ψ) of 0.8, and a set of different detection probabilities (p): 0.1, 0.5, and 0.9. Simulations were run for 5, 20, and 100 sampling sites, each scenario running over 5, 20, 50 survey nights and 1,000 iterations, respectively. Based on the estimated occupancy probabilities the root mean squared error (RMSE) was calculated for each scenario. The lower the RMSEs the more similar the estimated occupancy probabilities were to the actual occupancy probability used in a particular scenario. Hereby, a RMSE of 0.1 or below was taken as a threshold for adequate estimated precision. This level of precision is generally regarded as adequate in the current related literature for estimating occupancy probabilities (MacKenzie & Royle 2005; Guillera-Arroita *et al*. 2010). Notable here is that all simulations were run assuming nightly call counts to only being performed during 1 hour. The predictions should therefore be taken with some caution when comparing them to methodology that uses data collected over several hours per night, or where kiwi population density and structure vary from those at Whenuakite.

All statistical data analysis and simulation was conducted in R 3.4.0 (R Core Team 2017) using the following packages and their dependencies: lme4 (Bates *et al*. 2015), merTools (Knowles & Frederick 2016) and boot (Canty & Ripley 2017) for fitting and summarizing linear mixed effects models, plyr and ggplot2 (Wickham 2009, 2011) for data summary and visualization. The R package jagsUI (Kellner 2016) was used together with JAGS 4.2.0 (Plummer 2003) to conduct the Bayesian analysis of the occupancy model.

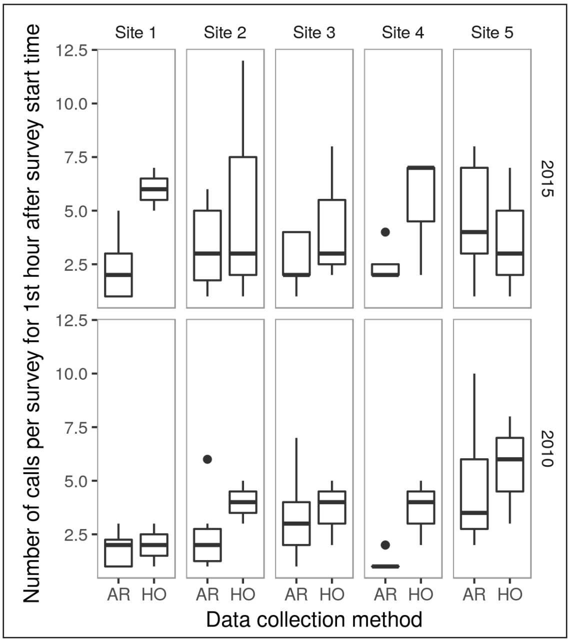

Figure 2. Box and whisker plot for the first-hour call counts from acoustic recorder (AR) and human observer (HO) collected data for the 5 different sites during the 2010 and 2015 call count surveys. Lower and upper limit of box indicating the range between 1st and 3rd quartiles, with centred bold line indicating the median of the data; Lower and upper whiskers indicating the minimum and maximum respectively, with points beyond whiskers indicating potential outliers (data points that lie beyond the ± 1.5 Inter Quartile Range).

RESULTS

Kiwi calls were detected by human observers and ARs at all sites during both survey seasons (Fig. 2). The number of calls per hour detected by human observers was generally higher than that detected by ARs and subsequent analysis at the same site during the first hour of recording (Fig. 2). The overall ratio of the number of calls per hour detected by ARs (during first hour of recording) to that detected by human observers was 1:1.52.

The multi-model inference indicated that the combination of parameters fitted to model 2 performed best in explaining the observed call count pattern, followed closely by model 1 (Table 2). The fixed effects common to both models were the interaction term between sampling year and data collection method, as well as the site the data were collected. In addition, model 1 also included the month of year parameter; however, as indicated by the slightly lower AICc weight, the month of year parameter did not add significantly to explaining the observed call count pattern. Rather, the extra number of model parameters in model 1 compared to model 2 meant that the AICc weight was comparably lower. Furthermore, none of the parameter combinations included in models 3, 4 or 5 provided a good explanation of the observed call count pattern. From this it is possible to infer that the main variation in call counts is due to variations between sites, rather than between different survey months.

A more detailed examination of the model 2 predictions supported the finding that human observers generally detected a higher number of calls during the first hour post survey start (sunset + 45 minutes) than ARs did at a given monitoring site (beta-estimate: 1.88, 95% CI: 0.67, 3.02). Furthermore, the model predicted overall differences in call counts between sites, particularly between (i) site 5 and site 1, and (ii) site 5 and site 4 (Tukey Contrasts: (i) beta-estimate: 1.95, 95% CIs: 0.43, 3.46; (ii) beta-estimate: 2.11, 95% CIs: 0.50, 3.71). Neither the survey year, nor the interaction term between survey year and data collection method were predicted to be statistically significant (year: beta-estimate: -0.31, 95% CIs: -1.13, 0.55; year:type: beta-estimate: -0.82, 95% CIs: -2.46, 0.76).

The occupancy model indicated that the average detection probability for human observers was about twice that of ARs (Table 3). Predictions for the detection probabilities for ARs and human observers stayed constant between the 2010 and 2015 survey seasons. In contrast, the model estimated the same probability of occupancy for both datasets. Similarly, high estimates for occupancy probability for the 2 different data collection methods may be due to the aforementioned ubiquitous spread of calls across all sites during both survey seasons.

For the simulated scenarios, the RMSE decreased with increasing number of sites and survey nights (Fig. 3). In these simulations, the number of sites had the greatest effect on RMSE, while the increasing number of survey nights produced a smaller decrease in RMSE. These results are highly dependent on the underlying detection probability. Scenarios with a low detection probability (0.1) required a higher number of survey nights to reduce their associated RMSE than when the detection probability was high (0.9).

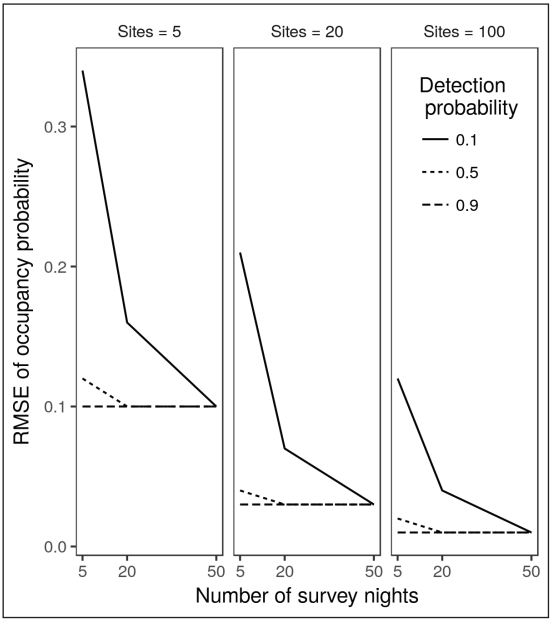

Figure 3. Comparison between number of sampling nights and the associated root mean square error (RMSE) estimates for occupancy probability, in relation to different number of survey sites. The estimates for RMSE gained from simulation are based on an occupancy probability of 0.8, and a detection probability of 0.1, 0.5 and 0.9. An RMSE of 0.1 or below is generally regarded as an adequate level of precision in the current literature (MacKenzie & Royle 2005; Guillera-Arroita *et al.* 2010).

Table 1. Models used as part of the multi-model inference. The intercept only is denoted with ~1 as fixed effect.

Model	Response	Fixed effects	Random effects (slope)
1	Call count	Year * Type + Site + Month	Year
2	Call count	Year * Type + Site	Year
3	Call count	Year * Type + Month	Year
4	Call count	Year * Type	Year
5	Call count	~ 1	Year

Table 2. Multi-model inference: * denotes an interaction term, while K refers to the number of model parameters, and AICc to the sample size corrected AIC value.

Model	Fixed effects	Fixed effects	K	neg log -likelihood	AICc	Delta AICc	AICc weight
1	Year * Type + Site + Month	Year * Type + Site + Month	11	-243.63	511.78	0.60	0.42
2	Year * Type + Site	Year * Type + Site	10	-244.55	511.18	0.00	0.56
3	Year * Type + Month	Year * Type + Month	7	-25212	519.27	8.10	0.01
4	Year * Type	Year * Type	6	-252.72	518.21	7.03	0.02
5	~ 1	~ 1	3	-258.65	523.51	12.33	0.00

Table 3. Results from occupancy model for detection (p) and occupancy (ψ) probabilities for different sampling methods and survey years, respectively. Estimates are based on a set of 5 sampling sites. Acoustic recorder estimates based on data collected during first hour of recording only.

Method	Year	Survey nights per site	Detection Probability (p) Mean	P Lower 95% CI	P Upper 95% CI	Occupancy probability (ψ) Mean	psi Lower 95% CI	psi Upper 95% CI
Acoustic recorder	2010	10	0.42	0.29	0.56	0.86	0.54	>0.99
	2015	10	0.48	0.35	0.62	0.86	0.54	>0.99
Observer	2010	3	0.94	0.79	>0.99	0.86	0.54	>0.99
	2015	3	0.94	0.80	>0.99	0.86	0.54	>0.99

DISCUSSION

While the call count data collected by human observers and ARs followed a similar pattern, human observers routinely recorded a higher number of calls during the first hour post survey start (sunset + 45 minutes) than ARs (an exception was site 5 in 2015 where AR median calls/hour was higher compared to observer median calls/hour, Fig. 2). Also this study accounted for shifts in call rates during different periods of the night by filtering both observer and AR data to only include those calls recorded during the first hour post survey start time, with no adjustment for potential differences in detection range for human observers or ARs being made. Digby *et al*. (2013) determined that simulated little spotted kiwi calls of both sexes were reliably detected from spectrogram inspection to at least 400 m, while human observers have been found to detect kiwi calls well beyond that distance. By potentially missing more distant kiwi calls, the ARs may have failed to identify the presence of kiwi at certain sites during the 2 sampling periods. In contrast, Stewart & Hasenbank (2012), and Zwart *et al*. (2014) demonstrated that ARs can provide similar results to, or even outperform human observers in detecting bird calls under certain circumstances. While no comparative study was available on the performance of different AR models used by this, or Zwart *et al*.'s study, the different outcomes in terms of sampling method may indicate that the effective sampling range of ARs depends on a variety of factors. These may include spectral analysis techniques, the sensitivity of the microphone and hardware used, the species monitored, the background noise level at the time of sampling, or the presence of acoustic barriers, such as tree trunks or steep hillsides, between the AR and the calling individual (Digby *et al*. 2013; Pryde & Greene 2016).

Furthermore, following the results from the multi-model inference the differences in month during which the different surveys were conducted did not affect the call count in a statistically significant manner. As no information on individual observers was available as part of this study, the effects of an individual observer's experience and ability to detect kiwi calls could not be tested. However, differences between individual observer ability to detect kiwi calls are likely to have contributed to the overall variance present in observer call counts. While observers in this study were experienced in detecting kiwi calls, and thus reducing the possibility of false positives, variation in their performance may stem from differences in their ability to detect faint calls, or to distinguish between individuals when multiple kiwi call at the same time. Spectral analysis of the sound files may also be affected by observer variation. While no observer bias during spectral analysis was assessed, this potential issue was minimised by having the same experienced observer utilising the same software settings for both years' data analysis. No measure of identifying false negatives for either data collected in the field or subsequent analysis was available as part of this study.

While some variation in the number of calls recorded per hour was found between sites during both survey seasons, kiwi were found to be present at all sites most of the time. This translated into a relatively high predicted occupancy probability of over 0.8, with a moderate to high estimate for the detection probability for human observers (0.94), and a low to moderate estimate for detection probability for ARs (0.42 and 0.48 for the 2010 and 2015 survey seasons respectively). In regards to the per site sampling effort, the number of repeated samplings met the suggested minimum requirements for human observers and ARs proposed by MacKenzie & Royle (2005): a site with a probability of occupancy of 0.8 should be sampled at least 2 times when the probability of detection is 0.9 or greater, or at least 4 times when detection probability is 0.5 or greater. In terms of the number of sampling sites, Guillera-Arroita & Lahoz-Monfort (2012) found that with decreasing detection probability the number of sampling sites required to gather reliable information on site occupancy increases. Likewise, in scenarios with rare or cryptic species, the lower occupancy and detection probabilities may make it necessary to increase the number of sampling sites to achieve the same estimator quality (MacKenzie & Royle 2005; Guillera-Arroita *et al*. 2010). Therefore, an increased survey effort may be required when surveying relict populations across large landscapes.

Based on the simulations conducted as part of this study, the predicted occupancy probabilities for data collected by human observers and ARs in the field were close to, or slightly above, the RMSE threshold of 0.1 for what is considered adequate sampling precision of the underlying site occupancy in the relevant literature (MacKenzie & Royle 2005; Guillera-Arroita *et al*. 2010). Looking at ways to improve the sampling precision in this applied setting, based on predictions from simulated scenarios, increasing the number of survey sites (e.g. from 5 to 20 sites for ARs) would improve the RMSE below the 0.1 threshold for both human observer and AR collected data (refer to Fig. 3). Increasing the number of sampling nights, however, would provide only a small gain in sampling precision of the underlying site occupancy for either human observers or ARs in this applied setting. It is important to note that this interpretation is based on a scenario that only uses data collected for 1 hour post sunset per night, as data collection over additional hours may yield higher nightly call counts that may increase the overall probability of detection and predicted occupancy probability.

Developing a survey design that takes into account the characteristics of the to-be-surveyed kiwi population is therefore important. Factors to consider at the design stage should include: expected distribution of population across landscape, the number of ARs required to cover a certain area, selection of sites offering similar sampling coverage, as well as the spacing between recorders. The latter is important to prevent double counting of calls by different ARs (pseudo-replication), and where subsequent analysis of call counts does not allow for filtering of replicate recordings. Furthermore, the survey design should also evaluate the number of hours of recording during each sampling night, as well as the number of sampling nights required to adequately estimate the probability of occupancy for certain sites.

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A video camera assessment of morepork (*Ninox novaeseelandiae*) diet and breeding success on Tiritiri Matangi Island

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Abstract: An observational study on the diet and breeding success of morepork (ruru; *Ninox novaeseelandiae*) was undertaken using video capture methods during the 2016-2017 breeding season on Tiritiri Matangi Island. The study investigated diet composition, frequency of prey deliveries, timing and frequency of chick provisioning, the behaviour of morepork and their young at 10 nest sites, and considered the possibility that morepork predation was having a negative impact on species of conservation importance. Tree wētā (*Hemideina* spp.) were found to be the most common prey type consumed at nest sites. Evidence of predation of bird species of conservation importance including stitchbird (hihi; *Notiomystis cincta*) was also found. Prey species continue to exhibit positive population growth rates, indicating predation rates are too low to have a significant destabilizing effect. However, as the population of moreporks has also grown, it is recommended that their impact on prey species be monitored.

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Key words: ruru, morepork, *Ninox novaeseelandiae*, dietary composition, breeding biology, island conservation, Tiritiri Matangi Island

INTRODUCTION

The morepork (ruru; *Ninox novaeseelandiae)* is a forest-dwelling owl native to New Zealand. Morepork are relatively common in New Zealand and are found distributed throughout areas of native forest, as well as within modified habitats such as farmland, pine plantations, and peri-urban green space (Stephenson 1998; Stephenson & Minot 2006). They are a small owl, approximately 29 cm long, weighing 175 g and have an average life span of approximately 6 years (Morgan & Styche 2012; Seaton & Hyde 2013). During the day they roost amongst the foliage of trees and epiphytes, and occasionally in crevices, on ledges, or in burrows (Denny 2009). After dusk, they leave their roosts to hunt (van Winkel 2008). They are territorial and have been found to defend a territory of 3.5 to 7.8 ha (Seaton & Hyde 2013).

Morepork exhibit a monogamous mating system with their breeding season running from September to January (Stephenson 1998; Seaton & Hyde 2013). The season begins with pairs roosting together, before moving to a nest, with egg laying beginning in October (Stephenson, 1998). Nests are usually within cavities of dead or live trees, but have also been found in burrows or scrapes on the ground, in thick clusters of epiphytes, in caves, tree forks, and in nest boxes (Stephenson & Minot 2006; Denny 2009; Seaton & Hyde 2013).

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Nest sites are often reused and once found can be checked annually (Stephenson 1998). Clutch size consists of 1–3 eggs, with a typical clutch size of 2 (Stephenson & Minot 2006). Hatching is asynchronous and eggs are incubated by the female for a period of 20–30 days (Seaton & Hyde 2013). During this time the female is fed on the nest by the male (Stephenson & Minot 2006). Nestlings are altricial and reach independence at approximately 91 days, fledging at approximately 35 days in December to January (Stephenson 1998; Seaton & Hyde 2013). Prior to fledging, both adults provide food for the young (Seaton & Hyde 2013).

Previous studies have found morepork to be opportunistic predators, making it likely their diet will vary according to differences in habitat, vegetation, and seasonal abundance of prey species (Lindsay & Ordish 1964; Denny 2009; Seaton & Hyde 2013). Macro-invertebrate species including wētā (Orthoptera), beetles (Coleoptera), cicadas (Hemiptera), moths (Lepidoptera), stick insects (Phasmatodea), and spiders (Araneae) are the core component of morepork diet (Cunningham 1948; Stephenson 1998; Haw & Clout 1999; Denny 2009; Seaton & Hyde 2013). They are also known to hunt for larger vertebrate prey including birds, lizards, and small mammals such as mice (*Mus musculus*), kiore (*Rattus exulans*), and ship rats (*Rattus rattus*) if present (Saint Girons *et al.* 1986; Stephenson 1998; Haw & Clout 1999; Haw *et al.* 2001; van Winkel 2008).

We studied a total of 10 morepork pairs over the 2016-2017 breeding season on Tiritiri Matangi Island, a 220 ha Scientific Reserve located in the Hauraki Gulf, 28 km north of Auckland and 3.5 km east of the Whangaparaoa Peninsula (Baber & Craig 2003; Galbraith & Cooper 2013). The objective of this study was to obtain more knowledge of the dietary composition and breeding success of the resident morepork population on the Island. We were particularly interested in the quantity of vertebrate prey that was being taken by morepork on Tiritiri Matangi Island with the hope of determining whether morepork are acting as a limiting factor for endemic bird populations, in particular stitchbird (hihi; *Notiomystis cincta*). The majority of stitchbird chicks fledged on the island are not recruited to the breeding population (McCready & Ewen 2017). The cause of this juvenile mortality is not well understood. It has been noted that morepork have the potential to increase the risk of mortality in local bird populations and a previous examination of nest contents on the Island found individually marked leg-bands originating from at least five stitchbirds, four of which were juveniles (Low 2010). There have been relatively few comprehensive scientific studies of morepork diet on offshore islands (Stephenson 1998; Denny 2009), and the effect they may have on small populations of endemic bird species has not been thoroughly investigated (but see Low 2010). Such research will lead to better understanding of the relative importance of native predators among all the factors that impact on these species.

METHODS

Data collection

The study took place between late October 2016 and late January 2017. Nests and roosts were located opportunistically. Researchers and volunteers on the island were asked to report any morepork sightings, unintentional disturbances of adult birds from nest sites and roosts, and instances of mobbing from other bird species. Seven nests were located by the time this study began in October, and 3 more were discovered during the course of the study, resulting in a total of 10 nests being studied on the Island. Roost sites were located in a similar manner. As noted by Stephenson (1998), the position of a roost is sometimes given away by the presence of 'white-wash' from bird faeces below the roost. This visual cue provided additional assistance locating roosts in the area surrounding nest sites.

Once nest sites had been located, four Bushnell HD NatureView cameras (model: 119440) were used to observe the morepork nests. Morepork activity was detected by a passive infra-red (PIR) motion sensor, at which time the camera was set to record a 15-second video. No-glow 'black' IR LEDs provided sufficient illumination for the camera to deliver black and white video in the dark. The following camera settings were used to capture videos: video size was 1920 x 1080 pixels, sensor level was high, LED control was low, night-time only capture, sound capture was on.

For each nest site, nest characteristics were recorded, and at least once a week nests were checked and further observational data collected and recorded on nest record cards. Approximate dates of hatching and chick fledging were estimated where possible if exact dates were not known. At the end of the season in January, breeding success was measured as the number of chicks fledged per breeding pair.

Diet was studied using direct field observations, footage from the motion detecting cameras, nest sampling, and analysis of regurgitated pellets consisting of indigestible material consumed by moreporks. A combination of these techniques has been proposed as the best method for determining owl diet during the breeding season (Southern 1969). As adults often consume small prey themselves at the point of capture while delivering large prey to chicks, this can result in a sampling bias if only one technique is used (Southern 1969). Pellets were collected opportunistically from below roost site and stored in bags labelled by site. Roost sites located near active nests were checked weekly, while other roost sites were checked only once. Once chicks had fledged, nests were scraped out and the material collected was searched through for prey remains. The remains were then bagged and labelled with the nest site and, along with the pellet samples, frozen to delay decay.

Data collection and storage

The following information was taken from the video footage and entered into an Excel spread sheet: the video reference number, site, date and time of video, sex of the bird if able to be determined, whether the bird was arriving or departing, whether a definite or probable food pass had occurred, the prey type (invertebrate, bird, or lizard), prey identification to the lowest taxonomical level possible, prey order, whether or not chicks had been fed, the prey they had eaten, any vocalisations, and any other notable behavioural observations.

As both sexes of morepork are similar in appearance and size, it is difficult to sex birds from external morphology alone (Haw & Clout 1999; Stephenson & Minot 2006). We determined the sex of birds where possible based on behavioural observations. It has previously been noted that only females seem to brood nestlings (Stephenson & Minot 2006). Therefore, in the camera footage, if there were 2 birds present with 1 in the nest and 1 arriving, we assumed the bird in the nest was female and the bird arriving was male. We also observed that male morepork did not seem to fully enter the nest, so if a single bird arrived and dropped down and fully entered the nest we assumed it was female. Likewise, if a bird jumped out of the nest and departed we also assumed it was female. In addition, if there were 2 birds present and the arriving bird dipped into the nest while the other bird reached up we assumed this to be a food pass, even if the item was not visible to the camera.

Data were exported into R 3.4.3 version 1.1.4193 (R Core Team 2017) and a Chi-square goodness-of-fit test was used to compare the observed frequency occurrence of activity, food passes and chick provisioning between early (1800 h – 2159 h), mid (2200 h – 0159 h), and late night (0200 h – 0600 h) with hypothesised equal frequency occurrences across these three time periods.

RESULTS

Breeding success

Nest floors comprised mainly soil, leaf litter, twigs, and wood dust material, with no additional material added. Nest height ranged from ground level (n = 4) to 1.5 m, with a mean height of 0.55 m (Table 1). Laying occurred from early October to early November, with eggs hatching from early November to early December, and chicks fledging in December and early January. Chicks hatched with whitish down and closed eyes. This white down was gradually replaced by grey down and around day 20 chicks started to acquire adult colouring.

Clutch size was determined for 8 nest sites, all of which had 2 eggs (Table 1). Two nests failed and were subsequently abandoned with no second breeding attempt detected. At the ICW site, 1 chick died from unknown causes approximately 8 days after hatching and subsequently disappeared from the nest. This was the only hatched chick that did not fledge. There was an average of 1.2 chicks hatched per nest (n = 8). The exact incubation period could not be determined but can be broadly estimated as between 16 and 31 days. Chicks had a nestling period ranging from a possible minimum of 25 days to a possible maximum of 39 days. A mean incubation and nestling period could not be calculated as we had only estimated dates for all but 1 site (B3) which had an incubation period of 27 days and a nestling period of 29 days. At this site the chick was observed back in the nest three days after fledging, suggesting that fledging may at times be

Table 1. Morepork nest site descriptions and 2016-2017 breeding season records on Tiritiri Matangi Island.

Nest site	Nest description	Height (m above ground level)	No. eggs	No. Young	No. fledged	Incubation period (days)	Nestling period (days)
AB	Small indent at the base of a pohutukawa tree (*Metrosideros excelsa)*	0.0	2	2	2	16-25	27-35
LIV	On ground inside the shell of a dead cabbage tree (*Cordyline australis*	0.0	2	1	1	NA	31-38
ICW	In small hollow at base of pohutukawa tree	0.0	2	2	1	26-31	33-38
B5	Cavity in dead cabbage tree	1.0	2	0	0	NA	NA
B21	Cavity in dead cabbage tree	1.5	2	0	0	NA	NA
Shortcut	In old red-crowned parakeet nest box with no roof	1.0	2	1	1	NA	25-33
B6	Cavity in dead cabbage tree	0.5	NA	2	2	NA	<34
B22	Burrow at foot of pohutukawa tree	0.0	2	1	1	NA	28-37
B3	Inside shell of dead cabbage tree	0.5	2	1	1	27	29
B22-H19	In cabbage tree	1.0	NA	2	2	NA	34-39

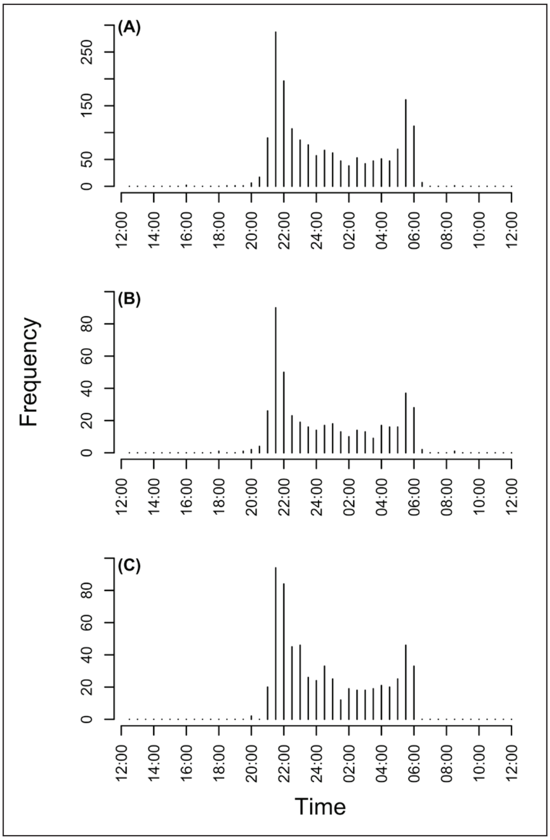

Figure 1. Nest visit and provisioning frequencies (per 30 minutes) recorded from 27 October 2016 to 06 January 2017: (A) All visits (recorded as arrival, departure or both, n = 1,732), (B) Provisioning chicks (n = 457), (C) Food pass events (includes to female on nest, n = 630).

a gradual process. The nest was checked again the following day and the chick was once again gone. Fledging is said to usually occur at around 35 days so 29 days is relatively early for a chick to fledge, although it is possible that nestling period may vary depending on food supply (Moon 2010). The mean fledging rate was 1.1 chicks per pair (n = 10).

Nest provisioning

Visitation rate to nests peaked following sunset with the largest number of visits occurring between 2100 h and 2200 h (Fig. 1A). There was another small increase just before sunrise between 0500 h and 0600 h (Fig. 1A). Frequency of food passes and chick provisioning followed a similar bimodal distribution with a prominent peak between 2100 h and 2300 h and a smaller peak between 0500 h and 0600 h (Fig. 1B, Fig. 1C). Despite the two peaks in activity around dusk and dawn, a Chi-squared analysis showed no significant difference in the frequency of visitation ($X^2 = 2.45$, $df = 2$, $P > 0.05$), food passes ($X^2 = 3.15$, $df = 2$, $P > 0.05$), or chick provisioning ($X^2 = 4.81$, $df = 2$, $P > 0.05$) among early (1800 h – 2159 h), mid (2200 h – 0159 h) and late night (0200 h – 0600 h) time periods. The maximum number of arrivals, departures, food passes, and instances of chick provisioning for one night at a single nest was 47, while the maximum frequency of the same activity recorded within an hour was 25. This was recorded between 2100 h and 2200 h.

Diet

In 30.2% of all food passes recorded, the prey was not able to be identified while in 28.7% it could only be identified as invertebrate (n = 630). We found that the majority (96%) of the prey items delivered to the nest that were captured by the camera and able to be identified were invertebrates (n = 440). Wētā made up 45.5% of observed invertebrate prey (n = 424) and 30.6% of prey recorded in total (n = 630). This was followed by Lepidoptera which made up 8.3% of invertebrate prey (n = 424), and 5.6% of prey recorded in total (n = 630). Birds made up 3.2% of all identified prey items delivered to the nest (n = 440), and 2.2% of prey recorded in total (n = 630). We have not attempted to assess the impact of differing biomass among prey items. Fourteen incidences of avian predation were observed. There may have been a further five, but the prey items were not clearly identifiable as birds or videos did not show footage of an arrival. Without observing the initial delivery of the item to the nest, we cannot be confident the footage is not of a previously cached prey item being consumed or fed to chicks, so these observations were excluded. During the study, we also experienced occasional technical difficulties with cameras running out of battery, video files corrupting, and at times not having cameras correctly positioned to capture activity at the nest. Furthermore, not all nest sites were monitored with cameras.

Pellet collection was largely unsuccessful with only 2.5 pellets collected beneath roost sites during the extent of the study. No pellets were observed being regurgitated during video footage. Examination of the pellets revealed only fragments of invertebrate exoskeletons.

All of the nest sites excavated contained bird remains, although some sites had a much higher proportion of bird remains than others (Fig. 2). Feathers were assumed to be evidence of predation as morepork are not known to add material to their nests (Stephenson 1998). The Shortcut nest site contained the remains of up to 13 birds although wings and legs could not be identified to species level. Tarsus measurements ranged from 23 mm to 33.8 mm. Stitchbird leg bands were found in two nest sites; whitehead (*Mohoua albicilla*) feathers were found at five nest sites; North Island saddleback (*Philesturnus rufusater*) feathers in three nest sites; red-crowned parakeet (*Cyanoramphus novaezelandiae*) feathers in two nest sites; North Island robin (*Petroica longipes*) feathers and a juvenile robin carcass in two separate nest sites; European blackbird (*Turdus merula)* feathers in two nest sites, and bellbird (*Anthornis melanura*), song thrush (*Turdus philomelos*), New Zealand kingfisher (*Todiramphus sanctus vagans*) and spotless crake (*Porzana tabuensis*) remains were each found in one nest site. Wētā remains were also common, excavated from 8 of the 10 nest sites. A total of 49 wētā mandibles were found at the B3 site alone. Some of the nests had relatively few easily identifiable remains and, since larger vertebrate prey items were easier to identify than small pieces of invertebrate exoskeletons, the percentage splits shown in Fig. 2 may not always represent accurate ratios of prey items.

DISCUSSION

Breeding biology

Our findings are consistent with those of Stephenson & Minot (2006) who observed morepork using a broad variety of nest sites on Mokoia Island, suggesting that they do not have overly specific nest requirements. The popularity of dead cabbage trees (*Cordyline australis*) suggests these may be favoured by morepork on Tiritiri Matangi Island, although, as most of the bush is less than 35 years old, it may be that dead cabbage trees are the most abundant acceptable sites. It is also possible these sites are being selected based on their cryptic characteristics, which may be advantageous as an avoidance strategy against mobbing by other birds (Denny 2009). Ground nesting was observed at four of the nest sites (Table 1). This is rarely observed on the mainland, probably due to risk of predation from introduced mammals.

The mean clutch size of 2 (n = 8), is consistent with published data (Imboden 1985; Stephenson & Minot 2006; Seaton & Hyde 2013). The mean fledging rate was slightly higher than that of 0.9 chicks per breeding pair (n = 10) recorded by Stephenson & Minot (2006) during the 1995-1996 breeding season on Mokoia Island. This may be due to differences in habitat quality as Mokoia Island was covered in low regenerating vegetation with very few natural cavities at the time of their study.

Looking at the frequency and pattern of activity and chick provisioning at nest sites, there was a peak in visits by adult morepork after sunset, followed by a steady rate of less frequent visits and another small peak before sunrise (Fig. 1A & 1B). This bimodal pattern of nocturnal visits has been found in other owl species (Stephenson & Minot 2006; Scriba *et al.* 2017). Gaps in our data caused by the difficulties with cameras made it impossible to calculate the mean visits per night for each site. However, our maximum of 47 is relatively low in comparison to the means of 81 and 91 per night recorded for flammulated owls (*Psiloscops flammeolus*) (another small owl with a primarily invertebrate diet) recorded in North America and Mexico (McCallum *et al.* 1995; Powers *et al.* 1996), although higher than the mean of 16.2 per night recorded for morepork by Stephenson (1998).

Following hatching, adults were observed feeding chicks from the bill. At nest AB, chicks began to independently consume invertebrate prey delivered to them by adults after the first six days. Small invertebrates were consumed whole while larger prey items such as wētā were held in the chick's foot while it tore off segments with its beak. Throughout the nestling period, we recorded at least 14 instances of avian prey being delivered to nest sites. Juveniles struggled to consume avian prey themselves. While the two chicks at AB were observed successfully plucking feathers from a bird left at the nest site, this was a slow process followed by the adult subsequently tearing the item up and feeding it to the chicks. Similar feeding behaviour was observed at other sites. It is possible that avian prey has developmental significance for the chicks and by learning to handle such prey they are better equipped for independence. At AB we also observed that one of the two chicks was dominant, consuming the majority of the food delivered during the first two weeks following hatching. As the chicks got older, however, this difference became less marked; both chicks consumed similar amounts of food and both fledged. As the study was purely observational, we did not weigh chicks or measure their growth, though if further research was undertaken this would provide valuable information.

Prey caching was observed throughout the course of the study. Both chicks and the female morepork at the AB site were often observed on video feeding on prey items found in the nest that had either not been consumed at the time of delivery or left only partially consumed. Whole and partially consumed wētā and avian prey items were also noted at various nest sites during field monitoring. This food caching behaviour was also observed during incubation and chick rearing during a study by Stephenson (1998). The rate at which food is delivered to the nest can limit reproductive success of birds (Krebs & Davies 1993), so short-term caching of prey may ensure more continuity of food supply to morepork chicks.

Once chicks were around 20 days old they became more active and could be observed waiting at the nest entrance for adults to return with prey, or moving around just outside the nest at ground-level sites. As chicks matured, we also observed numerous videos of chicks exercising their wings and allopreening between chicks and adults. An increase in activity was most notable in the nests at ground level where chick behaviour was clearly visible. At these sites chicks were observed venturing incrementally further (up to ~3 m) from the nest, exercising their wings, and occasionally climbing up nearby branches or onto fallen logs. Time spent active continued to increase the closer chicks got to fledging. At the B22 nest site, the chick was observed making short flights off a low branch (0.3 m above ground) a few days prior to fledging. Chicks in nests above ground level may not be able to move around as much or they may risk being unable to get back into the nest. This may give chicks at ground level sites an advantage in preparation for fledging, and consequently benefit morepork populations on predator-free islands where ground nesting is feasible.

One weakness of this study was our inability to sex the birds. Male and female morepork are indistinguishable in the field with no obvious size difference or difference in plumage (Stephenson 1998). This made it difficult to determine the parental care provided by each sex, or whether one sex delivered the most food. We could assume that following hatching it was the female that stayed on the nest for the majority of the time, departing infrequently for short periods probably to feed. However, these periods of parental absence grew longer as chicks matured and it became impossible to determine the sex of the bird delivering prey. Based on the incidence of videos with two adult birds present, it seems that both the male and the female deliver prey to the chick at least until fledging. Further studies would greatly benefit from the banding of at least one of the parents at each nest, so the sex of birds could be differentiated.

Diet

Our results provide evidence consistent with other studies that have found morepork to be primarily insectivorous (Imboden 1975; Stephenson 1998; Haw & Clout 1999; Haw *et al.* 2001; Denny 2009). Wētā were found to be the most common prey group, suggesting they were abundant on Tiritiri Matangi Island during the study period. However, it is also possible that large invertebrates were over-represented in our results due to the foraging behaviour of morepork during the breeding season. As noted by Denny (2009), if adult morepork are only able to deliver one prey item at a time to their nest, they may optimize foraging by consuming small invertebrate prey at the point of capture, while carrying more substantial prey items back to chicks.

The species of avian prey were not able to be determined from the video recordings, but during nest sampling we identified remains and/or feathers of stitchbird, whitehead, red-crowned parakeet, North Island robin, North Island saddleback, bellbird, European blackbird, song thrush, New Zealand kingfisher, and spotless crake. During nest monitoring we also recorded two song thrushes in the Shortcut nest, and one juvenile robin in the B3 nest. The remains of avian prey items are occasionally encountered away from morepork nest sites on Tiritiri Matangi. It is possible that remains with only the heads removed are morepork prey (Glue 1972; Brown & Mudge 1999). Examples encountered include common diving petrel (*Pelecanoides urinatrix*) and kōkako (*Callaeas wilsoni*) nestlings. There are no New Zealand falcons (*Falco novaeseelandiae*) on the Island.

We observed three incidences of predation on lizards; however, again the species were not able to be confidently identified from the video footage. Based on the size of the lizards it is likely that one was a gecko and the other two were skinks. No identifiable lizard remains were found at nest sites or roost sites. While lizards do not seem to be a common prey item for morepork, it is evident opportunistic predation does occur and may be more common when lizard abundances are high (van Winkel & Ji 2012). In earlier work on the Island, Raukawa gecko (*Woodworthia maculatus*) remains were found in the AB nest site (JRS *pers. obs.*). Other observers have reported morepork preying on nocturnal geckos (recorded as *Hoplodactylus* spp. possibly *Dactylocnemis pacificus* or a small *Hoplodactylus duvaucelii*) on Manawatawhi (Three Kings Islands) and Taranga Island (Hen Island) (Turbott & Buddle 1948; Chambers *et al.* 1955).

The predominantly insectivorous diet of morepork is probably facilitated by the low searching and handling times associated with such prey (Denny 2009). It was clear from the videos that handling time for birds was much greater than that for invertebrates, which were very quickly and easily ingested in comparison. Furthermore, morepork are thought to rely heavily on sound and motion when hunting (Denny 2009). As most potential avian prey is diurnal, this may reduce predation opportunities to dawn and dusk when some diurnal birds are active (Imboden 1975; Denny 2009). Our results support this with 11 of the total possible 19 observations of avian predation being recorded at dawn between 0500 h and 0600 h, and 6 at dusk between 2000 h and 2100 h. The remaining observations were recorded at 0437 h and 1517 h.

It has previously been noted that avian prey may be of particular significance as a food source for chicks (Imboden 1985), with adult morepork appearing to provide their young with more vertebrate prey than they consume themselves based on prey remains observed in nests (Stephenson 1998). While most avian prey delivered to nest sites was observed being fed to chicks, adult morepork were also occasionally seen feeding on them. Furthermore, adult morepork were observed leaving the nest with birds that had previously been delivered suggesting prey items were being taken to be consumed at roosts (Brown & Mudge 1999) or removed from the nest. If avian prey consumption is indeed increased during the morepork breeding season, it is expected that any impact on local bird populations would be most evident during this time. Some birds on Tiritiri Matangi use nest boxes which morepork are unable to access and this may provide protection before fledging and limit nest predation opportunities. Moving nest boxes that are in close proximity to known morepork nest sites is one strategy that might offer further protection. More research on diet outside of the nesting season would be of value in determining whether there is significant seasonal variation in vertebrate prey consumption.

We did not observe any pellets being regurgitated during video footage, which suggests they are primarily ejected at roost sites and/or during the day. Perhaps, to improve pellet collection in future studies, sheets or netting could be erected beneath known roosts. This has been noted as assisting in the collection of whole pellets, as those consisting entirely of invertebrate remains may otherwise shatter when they hit the ground (Imboden 1975; Saint Girons *et al.* 1986; Stephenson 1998). It would also reduce time spent searching for pellets amongst the leaf litter.

Other studies have found morepork pellets to consist almost entirely of invertebrate remains, while vertebrate remains are more common in nest sites (Imboden 1975; Stephenson 1998; van Winkel 2008). Similarly, we found a discrepancy between the number of avian prey items recorded on the cameras and the number found during nest sampling. This may be because nest sampling is biased towards the representation of vertebrate prey whose remains will persist for much longer than invertebrate remains (Denny 2009). As this is the first time that nest sites have been excavated, it is also possible that some remains uncovered were from previous breeding seasons, making it unwise to attempt to quantify predation rates from these results. It is also possible that our results were influenced by systematic error. As the cameras were set to record at night, evidence of avian predation that occurred in late morning or early evening may have been missed. Regardless, our results provide evidence of predation on endemic bird species and lizards. Offshore Islands such as Tiritiri Matangi may have higher avian and reptile predation rates than mainland New Zealand due to the increased availability of these prey types in the absence of mammalian predators.

Implications for conservation management

As a pest free island, Tiritiri Matangi is home to many small populations of endemic species of conservation importance, as well as establishing translocated populations. Exact numbers of

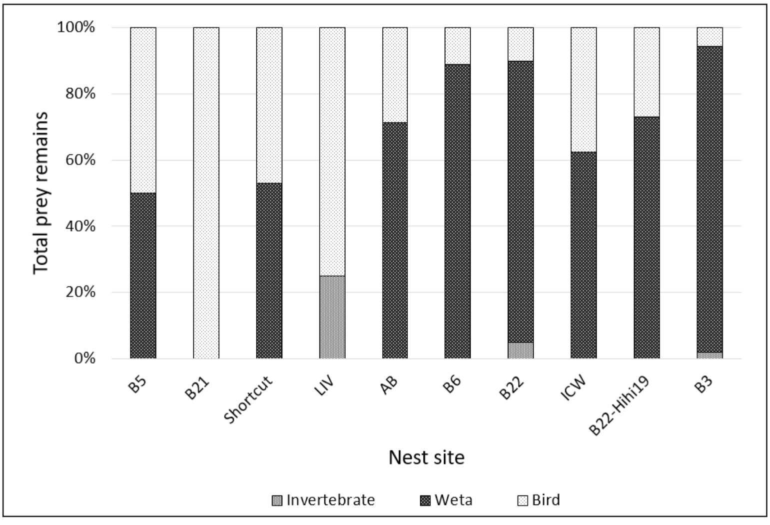

Figure 2. Percentage occurrence of invertebrate, wētā, and bird prey remains identified at each nest site when excavated after fledging (n = 10).

morepork on Tiritiri Matangi are unknown; however, using observational data from 2016-2017, we can estimate that there are around 20 breeding pairs. Our results indicate morepork diet on the Island consists predominantly of tree wētā and other common invertebrates. However, we have also found evidence of predation upon indigenous bird species including stitchbird, whitehead, red-crowned parakeet, North Island robin, saddleback, bellbird, and spotless crake. Natural predators such as morepork are an integral part of native ecosystems and are unlikely to have a significant destabilizing effect on established prey populations (van Winkel 2008). Nevertheless, morepork densities and their potential impacts on other species should continue to be monitored.

It has been proposed that translocated populations, especially captive-bred individuals, may be particularly at risk of predation due to unfamiliar habitat and/or loss of anti-predator responses (van Winkel 2008). Low (2010) suggested that survival differences between translocated stitchbird populations on Tiritiri Matangi and Mokoia Island were partially influenced by differing predation pressures from morepork. At the time of his study, morepork densities on Mokoia Island (average density of 0.393 ha^{-1} across the Island) were much higher than on Tiritiri Matangi (average density of 0.013 ha^{-1} across the Island) (Low 2010). It was also found that soil spore counts of *Aspergillus fumigatus* were much higher on Mokoia than Tiritiri Matangi (Low 2010; Perrott & Armstrong 2011). The common fungus, *A. fumigatus*, causes aspergilliosis in stitchbird and subsequent respiratory problems (Thorogood *et al.* 2013). While post-mortems have shown apergilliosis is a major cause of mortality for stitchbird (Perrott & Armstrong 2011), it is also possible aspergilliosis and morepork predation interact, resulting in increased losses. Stitchbird suffering from respiratory problems (or affected by other diseases) may be rendered more vulnerable to predation, and a loss of genetic diversity due to predation could reduce adaptive potential and the likelihood stitchbird will cope with stochastic events such as disease outbreaks or environmental changes (Frankham *et al.* 2002; Low 2010). Based on morepork location records from the 2017 kiwi call survey, single roosts and pair sightings from the 2016-2017 period, and nest site observations, morepork densities are now estimated as being much higher (~0.23 ha^{-1}) than when stitchbird first arrived on Tiritiri Matangi. However, the highly managed stitchbird population on Tiritiri Matangi continues to be maintained at an artificially high level (McCready & Ewen 2018) indicating that morepork predation is not excessively limiting. Further research that attempts to quantify predation rates and provide a more accurate estimate of morepork population numbers on the Island would be necessary to confirm this.

In conclusion, this study provides preliminary data for a better understanding of the diet and breeding success of morepork on an offshore island free of mammalian predators. Breeding pairs were found to have a mean fledging rate of 1.1 chicks per nest with the majority of chicks hatched surviving to fledging. Morepork diet observed at nest sites on Tiritiri Matangi was found to consist predominantly of wētā and other invertebrates over the breeding season. As noted, other studies have found that morepork are opportunistic predators, with optimal prey choice influenced by the relative abundances of species within their habitat. Further work on abundance of prey taxa would be needed to confirm opportunistic prey selection on Tiritiri Matangi. Our results suggest that, with their varied and mostly insectivorous diet, morepork are unlikely to pose a major threat to uncommon avian prey populations. However, if populations have been recently translocated, are already perilously small, or potentially rendered further vulnerable by disease, competition, reduced genetic diversity or nutritional deficiencies; morepork densities and the risk of predation should be taken into account. Further research is needed to provide a more accurate estimate of morepork population density, investigate survival of fledglings, quantify the impact of predation on conservation species and further investigate whether morepork are limiting juvenile recruitment of stitchbird on Tiritiri Matangi Island.

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An estimate of the Hutton's shearwater (*Puffinus huttoni*) population in the Kaikōura region using colour-marking in 2002 and 2014

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Abstract: In September 2002 and 2014 respectively, 2,077 and 1,704 prospecting Hutton's shearwaters were colour-marked on the ventral plumage at their breeding grounds at Kōwhai River, Seaward Kaikōura Ranges, New Zealand. Large numbers (425,516 in 2002, and 106,900 in 2014) of marked and unmarked birds were then counted from small boats off the Kaikōura coast between Haumuri Bluff and Ohau Point. A hypergeometric sampling model was fitted these counts, leading to population estimates of $\hat{N}$ = 459,290 (95% CI = 434,306-484,733) birds in 2002 and $\hat{N}$ = 590,407 (95% CI = 543,992–642,697) individuals in 2014. These estimates include both breeding and non-breeding birds and indicate that between 2002 and 2014 the population trend was about +2% per year.

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Keywords: Hutton's shearwater, mark-recapture, population estimates, *Puffinus huttoni*

INTRODUCTION

Hutton's shearwater (*Puffinus huttoni*; Mathews 1912) is currently classified by BirdLife International (2018) as "Endangered", and as "Threatened – Nationally Vulnerable" under the New Zealand Threat Classification system (Robertson *et al.* 2017). It is a small black-and-white shearwater (length 36–38 cm, weight 365 gm; Marchant & Higgins 1990) whose breeding grounds were unknown to the scientific community until 1965. Anecdotal reports from Maori, musterers, hunters, and Kaikōura locals indicated there were "muttonbirds" nesting in burrows high in the Seaward Kaikōura Ranges. Following up on these reports, Harrow (1965) confirmed breeding colonies of Hutton's shearwater in the headwaters of the Kōwhai River, between 1,200 and 1,800 m a.s.l. Extensive searching led to the discovery of nine further colonies, but only two (Kōwhai River and Shearwater Stream) remain today (Marchant & Higgins 1990; Cuthbert 2001; Sommer *et al.* 2009).

The reasons for the population decline of the Hutton's shearwater in the 20th century are not definitive. Deer, goats, and chamois have been observed breaking through the shallow friable soils into burrows and nest chambers (Harrow 1976). Stoats, although present in the Kōwhai colony, were not considered to occur in sufficient numbers to be a threat to the remaining colonies (Cuthbert & Davis 2002a). Cuthbert (2001, 2002) noted accessibility for, and evidence of, feral pigs in the colonies that had recently become extinct, and the relative inaccessibility to pigs to the Kōwhai River

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and Shearwater Stream colonies. Thus, Cuthbert (2001, 2002) concluded that predation and habitat destruction by feral pigs were likely the main causes of the population decline.

Another major threat to the continued existence of the Hutton's shearwater colonies is devastation by natural processes such as snow avalanches or debris avalanches/rock falls. Sherley (1992) reported that during his study two entire colonies had slipped away, and that erosion could cover burrows with alluvium. However, recent magnitude 5.7 (April 2015) and 6.2 (February 2016) earthquakes, about 50 km deep centred near St Arnaud 50 km to the northwest, did not produce any obvious land-sliding in the Kōwhai River (LKR *pers. obs.*).

To understand the current status of Hutton's shearwater and its vulnerability to catastrophic events, information on population size is needed. Several population estimates have been made since the mid-1980s. Sherley (1992) calculated the number of breeding pairs from burrow counts at quadrats in 17 of the 36 defined sub-colonies in the Kōwhai River and Shearwater Stream. He estimated a maximum of 134,400 breeding pairs less an unknown number of non-breeding pairs and unmated birds in active burrows. Correction factors for the total number of the burrows occupied by breeding pairs in the Kōwhai colony have been applied to Sherley's estimate to arrive at 94,000 breeding pairs (Taylor 2000). Later estimates gave a combined total of 106,000 breeding pairs (Shearwater Stream 8,000 and Kōwhai River 98,000 pairs; Cuthbert & Davis 2002b; Sommer *et al.* 2009). These studies focussed on breeding pairs and did not account for non-breeding birds at Kaikōura or young birds still in Australian waters (Waugh *et al*. 2013). More than half of a seabird population can be made up of non-breeding individuals (Warham 1996). Little is known about population trends, but a 20-year assessment, again based on burrow occupancy and breeding success, suggested the population at the Kōwhai River is increasing (Sommer *et al*. 2009).

Taylor (2000) recommended an assessment be made of Hutton's shearwater population using a non-traditional approach whereby a sample of the population at the breeding colony is colour-marked, and counts conducted at sea to obtain the ratio of marked and unmarked birds. This would allow for an estimate of the total population present in the Kaikōura region at that time, and the process should be repeated every 10 years to assess trends. Here, we present a study comparing estimates of the Hutton's shearwater population at Kaikōura made using this colour-marking technique in 2002 and 2014.

METHODS

Hutton's shearwaters return to the Kaikōura region from Australian waters in late-August (Harrow 1976; Marchant & Higgins 1990). By mid-September it is assumed that most birds have returned to New Zealand seas. In most seasons, a deep snow layer over the high altitude colonies prevents adults reaching their burrows in early spring. Therefore, large numbers of birds are found sitting on the surface at night and this is a mixture of breeding age and immature birds. The key advantage of sampling under snow conditions is ease of capture of birds off the surface. Another benefit is reduced damage to underlying burrows due to the deep snow cushioning the soft, friable, heavily burrowed ground. The technique works as it is not biased towards capturing mainly immatures on the surface as might happen later in the breeding season.

Tests of different types of colour-markers applied to the body plumage of Hutton's shearwaters were carried out by the Department of Conservation in September 2001. Water-based markers (e.g. Raddle™, Donaghys Limited) were considered too ephemeral as they washed off very easily, or faded rapidly on birds digging in snow or soils. Enamel spray paint had been used on black-browed albatross (*Thalassarche melanophris*) in the Falkland Islands (Thompson & Rothery 1991) and on shy albatross (*T. cauta*) in Australia with no discernible effect on these birds (Brothers *et al.* 1997). Following correspondence with overseas researchers who have used these products on seabirds we chose Dulux Spraykote (now Spraypak) Quick Dry™ enamel spray-paint. This paint is easy to apply, durable, and highly visible, but was expected to wear off the birds over a few weeks through repeated washing, diving, moving around in snow, and digging of burrows. The spray paint provides a surface coating on the outer feather layers only. Colour-marking followed the procedures listed in the New Zealand Bird Banding Manual (Melville 2011).

In 2002, the breast, belly, and underwings were marked; in 2014 the breast, belly, and under-tail coverts were marked as previous experience indicated little benefit in marking under the wings. Eight weeks after the marker was applied at the Kōwhai River capture site (10–12 November 2014), very few birds showed any discernible tinges of pink spray paint (LKR *pers. obs.*).

Field parties visited the Kōwhai River Hutton's shearwater colony (42°15′30″ S, 173°36′15″ E) between 16–20 September 2002 and 15–17 September 2014 (Table 1).

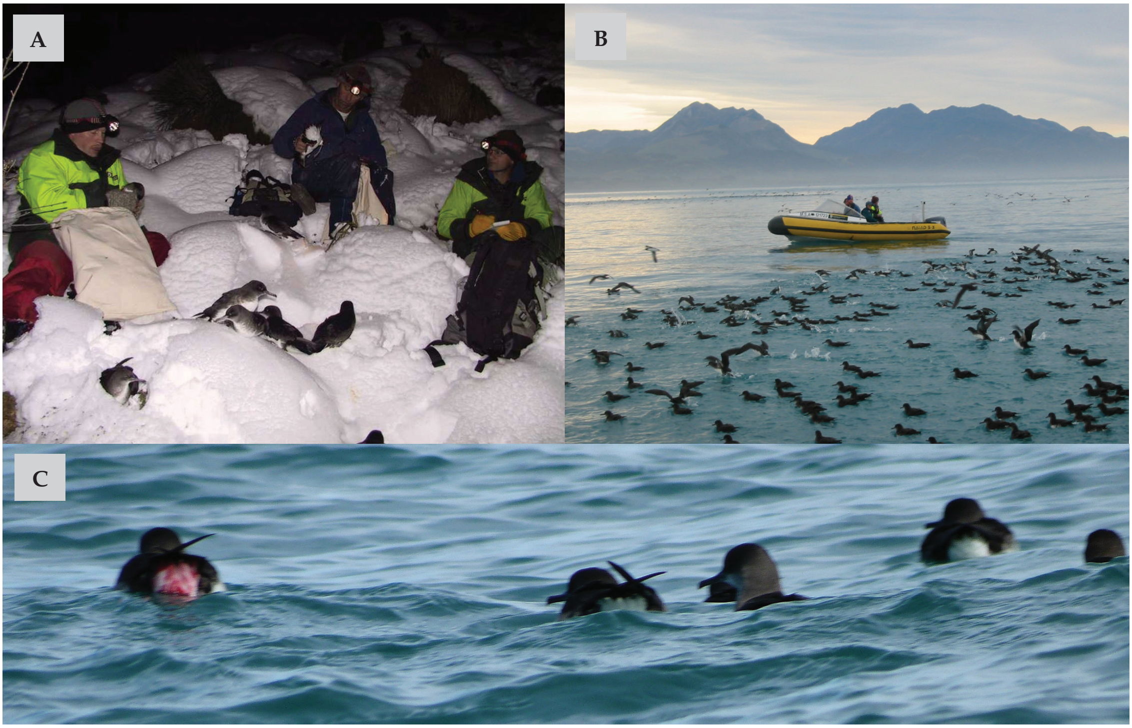

Figure 1. a) Field party, on the snow surface, collecting Hutton's shearwaters for marking in 2002 (Photo: Department of Conservation); b) Survey boat passing through a raft of Hutton's shearwater with observers searching for marked and unmarked birds (Photo: G. Taylor); c) Colour marked Hutton's shearwater on the water (Photo L. Rowe).

Birds return to the colony after dark at which time they were picked off the snow surface and placed in bird bags (Fig. 1a). They were held by one of the team who covered the head to prevent marker drift, marked by another member, and released. Accurate counts of birds marked with spray-paint were kept by field parties.

Immediately after the completion of the marking operation at the colony, observers started checking rafts of Hutton's shearwaters at sea using boat-based observations to count the birds on a daily basis. Multiple, large flocks of shearwaters (thousands of birds) were found each day between the Haumuri Bluffs to the south and Ohau Point to the north, and within 2 km of the shoreline. Up to four small boats on any given day were deployed and cruised slowly alongside or through the rafts (Fig. 1b). Observers on each boat looking out at different directions counted the numbers of unmarked and marked birds in a block and relayed these to a recorder (e.g. 200/0, 100/1, 86/0, 12/0, 130/1, etc.). Birds were counted as they flew off the water as the boat approached. Birds were only added to counts if the breast and belly could be clearly seen and, in 2014, if the under-tail coverts could be seen on birds swimming away from the boats (Fig. 1c).

The data were compiled into daily counts, and inference was carried out using a mark-resight model described as:

$$L(N|M, \qquad) = \prod_{i=1}^{days} \frac{\left(\frac{M}{m_i}\right)\left(\frac{N-M}{u_i}\right)}{\left(\frac{N}{m_i+u_i}\right)}.$$

where $L(.)$ denotes the likelihood function and N is the unknown population size. M = number of birds marked over the total number of days at the Kōwhai River. A series of counts (resighting sessions) were carried out over a number of days (*days*) indexed by $i = 1, \ldots\, days$, and the number of marked (denoted by m_i) and unmarked (denoted by u_i) birds was recorded. The resighting data were modelled as D independent draws of marked and unmarked birds from the population sampled without replacement. Data were regarded as replaced between days. This leads to the likelihood function proportional to the product of D hypergeometric distributions each with a common value for abundance. Approximate 95% confidence intervals were found by inverting a likelihood ratio test for $N = N_0$ where N_0 is the abundance under the null hypothesis.

Table 1. Summary of Hutton's shearwaters marked at the Kōwhai River colony and counted at sea.

	2002	2014
Dates sampled	16–20 September (4 nights)	15–17 September (2 nights)
Number of birds marked	2,077	1,704
Dates counted at sea	21–30 September (10 days)	17–20 September (4 days)
Number of unmarked birds counted at sea	425,516	106,900

RESULTS

The smaller numbers of birds marked and counted in 2014 were the result of bad weather curtailing the marking programme after 2 nights and gale force winds limiting the at-sea observations to 4 days from the planned 10 days (Table 1). In 2002 the estimated population size of Hutton's shearwaters was $\hat{N}$ = 459,290 (SE = 12,864; 95% confidence interval = 434,306–484,733). The estimated population size in 2014 was $\hat{N}$ = 590,407 (SE 26,678; 95% confidence interval = 543,992–642,697. As these confidence intervals do not overlap the inference is that the population of Hutton's shearwaters off Kaikōura in late September increased between 2002 and 2014. The estimated change in number of 131,117 birds, or 28.5%, corresponds to compounded annual growth of 2% per year.

DISCUSSION

Previous population estimates of Hutton's shearwater were 94,000 (Taylor 2000) and 106,000 (Cuthbert & Davis 2002b) breeding pairs. If, as has been suggested by Warham (1996), that more than half of a seabird population can be made up of non-breeding individuals, then there could be >400,000 birds in the Kaikōura population; this does not take into account the number of young birds still in Australian waters and yet to return. Our 2002 population estimate from our colour-marked bird modelling is about 460,000 birds, only 15% greater than that based on burrow counts which is very dependent on how close Warham's (1996) generalised estimate of non-breeders is for Hutton's shearwater.

Sommer *et al.* (2009) suggested there was an annual population increase of 1.7% in the 20 years to 2007 which was also consistent with population modelling (Cuthbert & Davis 2002b). If that increase is applicable through to 2014, and it is compounded over the period 2002–2014, there would be a population increase of 22.4% between counts; that is remarkably close to the increase measured here of 28.5% from our 2002 and 2014 colour marking exercises.

The population estimates for birds found off the Kaikōura coast in this study were much higher than estimates based on burrow counts, e.g. 106,000 pairs (Cuthbert & Davis 2002b). We suggest one of three reasons for this.

1) Our assumptions that (i) counts were independent and (ii) could be treated as sampling without replacement within a resampling session were violated. For example, there may have been inadvertent double counting of birds within a resighting session.
2) The non-breeding population approximates the breeding population as suggested by Warham (1996).
3) The estimates of burrowed surface area in Cuthbert & Davis (2002b) and Sommer *et al.* (2009) are inaccurate.

This study is unable to suggest which of these three scenarios is most likely and indeed all three may well be interacting to produce these results. We have some confidence that the shearwater flocks at sea mix randomly each day. In 2001, VHF radio-transmitters were attached to ten individual Hutton's shearwaters caught near the research hut to look at the flight paths the birds used to access the colony. These birds were checked for at sea each day near the Kaikōura Peninsula. The presence of individually radio-tagged birds at-sea changed daily. Also, most tagged birds went well beyond the VHF receiver range near Kaikōura (up to 20 km distance), only returning near land at dusk. From this we assumed that colour-marked birds would be mixing at random with unmarked birds from the entire species population each day rather than clustering into colony-specific flocks (GAT *unpubl. data*). The technique also works as it is not biased towards capturing mainly immatures on the surface as might happen later in the breeding season.

Thus, as long as this methodology and method of analysis is repeated, we consider this a scientifically and statistically robust method of estimating the population. By this we mean that we should be able to infer estimates of the population change, even if there is bias in our absolute abundance estimates. The increase we have estimated between 2002 and 2014 of 2% per year is in line with the increase in the breeding population in the Kōwhai colony between

1997 and 2008 (Sommer *et al.* 2009).

The methods adopted in this study allowed us to assess the total population of Hutton's shearwater in the Kaikōura region. The increase in total population is similar to the increase in breeding numbers (1.7% year^{-1}; Sommer *et al.* 2009). Therefore, the non-breeding and breeding populations are increasing at a similar rate. Prior to this study, there was concern as to whether stoat predation may be affecting different parts of the population disproportionately, depending on their onshore behaviour. Whereas Cuthbert and Davis (2002a) found that only 0.25% of breeding adults were killed by stoats each year, there was less certainty about impacts on other age groups. Birds in burrow chambers are not as easy for stoats to access and kill as birds sitting on the surface. Breeding birds therefore have some advantages within the nest and spending very limited time on the colony surface once the snow has melted. Pre-breeders by comparison spend large amounts of time at night sitting around calling, displaying, or sleeping on the ground and are considered at greater risk to stoat predation. Therefore, we wanted to determine the size of the total population, not just the birds occupying burrows to see if the non-breeding pool was being reduced by stoats. This does not appear to be the case and the observation that the population is growing supports Cuthbert's (2001) conclusion that stoats do not have an adverse impact on Hutton's shearwaters.

Utility of these data on estimating the impact of the 2016 Kaikōura Earthquake

The November 2016 magnitude 7.8 earthquake centred near Kaikōura was the largest earthquake in this region in over hundred years (United States Geological Survey 2016). It affected the northern half of the South Island and caused massive landslides and rockfalls within the Hutton's shearwater breeding colonies (M. Morrissey, Department of Conservation, *pers. comm.* 2016). The timing of the earthquake (at 0002 h, 14 November 2016 NZDT) coincided with the peak laying period for these shearwaters (Cuthbert 2001). We consider our population estimates of great value in assessing the impact of the November 2016 earthquake on Hutton's shearwater. A repeat colour-marking total population estimate is scheduled for September 2018.

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From wetlands to islands: morphological variation, plumage and song in Pacific island *Acrocephalus* warblers

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Abstract: *Acrocephalus* warblers occur across Eurasia, Africa, and Australasia, where they are typically migratory, wetland species, but also occur on islands as sedentary endemics in drier habitats, including forest and scrub. External morphology and song amongst Pacific island *Acrocephalus* warblers were investigated and comparisons made with *Acrocephalus* species elsewhere. There was a range of sizes between Pacific island *Acrocephalus* warblers, many being larger than migratory continental species. Bill:wing length ratios were higher in most Pacific species, and their wings more rounded, than most continental species, but less rounded than swamp-warblers of Africa and adjacent islands. Plumages of W and N Pacific species resembled reed-warblers elsewhere, but in SE Polynesia were more varied, brown or grey dorsally, shaded olive, yellow or rufous, and pale ventrally, shaded white, yellow or buff-white, with a melanistic morph on Tahiti. Spectrographic analysis showed a gradient of song complexity from continental and Marianas/Micronesia species (*A. hiwae, A. syrinx*), through to *A. taiti* and *A. vaughani* on the Pitcairn islands, which had no song. The mean frequency of Pacific island reed-warbler songs was inversely correlated with mean body size.

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Key words: *Acrocephalus*, body-size, evolution, islands, Pacific, reed-warbler, song

INTRODUCTION

Many *Acrocephalus* warblers (Passeri: Acrocephalidae) are well-known summer migrants that breed across the Palaearctic, and over half of the recognised species (55%) are endemic sedentary island species confined to islands or archipelagos (Dyrcz *et al*. 2016). Of 42 recognised *Acrocephalus* warbler species, 19 are continental, often migratory species, 19 occur (or occurred) on islands in the Pacific, and 4 occur on islands off Africa (Baker 1997; Dyrcz 2006; Kennerley & Pearson 2010; Leisler & Schulze-Hagen 2011; Dyrcz *et al*. 2016; Thibault & Cibois 2017). The 19 continental species typically inhabit wetlands, selecting breeding habitats in and around reeds or in other dense swamp or marshland vegetation (Dyrcz 2006; Kennerley & Pearson 2010; Dyrcz *et al*. 2016). Some may select drier habitats, such as trees with dense herbaceous undergrowth or scrubby thickets, e.g. *A. orinus*, *A. dumetorum* and some *A. palustris. Acrocephalus newtoni* on Madagascar also occurs in reeds and other wetland habitats, but *A. rodericanus* on Rodrigues Island and *A. sechellensis* on the Seychelles both occupy dry forest and scrub, while *A. brevipennis* on the Atlantic Cape Verde Islands occupies a broad range of dry habitats, as well as wetter situations in giant reed (*Arundo donax*) (Komdeur 1992; Showler *et al*. 2002;

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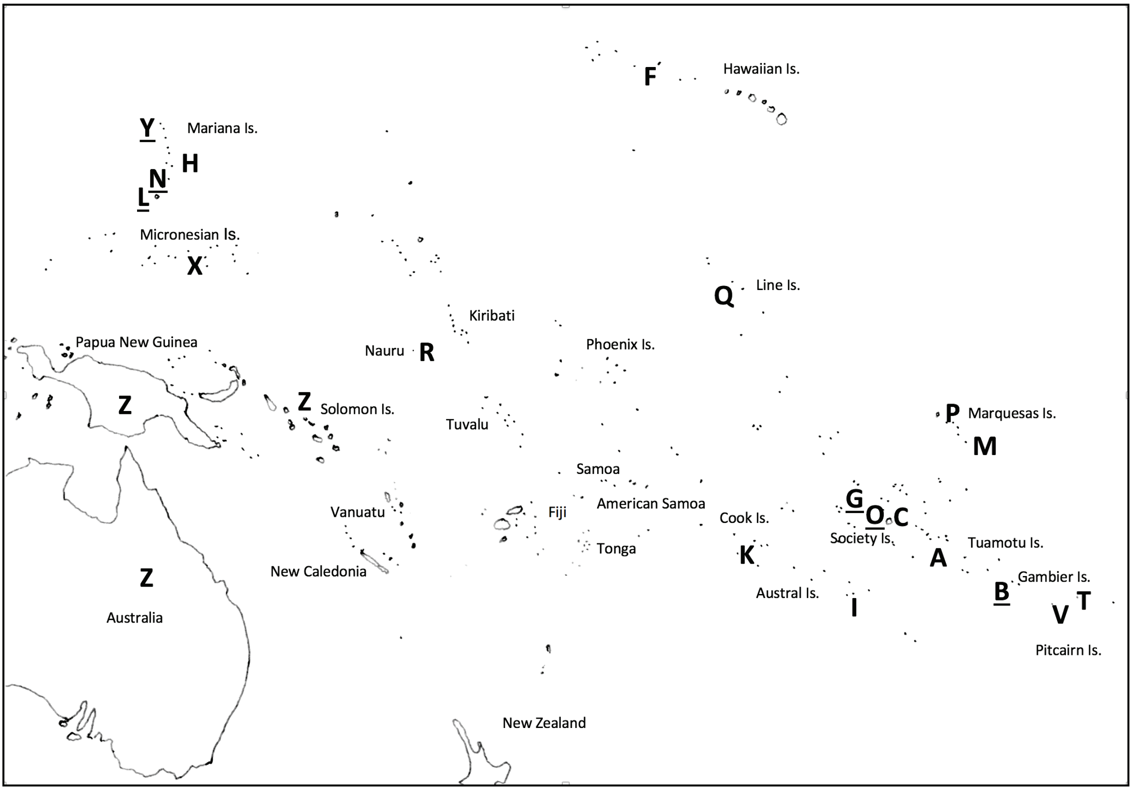

Figure 1. Indicative distribution of 20 *Acrocephalus* warbler species across the Pacific islands. Letter codes for species are: A = *atyphus;* B = *astrolabii;* C = *caffer;* F = *familiaris;* G = *musae;* H = *hiwae;* I = *rimitarae;* K = *kerearako;* L = *luscinius;* M = *mendanae;* N = *nijoi;* O = *longirostris;* P = *percernis;* Q = *aequinoctialis;* R = *rehsei;* T = *taiti;* V = *vaughani;* X = *syrinx;* Y = *yamashinae*. For reference, the broad distribution of *Acrocephalus australis* (coded Z) in Australia, Papua New Guinea, and the Solomon Islands is also shown. Codes for six extinct species are underlined.

Kennerley & Pearson 2010).

The Pacific islands (Fig. 1) on which 19 endemic *Acrocephalus* (formerly *Conopoderas*) warblers are known range from the Mariana Islands and the Hawaiian Leeward Islands in the north, south to the Line Islands (Kiritimati), Eastern Polynesia including the Cook Islands, then further south to the Austral, Gambier and Pitcairn islands (Pratt *et al*. 1987; van Perlo 2011; Thibault & Cibois 2017). In addition, *Acrocephalus* species occur in Australia, New Guinea, the Solomons, and SE and E Asia (Dyrcz 2006; Kennerley & Pearson 2010). No *Acrocephalus* species breed in New Zealand, although a vagrant male *A. australis* sang near Cheviot in November 2004 (Allen 2013; Heather & Robertson 2015). *Acrocephalus* warblers are absent from the larger, species-rich islands of Melanesia and Hawaii (Kennerley & Pearson 2010), apart from *A. australis* represented on Pacific islands in Melanesia by the subspecies *A. a. sumbae* (Dyrcz *et al*. 2016). Most Pacific island *Acrocephalus* warblers occupy dry habitats, such as forest and scrub, although some species also occupy habitats alongside lakes, ponds or rivers, e.g. *A. kerearako* and *A. syrinx*. In the Marianas, *A. luscinius* once occupied cane thickets near freshwater ponds, and *A. hiwae* occupies woodland and tall wetland vegetation and even mangroves (Kennerley & Pearson 2010), with habitat loss a leading factor limiting its populations (Mosher 2006; Camp *et al*. 2009). *Acrocephalus caffer* (Tahiti) and the extinct *A. longirostris* (Moorea) select (or selected) patches of Polynesian bamboo (*Schizostachyum glaucifolium*) near forest (Kennerley & Pearson 2010; *pers. obs.*), although this bamboo is considered as introduced in the Society Islands (Larrue *et al*. 2010).

The Pacific island *Acrocephalus* taxa have been the focus of increased research over recent years, resulting in re-interpretation of their phylogeny and taxonomic changes (Holyoak & Thibault 1977; Leisler *et al*. 1997; Thibault & Cibois 2006, 2017; Fregin *et al*. 2009, 2012; Cibois *et al*. 2007, 2008, 2011a,b; Leisler & Schulze-Hagen 2011; Fregin 2012; Saitoh *et al*. 2012). Kennerley & Pearson (2010)

Table 1. Pacific island *Acrocephalus* species and their IUCN Red List status (IUCN 2017).

Name	**Species**	**Pacific region**	**Red List status**	**Population trend**
Australian reed-warbler	*australis*	Melanesia	Least Concern	Stable
Guam reed-warbler	*luscinius*	Micronesia	Extinct	—
Saipan reed-warbler	*hiwae*	Micronesia	Critically Endangered	Decreasing
Aguijan reed-warbler	*nijoi*	Micronesia	Extinct	—
Caroline reed-warbler	*syrinx*	Micronesia	Least Concern	Stable
Kiritimati reed-warbler	*aequinoctialis*	Eastern Polynesia	Endangered	Decreasing[1]
S Marquesas reed-warbler	*mendanae*	Eastern Polynesia	Least Concern	Stable
Pagan reed-warbler	*yamashinae*	Eastern Polynesia	Extinct	—
Mangareva reed-warbler	*astrolabii*	Eastern Polynesia	Extinct	—
Nauru reed-warbler	*rehsei*	SE Micronesia	Vulnerable	Stable
Millerbird	*familiaris*	Hawaiian Islands	Critically Endangered	Stable
Pitcairn reed-warbler	*vaughani*	Eastern Polynesia	Endangered	Unknown
Henderson reed-warbler	*taiti*	Eastern Polynesia	Vulnerable	Stable
Cook reed-warbler	*kerearako*	Eastern Polynesia	Near Threatened	Decreasing
Rimatara reed-warbler	*rimitarae*	Eastern Polynesia	Critically Endangered	Decreasing
Forster's reed-warbler	*musae*	Eastern Polynesia	Extinct	—
Tahiti reed-warbler	*caffer*	Eastern Polynesia	Endangered	Decreasing
Moorea reed-warbler	*longirostris*	Eastern Polynesia	Extinct[2]	—
N Marquesas reed-warbler	*percernis*	Eastern Polynesia	Least Concern	Stable
Tuamotu reed-warbler	*atyphus*	Eastern Polynesia	Least Concern	Stable

[1] however, no declines on Kiritimati Island noted since 2007 (VanderWerf *et al*. 2016; Thibault & Cibois 2017)
[2] changed from IUCN Critically Endangered, following Thibault & Cibois (2017)

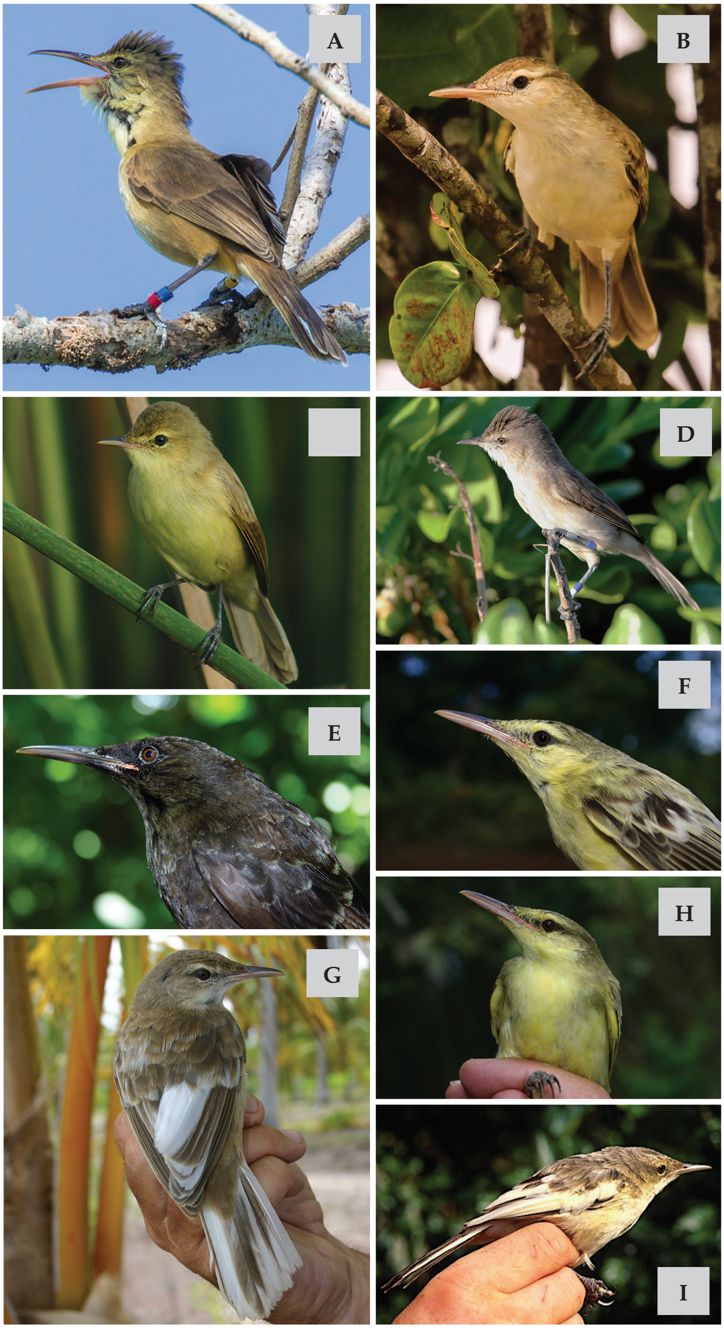

Figure 2. A selection of nine Pacific island *Acrocephalus* warblers. (A) *A. hiwae*, Saipan (photo: Lainie Berry); (B) *A. syrinx*, Weno, Chuuk (photo: Lainie Berry); (C) *A. kerearako kerearako*, Mangaia (photo: Gerald McCormack); (D) *A. familiaris kingi*, Laysan (photo: Cameron L. Rutt); (E) *A. caffer*, dark phase, Tahiti, (photo: A. Cibois & J-C. Thibault); (F). *A. percernis idae*, Ua Huka, (photo: A. Cibois & J-C. Thibault); (G) *A. atyphus atyphus*, showing leucism (white feathers), Takapoto, (photo: A. Cibois & J-C. Thibault); (H) *A. mendanae dido*, Ua Pou, (photo: A. Cibois & J-C. Thibault); (I) *A. vaughani*, Pitcairn, (photo: Elizabeth Bell, WMIL). The colour banded *A. familiaris kingi* (D) had been translocated from Nihoa to Laysan, the location of the extinct subspecies *A. familiaris familiaris*, to re-create a second millerbird population (Freifeld *et al.* 2016; Cameron L. Rutt, *pers. comm.*).

discussed the origin, distribution and extinction of Pacific island *Acrocephalus* warblers, regarding them as 'supertramp' species (Diamond 1974), but Cibois *et al*. (2011a) concluded that, while these species meet some of the 'supertramp' criteria in their aptitude for colonising remote archipelagos, their life-history characteristics do not fit the model. Leisler & Winkler (2015) examined *Acrocephalus* warblers on islands in the Atlantic, Indian, and Pacific Oceans, emphasising that their evolution pertained to more than the hitherto studied body size and bill dimensions.

Here, I follow the names and classification of Dyrcz *et al*. (2016), using additional information from Kennerley & Pearson (2010). Of the 20 species of Pacific island *Acrocephalus* warblers, which include *A. australis* from the Solomons (Fig. 1), six (30%) are extinct, eight (40%) are threatened, one (5%) is near threatened and five (25%) are of least concern; eight extant species are stable, five are decreasing and the population trend of one species is unknown (Table 1; IUCN 2017; Thibault & Cibois 2017).

Morphologically, these Pacific island *Acrocephalus* warblers vary widely across their area of distribution, such as in size, wing shape, and colour. For instance their lengths, from Dyrcz (2006), range from the 13 cm millerbird (*A. familiaris*) from Nihoa and Laysan to the 18 cm *A. luscinius* of Micronesia and 17–19 cm *A. atyphus, A. caffer, A. mendanae,* and *A. percernis* from Eastern Polynesia. More sedentary *Acrocephalus* warblers, including those on islands, have more rounded wings, while *Acrocephalus* warblers that migrate long distances have more pointed wings (Kennerley & Pearson 2010; Leisler & Schulze-Hagen 2011). However, Komdeur *et al*. (2004) found the Seychelles Warbler (*A. sechellensis*) did not differ from migratory warblers in its wing shape and wing loading, arguing that it showed morphological structures required for sustained flight, and may have a behavioural reluctance to disperse across the sea. More recently, Leisler & Winkler (2015) reported that *A. sechellensis* — freed from requirements of long-distance flight — was better able to adapt to highly cluttered habitats by having, *inter alia*, rounder, more slotted and broader wings than migratory *Acrocephalus* species.

Continental *Acrocephalus* warblers have streaked or uniform brownish plumage, but Pacific island species may have: yellow underparts (e.g. *A. caffer, A. kerearako, A. mendanae, A. percernis*), white (leucistic) feathers (e.g. *A. taiti, A. vaughani, A. rimitarae*), predominantly grey and white plumage (*A. aequinoctialis*), or, in *A. caffer,* a melanistic as well as typical colour morph (Fig. 2; Dyrcz *et al*. 2016).

Many *Acrocephalus* warblers exhibit a high degree of song complexity (Catchpole 1980; Parmenter & Byers 1991; Cramp *et al*. 1992; Kennerley & Pearson 2010), including mimicry of other species, e.g. the marsh warbler (*A. plaustris*) that breeds in Europe (LeMaire 1974; Bairlein *et al*. 2006; Catchpole & Slater 2008; Leisler & Schulze-Hagen 2011). Delivery rates and diversity of song syllables have been studied in various migratory *Acrocephalus* species (e.g. Catchpole 1980, 1983; Hasselquist *et al.* 1996; Bell *et al*. 1997, 2004; Borowiec & Lontowski 2000), as well as in some island species (e.g. Catchpole & Komdeur 1993). Island *Acrocephalus* species are reported to have simpler songs than mainland relatives, and variations in their song patterns across the Pacific have been briefly presented (Bell & Perfect 1994; McPherson 1998; Bell 2001; Bairlein *et al*. 2006; Kennerley & Pearson 2010). The song frequency of birds is negatively correlated with body-size in some species (e.g. Wallschläger 1980; Badyaev & Leaf 1997; Mahler & Gil 2009), and as Pacific island *Acrocephalus* species vary in size (Dyrcz 2006), they provide an opportunity to test this inverse size-song frequency relationship.

Here, I examine in further detail morphological variation and song patterns in Pacific island *Acrocephalus* warblers, comparing them with congeneric species elsewhere. Two broad questions are addressed: (1) How variable are shapes, sizes and colours of Pacific island *Acrocephalus* species, and how do they compare with *Acrocephalus* species elsewhere? (2) How variable and complex are Pacific island *Acrocephalus* warbler songs, how do they compare with *Acrocephalus* species elsewhere, and how do their song frequencies relate to body size?

METHODS

Measurement of museum specimens

To obtain data on size variation among Pacific island and continental *Acrocephalus* species, morphometric data were obtained from seven museums (Bishop Museum, Honolulu; British Museum of Natural History, Tring; California Academy of Sciences, San Francisco; Muséum National d'Histoire Naturelle, Paris; Museum of Vertebrate Zoology, Berkeley; Smithsonian Institution National Museum of Natural History, Washington DC; Te Papa Tongariro Wellington).

With measurements following Svensson (1975), the following variables were recorded, where available, from most specimens: data entry number (chronological), taxon code, location code, museum code, sex code, age code, year collected, wing-length (mm) using maximum flattened chord, tail length (mm), tail graduation as outer-tail feather tip to longest tail feather tip (mm), bill to skull (mm), bill to feathers (mm), bill to nostril (mm), bill depth (mm), bill width (mm), tarsus length (mm), 1st toe claw length (mm), 1st toe claw depth (mm), 1st toe length excluding claw (mm), 1st toe length including claw length (mm), 3rd toe claw length (mm), 3rd toe claw depth (mm), 3rd toe length excluding claw (mm), 3rd toe length including claw length (mm).

Plumage condition of each specimen was noted, including whether or not it was in moult (if so, which area – body, wings or tail), and the degree of feather wear from fresh to abraded. Damaged or moulting museum specimens resulted in some measurements not being taken so these data were unavailable for multivariate analysis. For each specimen, the colours of the plumage and soft-parts were recorded, and for comparison with additional mainland *Acrocephalus* species, supplementary data were obtained from Kennerley & Pearson (2010).

The ascendant system of numbering primaries (from outer distal to inner proximal) was used in wing feather examination, e.g. to measure wing-formulae (see Witherby *et al*. 1943; Svensson 1975; Williamson 1976; Kennerley & Pearson 2010; Shirihai & Svensson 2018), rather than the descendent system generally used in moult studies and elsewhere (see Ginn & Melville 1983; Jenni & Winkler 1994; Deutsche Ornithologen-Gessellschaft 2011; Bell 2015). In *Acrocephalus* warblers, the first primary is small or minute (Kennerley & Pearson 2010) and its length was compared to that of the longest primary covert (mm: greater or less than). The wing formula was recorded for ascendant primary feathers 2–10, including relative feather-length (mm) from wing point, as well as primary emargination (primary nos. and emargination lengths (mm)), primary notching (primary nos. and notch lengths (mm)), and the position of the 2nd primary relative to other primaries. From examination of wing data, wing shapes can be compared. For analysis, where a range of primaries was recorded between individuals of a species, the mid-point primary number was taken, (e.g. 5 if range 4–6; 3.5 if range 3–4) to simplify graphical representation of the relationship between the position of the wing-point primary and the inner primary (occasionally secondary) equivalent to the tip of the 2nd primary (Fig. 5).

Recording of songs and calls

Field recordings of songs of Pacific island *Acrocephalus* warblers were made as follows: *A. kerearako kaoko* on Mitiaro (Cook Is.) and *A. caffer* on Tahiti (Society Is.) by the author; *A. kerearako kerearako* on Mangaia (Cook Is.) by members of the Ornithological Society of New Zealand; *A. familiaris kingi* on Nihoa (Hawaiian Leeward Is.) by Sheila Conant; *A. percernis percernis* on Nuku Hiva (N. Marquesas Islands) and *A. mendanae mendanae* on Hiva Oa (S. Marquesas Is.) by Rod Morris; *A. vaughani* on Pitcairn Is. by Bruce Robertson; and *A. taiti* on Henderson Is. by Jim Jolly. Sound spectrograms from a selection of these recordings were reproduced by Kennerley & Pearson (2010) after being lodged in the McPherson Sound Library (McPherson 1995, 1998). The late Ralph Shreiber kindly supplied song information for *A. aequinoctialis* from Kiritimati Is. (see Milder & Schreiber 1989).

In the Pacific, both cassette and DAT tape recorders were used to record warbler songs and calls, particularly a portable Sony TCD-D10 ProII DAT recorder with a Telinga parabolic microphone. Other *Acrocephalus* song recordings were made in Europe (e.g. Bell *et al*. 1997, 2004), while songs (or calls) were also sourced from the following bird sound libraries: the British Library of Wildlife Sounds, London, UK; the Florida Museum of Natural History Bird Sounds Library, University of Florida, Gainesville, Florida USA; the Macaulay Library of Bird Sounds, Cornell University Laboratory of Ornithology, Ithaca, NY, USA; the McPherson Natural History Unit Sound Archive, Ashburton, NZ; the Television New Zealand Natural History Unit sound library, Dunedin, NZ; and the National Biodiversity Center's Xeno-canto web-site. The quality of these library sound recordings varied, but those of better-quality were selected to provide samples additional to the field recordings described above.

Morphometric analysis

For statistical comparison of Pacific island *Acrocephalus* warbler morphometrics, principal component analyses (PCA) using XLSTAT were undertaken, while other statistical analyses were done using both XLSTAT and StatPlus:mac Pro. A wide range of combinations of variables were run using PCA and the most informative set used to compare morphometrics across species (Figs. 3 & 4). The chosen combination of PCA variables balanced good representation of both species and variables, given that some had to be excluded in damaged and/or moulting specimens.

Bioacoustic analysis

Songs (or calls) of a selection of individual *Acrocephalus* warblers from Pacific islands and adjacent mainland areas were analysed using AviSoft SASLab and Raven Pro version 1.5 sound analysis software on PC and Mac computers. A song-element coding system, previously used for European *Acrocephalus* species, was used to identify and classify individual syllable element types on printed output of spectrograms (see e.g. Catchpole 1979; Bell *et al*. 1997, 2004; Catchpole & Slater 2008). The following song variables were calculated: mean maximum frequency (kHz); mean minimum frequency (kHz); mean frequency (kHz); and frequency range (kHz). For visual comparison, 3–3.5 second sound spectrograms were compared, and for quantitative comparison, samples over a standard 36 second recording period were analysed to provide data on: mean time in song (seconds); mean no. syllables; mean no. syllable types; mean no. syllables per second overall (36 second sample); mean no. syllables per second of song; and percentage of time in song.

RESULTS

External morphometrics

Morphometric variation

From 139 museum specimens, morphometric data were obtained for 16 Pacific island *Acrocephalus* species (following Dyrcz *et al*. 2016) as follows: 6 Guam reed-warblers (*A. luscinius,* extinct); 9 Saipan reed-warblers (*A. hiwae*), 5 Caroline reed-warblers (*A. syrinx*), 5 Kiritimati reed-warblers (*A. aequinoctialis*), 6 Southern Marquesas reed-warblers (*A. mendanae*), 7 Pagan reed-warblers (*A. yamashinae,* extinct), 2 Mangareva reed-warblers (*A. astrolabii,* extinct), 1 Nauru reed-warbler (*A. rehsei*), 51 millerbirds (*A. familiaris*, including 16 of the extinct nominate subspecies *familiaris* from Laysan), 11 Pitcairn reed-warblers (*A. vaughani*), 3 Henderson reed-warblers (*A. taiti*), 6 Cook reed-warblers (*A. kerearako*), 1 Forster's reed-warbler (*A. musae*, extinct), 8 Tahiti reed-warblers (*A. caffer*), 4 Northern Marquesas reed-warblers (*A. percernis*), and 14 Tuamotu reed-warblers (*A. atyphus*). A principal component analysis plot for measurements of museum specimens from the 16 Pacific island *Acrocephalus* species illustrates morphometric variation amongst them (Fig. 3).

The first two axes explained 96.9% of the variance. Increasing size is evident along PC axis 1 which corresponded to all measurements and explained most of the variance (85.8%). Axis 2 was mainly composed of bill lengths and tail length, explaining 11.1% of the variance (Fig. 3), and a bivariate plot of two of these measurements (tail-length and bill-to-feathers length) was used to further illustrate their relative sizes (Fig. 4). *Acrocephalus familiaris* was distinctly smaller than other taxa (PC1 axis), while *A. caffer* and single *A. astrolabii* and *A. musae* specimens were largest (Fig. 3). *Acrocephalus mendanae*, *A. percernis*, *A. atyphus*, *A. luscinius*, and *A. hiwae* were also relatively large, while species clustered in an intermediate position were *A. syrinx*, *A. rehsei*, *A. aequinoctialis*, *A. yamashinae*, *A. kerearako*, *A. vaughani*, and *A. taiti*. Contributing to shape variation (PC2 axis) were particularly *A. luscinius*, and *A. hiwae* with relatively long bills, and *A. taiti* and *A. vaughani* with relatively longer tails and tarsi and relatively smaller bills (Figs. 3 and 4).

A feature of many Pacific island *Acrocephalus* species was their relatively large bill size (Figs. 2–4; Dyrcz 2006; Kennerley & Pearson 2010; Dyrcz *et al*. 2016). For comparison with other *Acrocephalus* warblers, ratios of mean bill-to-skull length to mean wing-length were determined for all the world's *Acrocephalus* species (see Appendix). Ratios were highest in Pacific island species, except for *A. taiti*, *A. vaughani* and *A. aequinoctialis*, reflecting the proportionately larger bills in most Pacific island *Acrocephalus* warblers. Clearly both wing-size and wing-shape also affect these ratios, and wing-shape is considered next.

Wing formula and wing-shape

Wing-formulae were determined for a range of *Acrocephalus* species. Resident species, including those on islands, had more rounded wings, and generally, they have primaries 3–6 emarginated, often primaries 3–5. Long-distance migrants tended to have longer wings with fewer primaries emarginated, usually primary 3, sometimes 4 (Kennerley & Pearson 2010). Consequently, the position of the wing-point, and of the inner primary (or secondary) equivalent in length to the 2nd primary, tended to be more proximal on the bird in resident species, and more distal in migratory species.

When positions of the wing-point and the flight feather equivalent to the tip of the 2nd primary were compared (Fig. 5) for four *Acrocephalus* species groups — resident African species (including islands), resident Pacific island species, round-winged migratory or sedentary continental species, and long-winged continental migrants — there was a significant correlation between the two wing measures (Pearson $r = 0.8691$, $df = 34$, $p < 0.001$) and differences occurred between most groups for both wing measures (Mann-Whitney U-tests, $p = 0.124$ to $p < 0.001$).

Continental migrant *Acrocephalus* warblers with longer, more pointed, wings had equivalent primary measures most distally positioned (*arundinaceus, griseldis, orientalis, paludicola, palustris, schoenobaenus, scirpaceus*). Next in the sequence were rounder-winged migratory or more sedentary continental species (*agricola, australis, bistrigiceps, dumetorum, melanopogon, orinus, sorghophilus, stentoreus, tangorum*). Resident Pacific island reed-warblers (*aequinoctialis, atyphus, caffer, familiaris, kerearako, luscinius, mendanae, rimitarae, syrinx, taiti, vaughani*) were round-winged, but less so than the African species (*brevipennis, gracilirostris, newtoni, rodericanus, rufescens, sechellensis*) which had markedly rounded wings. The aptly named 'blunt-winged warbler' (*A. concinens*), a continental species, fell amongst some Pacific island species (Fig. 5; Kennerley & Pearson 2010).

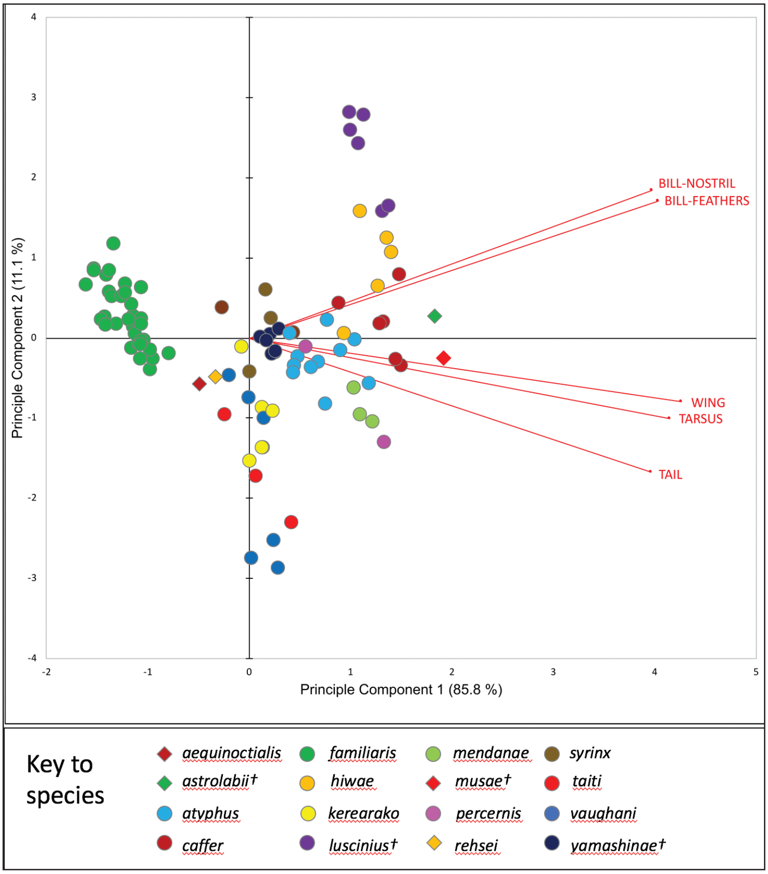

Figure 3. Principal component analysis plot for five log-transformed measurements of museum specimens from 16 Pacific island *Acrocephalus* species. The measurements were wing-length, tail-length, bill-to-feathers, bill-to-nostril, and tarsus-length. The five lines show the projections of the five variables in the factors space. Symbols for most species are circles, but diamonds are used for four single individuals. † indicates extinct species.

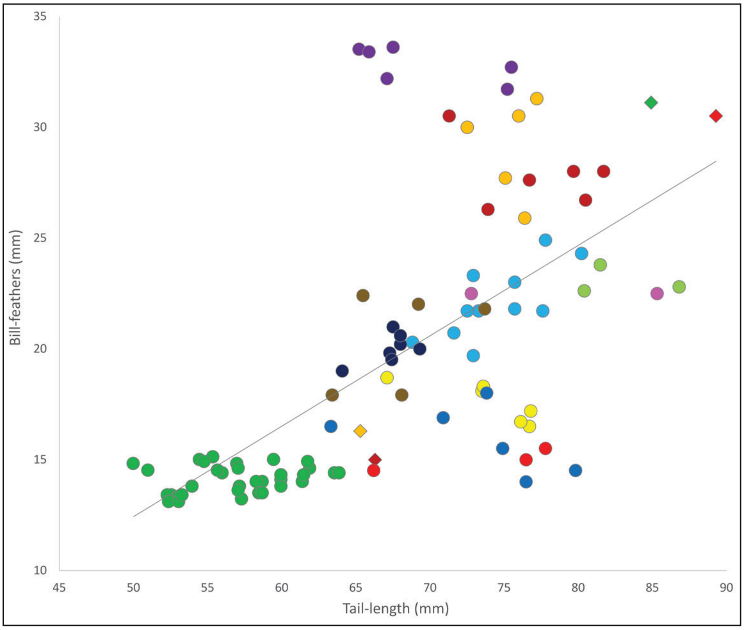

Figure 4. Scatter plot (with regression line) of tail-length and bill-to-feathers length for museum specimens of 16 Pacific island *Acrocephalus* species. Symbol codes for species are shown in Fig. 3.

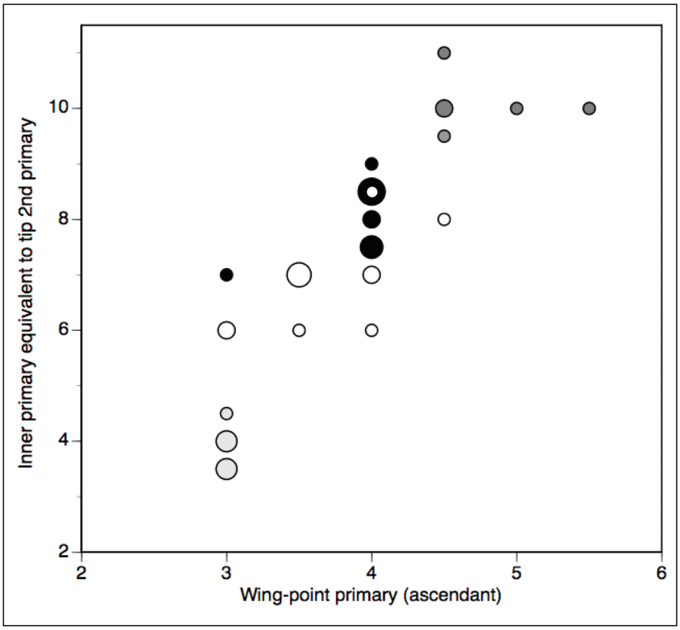

Figure 5. The positions of the wing-point primary plotted against the inner primary (occasionally secondary) equivalent to the tip of the 2nd primary (numbered ascendantly) in *Acrocephalus* warblers, the size of circles indicating the number of species (range 1–4). Four main *Acrocephalus* groups are differentiated: light grey = long-winged continental migrants; white = other continental species, often migratory; black = Pacific island species with rounded wings; dark grey = species from Africa and its offshore islands with markedly rounded wings. Those species with rounder wings tend to have both the wing-point and the primary equivalent to the 2nd primary more proximally positioned on the bird, while these primaries are more distal in species with longer wings, especially some long-distance migrants ($r = 0.8691$, $df = 34$, $p < 0.001$). Data from Kennerley & Pearson (2010) and present study.

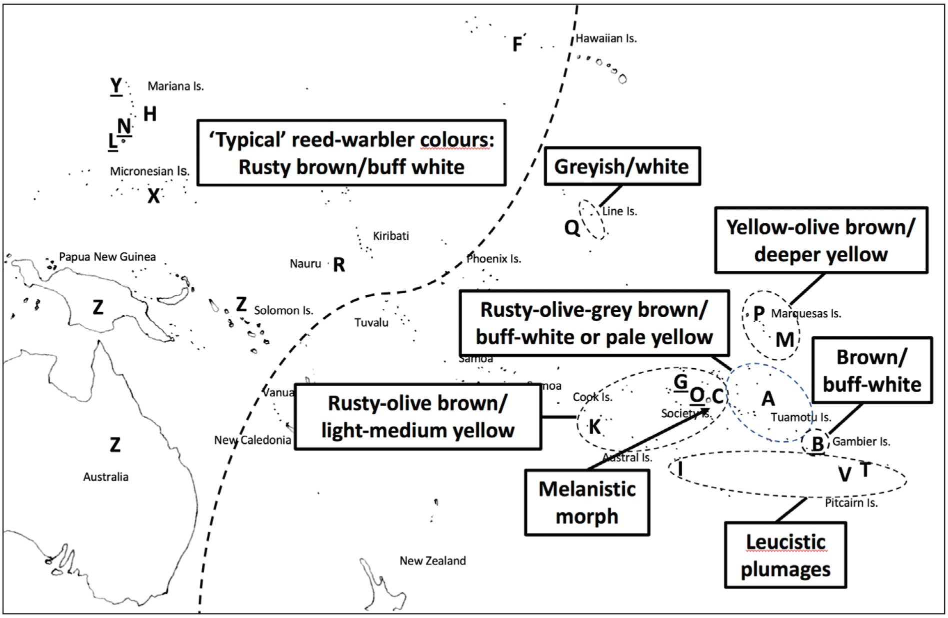

Figure 6. Predominant colours of *Acrocephalus* warblers across the Pacific based on examination of museum specimens, expressed mostly as dorsal colour/ventral colour. Letter codes for species as in Fig. 1. Data from present study, supplemented with information from Dyrcz (2006), Kennerley & Pearson (2010) and Dyrcz *et al.* (2016).

Plumage colour

The colours of Pacific island *Acrocephalus* warblers (Figs. 2 & 6) fell into two main groups: (1) species from the N and W Pacific islands (Hawaii, Marianas, Micronesia, and Solomons) which were uniform brownish dorsally and pale buff ventrally, akin to *Acrocephalus* species outside the Pacific (Fig. 2A,B,D; Dyrcz *et al*. 2016); (2) species that occur across E Polynesia which departed from the typical and relatively uniform 'reed-warbler' pattern, which were predominantly brown or grey dorsally, variously shaded olive, yellow and rufous, and paler ventrally, variously shaded white, yellow or buff — *A. percernis* and *A. mendanae* of the Marquesas islands (Fig. 2F,H) were particularly yellow ventrally, while in Kiritimati *A. aequinoctialis* was distinctly greyish dorsally and whitish ventrally (Fig. 6). In *A. atyphus* large colour variation was found in almost all atolls (Cibois *et al*. 2011c; A. Cibois *pers. comm.*).

South east Polynesian species also had pale edgings to the feathers, particularly on the mantle and upper wing coverts. In N and W Pacific species (group 1), these edgings appeared more uniform, although slightly paler brown edging occurred (in *australis, familiaris, hiwae, luscinius, nijoi, rehsei, syrinx* and *yamashinae*); also in *A. astrolabii*, evidently from Magareva in the Gambier Islands, SE Polynesia (Dyrcz 2006; Cibois *et al*. 2011b; Thibault & Cibois 2017). Some populations of adjacent *A. atyphus* in the Tuamotus also showed less marked feather edging, as did *A. aequinoctialis* and *A. kerearako* (Fig. 2C). In remaining, often larger, Polynesian species, pale yellow or yellow-white edging to dorsal feathers were clearly evident. The occurrence of white feathers (leucism) was a feature of the southern *A. rimitarae, A. taiti*, and *A. vaughani* (Fig. 2I & Fig. 6). In some specimens of *A. atyphus* (Fig. 2G), *A. caffer*, *A. familiaris* (Laysan subspecies *familiaris*), *A. kerearako, A. mendanae* and *A. percernis* some white feathers were also seen. On Tahiti *A. caffer* was dimorphic, being either a 'typical' olive brown/light yellow or, less frequently, a melanistic dark brown (Fig. 2E). In some species predominant colours differed between and within islands, e.g. in *A. atyphus* (Cibois *et al*. 2011c), and with age, e.g. in *A. vaughani* and *A. rimitarae* (Thibault & Cibois 2006).

Song patterns

Song spectrograms

Short sound spectrogram samples of song (or calls) of ten Pacific island *Acrocephalus* warblers and, for comparison, two continental species from the W Pacific (*A. australis, A. orientalis*), exemplify differences between species (Fig. 7). There was a gradient of song complexity from continental and Marianas/Micronesia species (*hiwae, syrinx*), through to *A. taiti* from Henderson and *A. vaughani* from Pitcairn, which had no song but simpler harsh calls. Short bursts of song with intervals of no song were a feature of *A. familiaris* from Nihoa and *A. aequinoctialis* from Kiritimati, while a characteristic of the song repertoires of SE Polynesian *Acrocephalus* species (*kerearako, caffer, mendanae, percernis*) was the inclusion of 'churr' syllables. The relatively accomplished song of the 'nightingale' reed-warbler (*A. hiwae*) from Saipan was evident (Fig. 7).

Song complexity and delivery rate

Analyses of 36-second sound spectrogram samples of 13 Pacific island *Acrocephalus* warblers, plus *A. australis* and *A. orientalis* for comparison, revealed clear variation across the Pacific region, with similarity between some geographically adjacent groups (Table 2).

The most southern species on Henderson and Pitcairn evidently lacked a complex song and only uttered simple calls, generally varying only slightly in duration and amplitude — 1–3.5 syllable types s^{-1}, rather than the more complex series of syllables typical of the songs of most other Pacific island *Acrocephalus* species (Fig. 7; Table 2). No songs, only calls, of *A. rimitarae* were analysed. Amongst the other species examined, song syllable diversity and delivery rates varied, but overall most had less diversity than the migratory *A. orientalis* which had a higher syllable count and rate of syllable delivery (Table 2). The mean syllable diversity was highest in *A. hiwae* from Saipan; however, again reflecting its popular name 'nightingale reed-warbler' (e.g. Mayr 1945; Pratt *et al.* 1987).

The percentage of time in song was highest in *A. orientalis, A. kerearako* and *A. percernis,* but relatively low in song samples of *A. aequinoctialis, A. familiaris* and *A. rehsei.* Despite *A. familiaris* having a low song delivery rate overall, when syllable delivery was measured in relation to the time in song, it had the highest value – short, fast syllable deliveries with long intervals between them (Table 2). *Acrocephalus aequinoctialis* from Kiritimati had a distinctive and much simpler song than most *Acrocephalus* species (see Milder & Schreiber 1989), with the lowest percent time in song and low syllable diversity – the poorest of the Pacific island *Acrocephalus* songs, excluding *A. taiti* and *A. vaughani* with no song, and perhaps *A. rimitarae* with limited song (see Thibault & Cibois 2006). Although data were limited, the mean syllable delivery rate and syllable diversity were lower in *A. mendanae* from the S Marquesas than in *A. percernis* from the N Marquesas. *Acrocephalus caffer* was intermediate between the two Marquesan species. *Acrocephalus australis*, from both E Australia and the Solomons, had a relatively high syllable diversity but a relatively moderate delivery rate (Table 2).

Table 2. Song syllable diversity and delivery rates from 36-second samples of Pacific island *Acrocephalus* warbler songs. For comparison, samples from *A. orientalis* (Japan) and *A. australis* (E Australia and Honiara Island) are also included. Species are ordered by declining mean no. of song syllables over the 36-second period.

Species	Location	Sample size (n)	Mean (±SE) song time (seconds)	Mean (±SE) no. syllables	Mean (±SE) no. syllable types	Mean (±SE) no. syllables per second overall	Mean (±SE) no. syllables per second of song	Percent time in song
orientalis	Japan	2	31.3 ± 2.3	126.5 ± 3.4	18.0 ± 0.4	3.5 ± 0.3	4.0 ± 0.0	86.9
hiwae	Saipan	5	27.4 ± 1.8	124.8 ± 4.9	32.8 ± 0.6	3.5 ± 0.3	4.5 ± 0.1	76.1
percernis	N Marquesas	4	30.9 ± 0.8	119.5 ± 3.1	20.0 ± 0.4	3.3 ± 0.2	3.9 ± 0.1	85.7
kerearako	Mangaia & Mitiaro	9	31.0 ± 0.6	114.9 ± 5.9	14.9 ± 1.1	3.2 ± 0.2	3.7 ± 0.2	86.1
syrinx	Truk	5	23.8 ± 2.6	94.0 ± 7.2	15.2 ± 0.6	2.6 ± 0.5	3.8 ± 0.2	66.2
australis	Australia & Solomons	5	19.9 ± 1.9	89.2 ± 9.5	20.2 ± 3.2	2.5 ± 0.3	4.5 ± 0.1	55.4
rehsei	Nauru	3	17.3 ± 4.0	89.0 ± 11.1	19.7 ± 1.3	2.5 ± 0.6	5.0 ± 0.1	48.1
caffer	Tahiti	5	29.6 ± 1.4	82.4 ± 0.3	13.2 ± 0.3	2.3 ± 0.3	2.8 ± 0.1	82.2
atyphus	Tuamotus	2	28.1 ± 7.9	80.5 ± 9.7	18.0 ± 1.9	2.2 ± 0.9	2.7 ± 0.2	78.0
familiaris	Nihoa	3	13.5 ± 2.9	75.7 ± 11.5	12.0 ± 0.6	2.1 ± 0.5	5.3 ± 0.4	37.4
mendanae	S Marquesas	5	25.4 ± 2.3	71.8 ± 4.2	10.6 ± 0.4	2.0 ± 0.4	2.8 ± 0.1	70.5
*rimitarae**	Rimatara	2	33.3 ± 2.7	38.0 ± 2.9	1.0 ± 0.0	1.1 ± 0.4	1.1 ± 0.4	92.5
aequinoctialis	Kiritimati	2	9.0 ± 2.1	35.5 ± 5.4	3.5 ± 0.1	1.0 ± 0.2	3.9 ± 0.3	24.9
*taiti**	Henderson	2	23.3 ± 5.7	30.0 ± 0.6	3.5 ± 0.6	0.8 ± 0.1	1.4 ± 0.3	64.8
*vaughani**	Pitcairn	2	23.7 ± 8.8	28.0 ± 0.3	1.0 ± 0.0	0.8 ± 0.0	1.4 ± 0.7	65.8

* only simple calls, no song

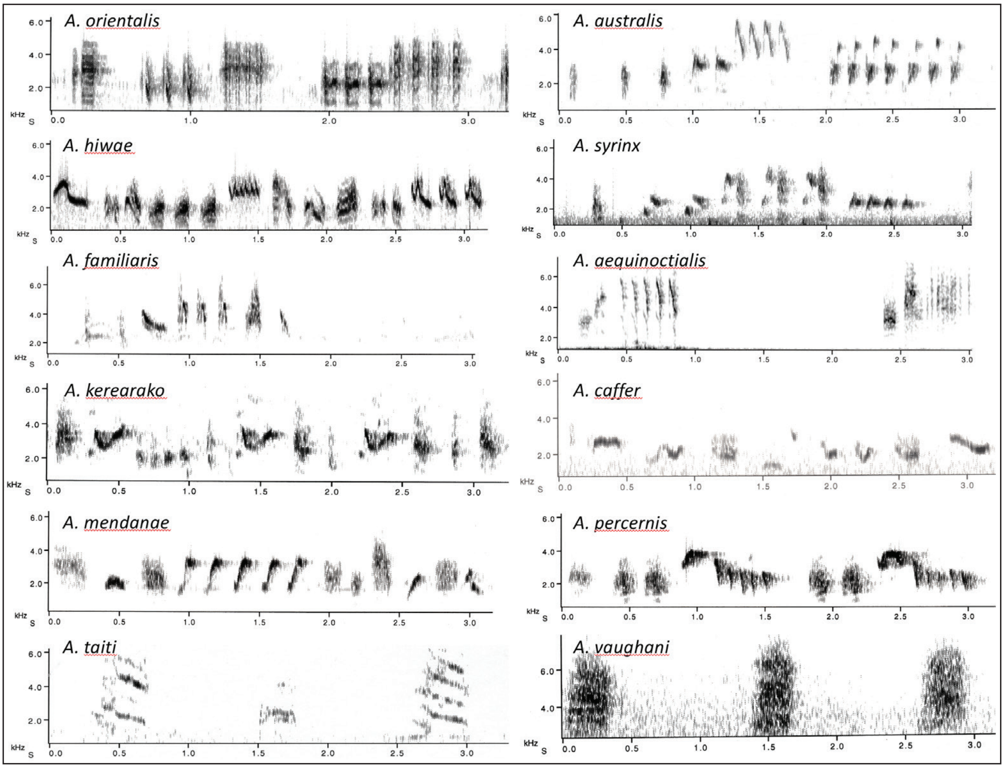

Figure 7. Sound spectrograms of ten Pacific island *Acrocephalus* warblers and, for comparison, two continental species from the W Pacific (*A. australis, A. orientalis*). Note harsher 'churr' notes in many species (e.g. *A. caffer*, *A. kerearako*, *A. mendanae*, *A. percernis*).

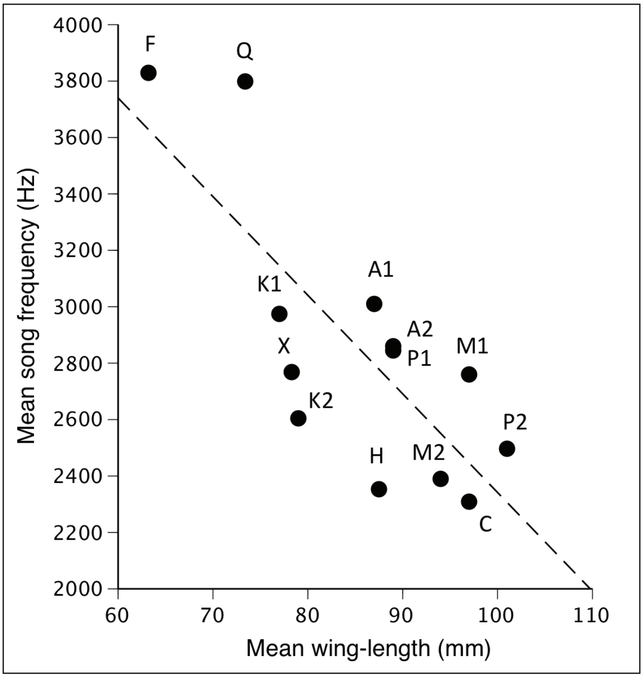

Figure 8. Mean song frequency is inversely correlated with mean wing-length in Pacific island *Acrocephalus* warblers (Pearson r = –0.608, df = 11, $p < 0.02$). Viewed downwards with decreasing mean frequency, the points plotted represent: F = *A. familiaris kingi* (Nihoa); Q = *A. aequinoctialis aequinoctialis* (Kiritimati), A1 = *A. atyphus eremus* (Anuanurunga); K1 = *A. kerearako kerearako* (Mangaia); A2 = *A. atyphus ravus* (Makatea); P1 = *A. percernis idae* (Ua Huka); X = *A. syrinx* (Chuuk); M1 = *A. mendanae consobrina* (Mohotani); K2 = *A. kerearoako kaoko* (Mitiaro); P2 = *A. percernis percernis* (Nuku Hiva); M2 = *A. mendanae dido* (Ua Pou); H = *A. hiwae* (Saipan); C = *A. caffer* (Tahiti). Samples of *A. taiti* (Henderson), *A. vaughani* (Pitcairn) and *A. rimitarae* (Rimatara) were excluded as no song was recorded.

Song frequency and body-size

While there was variation in the frequency range of different syllables in the song, overall the mean frequencies of song syllables for Pacific island populations were inversely correlated with mean body size: for example, the smallest species, *A. familiaris* of Hawaii (Nihoa) had the highest mean frequency and larger species, like *A. caffer* (Tahiti) and *A. hiwae* (Saipan), had song syllables in the lower mean frequency range (Fig. 8).

The frequency 'sound window' (mean maximum frequency – mean minimum frequency) was 4.8 kHz in the continental *A. orientalis*, but narrower in Pacific island *Acrocephalus* warblers. In songs or calls of *A. aequinoctialis, A. taiti* and *A. vaughani* the mean frequency range was 3.4–4.3 kHz. In other Pacific island species, it was lower, in descending order: 3.2 kHz (*A. familiaris*); 3.0 kHz (*A. atyphus*); 2.7 kHz (*A. australis* and *A. mendanae*); 2.3 kHz (*A. percernis*); 2.0 kHz (*A. kerearako*); 1.7 (*A. syrinx*); 1.5 (*A. hiwae*); and 1.3 (*A. caffer*).

DISCUSSION

The focus of this study was to quantify and interrelate measures of morphological variation and song patterns in Pacific island *Acrocephalus* warblers, recognising that there have already been a range of studies describing their biology, phylogeny, systematics, behaviour, and ecology (e.g. Holyoak & Thibault 1977; Kennerley & Pearson 2010; Leisler & Schulze-Hagen 2011; Leisler & Winkler 2015; Thibault & Cibois 2017). In some instances, these warblers are the sole passerines on an island (e.g. *A. aequinoctialis, A. rehsei, A. taiti, A. vaughani*), and as residents on isolated islands or archipelagos, they differ behaviourally, ecologically, and morphologically from most *Acrocephalus* warblers elsewhere in the world. Over much of their global range, *Acrocephalus* warblers are migratory and associate with wetland habitats, including reeds from which reed-warblers get their name. On Pacific islands, such habitats are often not available, so these 'reed-warblers' have adapted to drier situations, including rank vegetation, scrub and forest (Dyrcz 2006; Kennerley & Pearson 2010; Leisler & Schulz-Hagen 2011; *pers. obs.*).

Morphologically, Pacific island reed-warblers ranged in size from the relatively small *A. familiaris* (superficially resembling the migratory common reed-warbler *A. scripaceus*), to relatively large warblers of Micronesia (e.g. *A. hiwae* and *A. luscinius*) and Eastern Polynesia (*A. caffer*, *A. longirostris, A. mendanae*, *A. musae*). Craig (1992) noted that greater size is typical of island forms that may confront competitively impoverished or food-limited environments, although the small *A. familiaris* also inhabits a food-limited environment. The relative bill size was also greater in these species (*A. caffer, A. hiwae, A. luscinius, A. longirostris, A. musae*). In general, Pacific island *Acrocephalus* warblers had shorter, more rounded, wings than their continental counterparts (Fig. 5; Kennerley & Pearson 2010), suggesting different flight capability (Leisler & Schulze-Hagen 2011; Leisler & Winkler 2015). Pratt *et al*. (1987) described the flight as 'weak and fluttering' in *A. aequinoctialis* and *A. familiaris*, and 'slower and weaker than that of larger reed-warblers' in *A. atyphus*. On Tahiti, fluttering flight was a feature of *A. caffer*, while on Mitiaro Island in mid-February, an *A. kerearako* in heavy moult was virtually flightless (*pers. obs.*). Leisler & Schulze-Hagen (2011) remind us that in temperate continental *Acrocephalus* species, the longer the migration route, the longer and more pointed their wings, while in dense vegetation rounded wings are an advantage. Regarding tarsus length, Murphy & Matthews (1929) noted that *A. vaughani* is 'set well apart from other [Pacific] members of the genus by at least one structural characteristic, namely, the greater proportionate length of the tarso-metatarsus' (tarsus) — a difference evident in this study (Fig. 3).

Leisler & Schulze-Hagen (2011) suggested that overall the morphologies of island *Acrocephalus* warblers point towards terrestrial living and a more acrobatic use of the substrate (tarso-metatarsus diameter), a reduction in longer flights but greater manoeuvrability (wing traits), as well as a diminished role for aerial feeding and closer contact with various substrates during extractive foraging (rictal bristles). Leisler & Winkler (2015) later noted that the evolution of island *Acrocephalus* warblers is beyond just 'bills and masses', stressing that their evolution pertained to all functional complexes, and not only previously studied body size and bill dimensions, concluding that shape-related morphological evolution of island species is characterised by changes in the hind limb, flight, and feeding apparatus. Birds on islands converged to a morphology with strong legs, shorter rictal bristles, and rounder, more slotted and broader wings. However, body size and bill dimensions did not contribute to the separation of continental and island forms because of their high variance among islands, although bills tend to be longer on islands. They suggested that 'vegetation clutter' is the major driving force for variation in body size (Leisler & Winkler 2015). Wings of island birds hardly varied among islands; Leisler & Winkler (2015) concluding that this was not surprising due to a lack of adaptive features associated with long distance flights, and attributed a tendency towards shorter rictal bristles in island warblers to the diminished role of aerial feeding, and to closer contact with various substrates in the course of extractive foraging.

Noting a shift towards stronger legs in several insular species, they saw this as remarkable, as reed-warblers on continents have even stronger legs than other passerines of comparable size, noting that this trait correlates with feeding techniques associated with broad habitat use (Leisler & Winkler 2015).

The colour of the more northern island *Acrocephalus* species in the Marianas, Micronesia and Hawaii broadly resembled the colour of reed-warblers elsewhere, but in SE Polynesia their colouration was more varied, including more yellow and/or white in the plumage (Fig. 6). Such shifts from 'typical' reed-warbler colours suggests different selection pressures on reed-warblers that generally no longer live in reeds. In the Line Islands (Kiritimati) the plumages were shades of grey and white (*A. aequinoctialis*; Fig. 6), while on Pitcairn, Henderson and Rimatara, leucism (white feathers) occurred (*A. taiti, A. rimitarae, A. vaughani*; also in some *A. atyphus* – see Fig. 2G,I). On Tahiti, *A. caffer* had a less common melanistic morph (Kennerley & Pearson 2010; Cibois *et al.* 2012; Fig. 2E; *pers. obs.*). A dark morph also occurs in *A. stentoreus* in the Middle East, forming approximately 5% of the population there (Laird 1992; Svensson 2009; Kennerley & Pearson 2010; Shirihai & Svensson 2018). The pattern of leucism was different between *A. taiti, A. rimitarae* and *A. vaughani*, affecting primarily the anterior body plumage, secondaries, and rectrices of *A. taiti*, the primaries, secondaries, and rectrices of *A. vaughani*, and scattered parts of the plumage of *A. rimitarae* (Murphy & Mathews 1929; Holyoak 1978; Graves 1992; Thibault & Cibois 2006). In all three taxa, leucism appeared to progress with age. Graves (1992) suggested that there was no evidence that leucism was a consequence of songlessness or vice-versa.

While the complexity and delivery rate of song syllables have been studied in a range of migratory *Acrocephalus* species (e.g. Catchpole 1980, 1981a; Hasselquist *et al*. 1996) and a few island taxa (e.g. Catchpole & Komdeur 1993), song complexity in resident Pacific island reed-warblers has received less attention (but see, e.g. Milder & Shreiber 1989). The generally more complex songs of the Old World warblers, including the Acrocephalidae, may have evolved under the pressures of sexual selection or during the process of speciation (Barlein 2006).

Song contrasts are most striking when they concern close relatives, as within the genus *Acrocephalus*, and whether or not a bird migrates has been identified as an important factor influencing song learning strategies (Catchpole & Slater 2008). While here 49 individual song spectrograms were examined for various Pacific island *Acrocephalus* species, and comparisons made with *A. australis* and *A. orientalis*, only a few individuals were sampled for some species. But, given this qualification, contrasting and comparable trends did emerge from spectrographic analysis (Fig. 7; Table 2). Song syllable diversity and delivery rates varied, but overall they had lower syllable diversity than the migratory *A. orientalis* (Table 2). On Kiritimati in the Line Islands *A. aequinoctialis* had a relatively simple song (see Milder & Schreiber 1989), on Nihoa Island *A. familiaris* gave rapid bursts of song at intervals, and on Saipan *A. hiwae* had the most complex song — Mayr (1945) described the 'nightingale' reed-warbler of the Marianas as a 'beautiful singer', implying such a varied and musical repertoire. The three southernmost species had either no song (*A. taiti* and *A. vaughani*), or limited song (*A. rimitarae*), mostly uttering simpler, harsh call notes (Fig. 7; Table 2; Thibault & Cibois 2006).

How do Pacific island *Acrocephalus* songs compare with long-distant migrant *Acrocephalus* species other than *A. orientalis* (Table 2)? Two well-researched European species that winter in Africa, known to have elaborate song repertoires, are the marsh warbler (*A. palustris*) and the sedge warbler (*A. schoenobaenus*; Lemaire 1974; Catchpole 1980, 1981a; Simms 1985). Males of both species have greater song syllable diversity and delivery rates than the resident Pacific island *Acrocephalus* warblers (Table 2). For example, in Poland the mean (± SE) song syllable delivery rate of 23 male *A. palustris* was 5.00 (± 0.17) syllables s^{-1} (range 3.11–6.30 syllables s^{-1}; data from Bell *et al*. 2004), while over 15 min of continuous song a male *A. palustris* in Worcestershire, UK, sustained a generally linear output of 66.2 *new* syllable elements min^{-1} (Bell *et al*. 2004). This comparison is at the higher level of syllable diversity for *Acrocephalus* warblers, Simms (1985) noting (p. 220) that a top singer among marsh warblers 'has no real peer among the *Acrocephalus* warblers'. The migratory *A. shoenobaenus* also has a complex repertoire (Catchpole 1980, 1981a; Simms 1985). In Poland, males had a mean (± SE) overall syllable delivery rate of 3.61 (± 0.24) syllables s^{-1} overall (range 2.02–4.69 syllables s^{-1}), and 4.24 (± 0.22) syllables s^{-1} (range 2.40–5.14 syllables s^{-1}) if between-song intervals were excluded (Bell *et al*. 1997). In this comparison, song complexity and delivery rates were generally higher than in Pacific island *Acrocephalus* species, except for *A. australis, A. familiaris, A. hiwae* and *A. rehsei* which had higher mean syllable delivery rates for time in song, but not higher mean syllable delivery rates overall (Table 2).

Numerous studies indicate that large repertoires are driven by sexual-selection, some field studies showing correlations between repertoire size and breeding success (e.g. Searcy 1984; Catchpole *et al*. 1986; Baker *et al*. 1987; Searcy & Yasukawa 1990;

Searcy 1992; Mountjoy & Lemon 1996; Bell *et al*. 1997, 2004; Buchanan & Catchpole 1997; Lampe & Espmark 2003), but that was not always the case (e.g. Beecher *et al*. 2000), or has been questioned (e.g. Darolová *et al*. 2012). Amongst *Acrocephalus* species, the migratory *A. palustris* with its particularly complex and varied repertoire, appropriates syllables from other species into its repertoire, both from its European breeding grounds and from its African winter quarters (Dowsett-Lemaire 1979). It is the latest trans-Saharan migrant *Acrocephalus* species to arrive on its European breeding grounds (Catchpole 1980, 1981a), and there is a high premium placed on the male to quickly attract a mate, which might have driven sexual selection for development of its particularly complex song. Song functionally therefore evolved primarily for mate attraction (inter-sexual selection), more than for territorial advertisement (intra-sexual selection), more elaborate songs resulting in higher breeding success, involving polygyny in some species, and invoking the idea of male song being an 'acoustic peacock's tail' (Catchpole 1980, 1981a,b; Hasselquist *et al*. 1996; Bell *et al*. 1997, 2004). Other migratory *Acrocephalus* warblers, including *A. orientalis* and *A. schoenobaenus*, also face pressures of time to attract a mate and initiate breeding. In a review of the relationship between latitude, migration and the evolution of bird song complexity, Najar & Benedict (2018) concluded that there was no strong evidence that song complexity increases with latitude and/or migration in all birds, although it did in some species, as evidenced by *A. palustris* and *A. schoenobaenus*.

For resident island *Acrocephalus* species, the situation is very different, as such time constraints do not apply in tropical and subtropical regions where extended breeding throughout much of the year occurs (Kennerley & Pearson 2010). In an island study of *A. sechellensis* on the Seychelles, Catchpole & Komdeur (1993) found that this resident reed-warbler is a cooperative breeder in a saturated, island environment, with a song structure differing significantly from migratory European marshland *Acrocephalus* species. Song was transmitted within a more restricted frequency range which propagated more effectively through tropical forest. Males had a relatively short, simple song, used for territorial defence throughout the year, but they also had a complex repertoire of song types, with song activity peaks before and declines during breeding, suggesting an inter-sexual function — mate-attraction. Catchpole & Komdeur (1993) concluded that the demands of tropical island life are reflected in both the structure and function of male song in *A. sechellensis*. Leisler & Schulze-Hagen (2011) suggested that simpler songs in Pacific island *Acrocephalus* populations, comprising shorter signals, might have been selected for to facilitate individual recognition of familiar resident neighbours. They noted that such songs are more strongly coded for estimating distance and for individual recognition, with a much-reduced function of attracting a partner through greater song complexity.

On Kiritimati, Milder & Shreiber (1989) reported that in the absence of other Pacific land birds and natural predators, vocal signals of *A. aequinoctialis* were simple compared to most *Acrocephalus* species, and suggested that this was the result of a lack of interspecific interactions, a monogamous life-style, large permanent territories, open dry habitat and limited interaction among neighbouring individuals. On Saipan, however, *A. hiwae* is extremely territorial, singing from exposed treetops, interior thickets, or stems of elephant grass (*Pennisetum purpureum*), male defensive behaviour including song and pursuit (Craig 1992; Rounds & Radley 2018). Contrasting with mainland *A. orientalis* and *A. arundinaceus*, *A. hiwae* had polygyny largely or entirely absent, much larger territories, upland rather than marshes as the principal breeding habitat and body size, particularly bill size, greatly increased. A shift to upland habitats may account for these differences in social behaviour and territory size. Mosher & Fancy (2002) found nests of *A. hiwae* within three habitat types: upland introduced tangan-tangan (*Leucaena leucocephala*) forest, a native mangrove (*Bruguiera gymnorrhiza*) wetland, and a native reed (*Phragmites karka*) wetland. Nesting substrates included five native and two introduced tree species and one native reed species. Kennerley & Pearson (2010) noted that *A. hiwae* showed a distinct preference for tangan-tangan woodland, and mosaics of tangan-tangan and sword grass (*Miscanthus floridulus*) or elephant grass, but otherwise chose wetlands.

Holyoak (1978) reported that on Henderson *A. taiti* gave a variety of chirping calls but no song. However, Graves (1992) suggested that the lack of song may be a matter of interpretation, noting that most of its vocalisations were high pitched (4–8 kHz) single notes of short duration (<0.13 set), but there were also series of thin, longer notes (l–5 set) given by adult territorial birds, albeit in an unknown context, that resembled song (his Fig. 6). He observed that these vocalisations could be clearly heard at 25 m above the white noise of wind and surf (both predominately 0–3 kHz) along beaches, and probably functioned in inter-territorial communication, given the small territory size of *A. taiti*.

There have been conflicting reports about whether *A. rimitarae* has a song. It was reported as emitting a variety of chirping calls, but no song by Barlein (2006). Thibault & Cibois (2006), however, reported that males sang regularly in the early morning, the evening, or during bright moonlit nights, but rarely during midday, even during the breeding season, quoting Quayle (ms) who wrote: 'Here is a warbler singing with all the variation and harmony of Marquesan or Tahitian varieties'. Kennerly & Pearson (2010) noted that *A. rimitarae*, unlike its counterparts on Pitcairn and Henderson, has a recognisable song described as a succession of low and short whistling notes, less powerful and elaborate than songs of *A. caffer* or *A. atyphus*, and was typically of shorter duration. Dyrcz & Sharpe (2018) report its description as a loud 'chack-chack', with a variety of chirping calls, and noted that while the latter are recognised as a song by some authors, 'true song' was not recorded.

Tameness is another feature of many endemic island birds, and is evident in some Pacific island reed-warblers. For example, on the extinct Laysan millerbird, *A. familiaris familiaris*, Schauinsland (1899), quoted by Bailey (1956), remarked that 'one of these little singers once chose the edge of my open book for its perch, and gave forth its best song'. Elsewhere, *A. aequinoctialis* and *A. vaughani* were described as 'bold and inquisitive' and *A. atyphus* and *A. mendanae [percernis]* as 'easily "squeaked up" ...', while, in contrast, *A. luscinia* [*hiwae*] and *A. syrinx* were described as skulkers, the Nihoa millerbird *A. familiaris kingi* as 'A secretive denizen' and *A. caffer* as 'usually shy and difficult to observe' (Pratt *et al*. 1987), although I found the song posts of *A. caffer* were typically high up (usually in bamboo) rather than in a skulking position lower down. On Mitiaro Island *A. kerearako* was relatively approachable (*pers. obs.*).

Body size is known to be negatively correlated with song frequency measures in birds (e.g. Wallschläger 1980; Badyaev & Leaf 1997; Mahler & Gil 2009; Tietze *et al*. 2015). The low frequency range of a species may be limited by body size (Ten Cate 2004) — e.g. in the small leaf warblers (Phylloscopidae) body size was a constraint on song frequencies, independent of phylogeny (Tietze *et al*. 2015). Frequency (or pitch) not only indicates body size across different species, but also within a species — e.g. the larger the male purple-crowned fairy-wren (*Malurus coronatus coronatus*) the lower the pitch of its song (Hall *et al*. 2013). In Pacific island reed-warblers, the song of the 13 cm long *A. familiaris* from Nihoa was described as 'metallic and bubbling' (Shallenberger 1981) and the 15 cm *A. aequinoctialis* had songs of limited syllables usually beginning with a distinctive 'cha chē', with the 'chē' high-pitched (Milder & Shreiber 1989). In contrast, the song of the 17–19 cm *A. caffer* on Tahiti was of lower frequency, with mellow notes (reminiscent of some *Turdus* thrushes), while the song of *A. hiwae* was described as a slow, loud, varied but simple melody, range 1–5 kHz, not dissimilar to the song of a Eurasian blackbird (*Turdus merula*), but sounding harsher and less melodic and containing short and fluty warbling sections (Kennerly & Pearson 2010). Over a range of measurements of frequency and size, there was therefore an inverse relationship (see Fig. 8).

However, size alone does not influence song frequency, the environment through which the sound is transmitted also plays a part (Morton 1975; Catchpole & Slater 2008). When comparing *A. sechellensis* with the migrant *A. scripaceus*, Catchpole & Komdeur (1993) found that the frequency range was much reduced in the island species, and approximated the 'frequency window' for optimal transmission in tropical forest (Morton 1975). Many Pacific island *Acrocephalus* species also inhabit forest and scrub habitats, rather than more open wetland habitats (Kennerley & Pearson 2010), and their frequency ranges (Fig. 7) are also relatively narrow and generally reflect the <4 kHz sound window that Morton (1975) described for low forest. The higher frequencies in *A. aequinoctialis* and *A. familiaris* songs may also reflect their more open habitats (Morton 1975), while the harsh, high frequency calls of *A. taiti, A. rimitarae* and *A. vaughani* may facilitate sound transmission against a background of wind and ocean noise in SE Polynesia, as Graves (1992) suggested.

Using sequences of mitochondrial DNA (cytochrome *b*, ND2, and ATP8 genes), Cibois *et al*. (2011a) concluded that Pacific island *Acrocephalus* warblers did not form a monophyletic group, since the extinct *A. luscinius luscinius* from Guam fell outside the main Pacific radiation. The remaining Pacific taxa were divided into two clades: one clade including all other reed-warblers from Mariana/Micronesia and Australia, and two Polynesian taxa from the Line Islands (*A. aequinoctialis*) and S Marquesas (*A. mendanae*); the other clade including all remaining Polynesian taxa. Adding to earlier studies of Pacific island *Acrocephalus* species (e.g. Holyoak & Thibault 1977; Thibault & Cibois 2006; Cibois *et al*. 2007, 2008), they revealed a more complex pattern of colonisation of the Pacific islands by *Acrocephalus* warblers than stepping-stone colonisation previously invoked, notably that the Mariana, Marquesas and Society taxa are polyphyletic and that the Australian reed-warbler (*A. australis*) represents 'reverse colonisation' from island to continent. The present study found some similarities between *A. australis* and Pacific island *Acrocephalus* species (Fig. 6; Table 2), but the phylogenetic difference between the northern (*A. percernis*) and southern Marquesas (*A. mendanae*) was not evident from their broadly similar morphometrics and colouration (Figs. 2–4), but *A. mendanae* had a less elaborate song (Table 2). Although data were limited, the mean syllable delivery rate and syllable diversity were lower in *A. mendanae* than in *A. percernis*, but sampling from a greater number of islands in the Marquesas Archipelago could possibly show different dialects rather than a clear difference between two species. Similar morphological characters may reflect their broadly similar environments as the two species are in close geographical proximity (Fig. 1). Thibault & Cibois (2017) suggested that for these two species this similarity reflected a higher influence of ecology than of phylogeny and that within the Marquesas Archipelago birds on dry and smaller islands tend to be smaller than those on larger islands, irrespective of their phylogenetic origin. The *Acrocephalus* species across Micronesia, while manifesting some marked differences (e.g. in body and bill size – see Mayr 1945), are collectively more typical *Acrocephalus* species in terms of their general colouration and type of song.

In conclusion, insularity has resulted in extensive speciation of *Acrocephalus* warblers across the Pacific. Since Darwin's studies of finches on the Galapagos Islands (Darwin 1859; Lack 1947; Grant *et al*. 1985), studies of avian evolution have often focussed on islands and archipelagos, including elsewhere in the Pacific such as Hawaii and New Zealand (e.g. Fleming 1962, 1975; Bock 1973; Lerner *et al*. 2011). Islands are simplified, isolated ecosystems, providing an ideal set-up to study evolution, including bird song (Morinay *et al*. 2013). The Pacific island reed-warblers are more widely distributed than on single archipelagos, and there are further opportunities for behavioural, ecological and evolutionary research on them across a range of spatial scales, adding to studies already undertaken (e.g. Cibois *et al*. 2007, 2008, 2011a; Leisler & Schulze-Hagen 2011; Leisler & Winkler 2015), and addressing how the birds might have adapted to island environments far removed from the wetland habitats occupied by their continental counterparts.

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Appendix. Ratios of bill (to skull) length/wing-length in the world's *Acrocephalus* species. Species are in increasing order of ratio values. Ratios are highest in most Pacific island species (shown in bold), although they are lower in *A. taiti, A. vaughani* and *A. aequinoctialis*. Species names follow Dyrcz *et al*. (2016), data are sourced from this study and from Kennerley & Pearson (2010), Cibois *et al*. (2011b) and Saitoh *et al*. (2012).

Species	Bill/wing ratio	Status
paludicola	0.215	Palaearctic migrant
schoenobaenus	0.220	Palaearctic migrant
taiti	**0.226**	**Resident (Pacific island)**
palustris	0.231	Palaearctic migrant
arundinaceus	0.237	Palaearctic migrant
vaughani	**0.244**	**Resident (Pacific island)**
sorghophilus	0.248	Asian migrant
scirpaceus	0.256	Palaearctic migrant
bistrigiceps	0.256	Asian migrant
agricola	0.256	Palaearctic migrant
aequinoctialis	**0.260**	**Resident (Pacific island)**
griseldis	0.261	Palaearctic migrant
melanopogon	0.261	Partial migrant
gracilirostris	0.264	Resident (Africa)
sechellensis	0.265	Resident (Seychelles Is.)
orientalis	0.270	Asian migrant
newtoni	0.272	Resident (Madagascar Is.)
australis	0.273	Resident (Australasia)
dumetorum	0.274	Palaearctic migrant
concinens	0.274	Asian migrant
tangorum	0.280	Asian migrant
rimitarae	**0.282**	**Resident (Pacific island)**
rodericanus	0.284	Resident (Rodrigues Is.)
rufescens	0.294	Resident (Africa)
kerearako	**0.296**	**Resident (Pacific island)**
familiaris	**0.300**	**Resident (Pacific island)**
stentoreus	0.302	Migrant
brevipennis	0.305	Resident (Cape Verde Is.)
percernis	**0.307**	**Resident (Pacific island)**
rehsei	**0.313**	**Resident (Pacific island)**
orinus	0.314	Palaearctic migrant
atyphus	**0.315**	**Resident (Pacific island)**
***yamashinae*†**	**0.317**	**Resident (Pacific island)**
mendanae	**0.323**	**Resident (Pacific island)**
***nijoi*†**	**0.324**	**Resident (Pacific island)**
syrinx	**0.329**	**Resident (Pacific island)**
caffer	**0.360**	**Resident (Pacific island)**
***longirostris*†**	**0.364**	**Resident (Pacific island)**
***musae*†**	**0.371**	**Resident (Pacific island)**
***astrolabii*†**	**0.379**	**Resident (Pacific island)**
hiwae	**0.400**	**Resident (Pacific island)**
***luscinius*†**	**0.432**	**Resident (Pacific island)**

† extinct

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Estimates of local occupancy for native land birds from the New Zealand bird atlases

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Abstract: We describe the creation of a standardised set of data from the two national atlases of bird distribution compiled by the Ornithological Society of New Zealand. The data provide estimates of local occupancy probability for each of 64 taxa of native land birds, in each of 2,155 grid squares covering the North, South, and Stewart islands, in two measurement periods (September 1969 – December 1979, and December 1999 – November 2004). Because these local occupancy estimates were derived on an identical basis for each bird taxon and each time period, they enable unbiased comparisons between time periods and among species. Links to permanent data repositories of the original and standardised data are provided.

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Key words: occupancy models, standardised bird atlas data

INTRODUCTION

Research on and management of native birds in New Zealand has amassed considerable knowledge of bird species distributions and conservation ecology. However, the only data sets that have recorded the spatial distributions of all bird species across the whole nation are two national atlases of bird distribution compiled by the Ornithological Society of New Zealand (OSNZ; Bull *et al*. 1985; Robertson *et al*. 2007). These data potentially provide the only spatially explicit, nationally comprehensive, all-species, multi-decade (25-year) view of the status of and trends in New Zealand's avifauna.

To date, the two OSNZ atlases have not been particularly widely used to inform the strategic management of New Zealand birds. In part, this may be because comparisons between the two measurement periods is complicated by two non-standard aspects of the data: (1) the different spatial systems and locations of the sampling units in the different atlases (imperial vs metric grid squares), and (2) differences in the levels of effort applied across the nation between and within each of the two surveys. To overcome these obstacles and enable robust comparisons between the distributions and occupancies of the native birds in each atlas, we created a standardised set of data. In this paper we, (1) describe the process we used to create the standardised dataset, and (2) provide links to a permanent data repository where it can be accessed for use.

METHODS

Raw data

Our raw data were collated in two national atlases of bird distribution compiled by the OSNZ (Bull *et al*. 1985; Robertson *et al*. 2007). Field surveys for the first atlas were conducted from September 1969 to December 1979 (1969–1979) and for the second atlas from December 1999 to November 2004 (1999–2004). We refer to these two atlases as Atlas 1 and Atlas 2, and to the two collection time periods as the first and second 'measurement periods', respectively.

Observers for Atlas 1 (OSNZ members in

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association with the Ecology Division of the then Department of Scientific and Industrial Research (DSIR) and the Wildlife Service of the Department of Internal Affairs) recorded observations in 96% of the 3,675 10,000 yard grid squares of the then NZMS1 national grid in the imperial coordinate system (Bull *et al*. 1985; Scofield *et al*. 2012). Surveys for Atlas 2 (Robertson *et al*. 2007) commenced 20 years after Atlas 1 was published. Observations were recorded in 10,000 m (10 × 10 km) squares on the national grid defined in the metric New Zealand Map Grid (NZMG) coordinate system. Record sheets were submitted from 96.4% of the 3,192 10 × 10 km grid squares in New Zealand (Robertson *et al*. 2007).

Observers could return either complete or incomplete record sheets (referred to as 'cards' in the first atlas) for a square. Complete sheets (or 'full lists') were those considered to be a complete list for the grid by the observer, indicating their opinion that they had invested sufficient effort to cover the whole square and had recorded all taxa that were present within it. In complete sheets, absences (non-detections of a bird species) are expected to reflect a true failure to detect a bird in a given grid, while incomplete sheets (or 'part lists') represent partial geographic or fauna coverage of a square by the observer, so that any absences are unreliable. In Atlas 1, observers started a new sheet for a square each calendar month, recording only start and end dates of observations on each sheet, so that effort can only be estimated as the number of days in the interval. In Atlas 2, observers were required to start a new sheet every quarter, and they directly estimated the number of full days spent recording observations, as well as the start and end dates of observations. The numbers of complete sheets returned for the different grid squares across the country varied greatly within each measurement period and between measurement periods.

On completing the publication of Atlas 2 in 2007, the OSNZ recreated electronic files of data collected for Atlas 1, which had been unwittingly destroyed in the early 1980s. They made the data from both atlases available for research on request to the OSNZ on a cost-recovery basis. The data were supplied to us as Microsoft Access databases.

Deriving estimates of occupancy from atlas data

We used a two-stage modelling process to overcome the challenges presented, first by the different levels of observer effort across grid squares within each measurement period, and second by differences in the spatial locations of the grid squares between the two measurement periods.

In stage 1 we used a Bayesian modelling process to fit two occupancy models for each land-bird taxon (one for each measurement period, 1969–1979 and 1999–2004), which provided estimates of the bird's probability of occupancy in each grid square that was sampled. In stage 2, the fitted estimates were then interpolated to a common 10 × 10 km grid.

Some areas – including the Chatham Islands and many offshore islands – were not covered in one or both of the atlases. These areas were not included in our common grid, and no estimates of local occupancy were derived for them. Appendix 1 provides a glossary of technical terms used in the methods that follow.

Stage 1: Fitting occupancy models

In stage 1 we adopted an occupancy modelling approach to address differences in effort. Occupancy models recognise that the detection of species by observers is imperfect: often the probability of detecting a species that is actually present is much less than 1.0 (MacKenzie *et al*. 2002; Bailey *et al*. 2014). Non-detection of a species at a site does not mean that the species is truly absent, because it may be a false absence. Furthermore, detectability can vary not only among species but also across observers, and also as a result of other factors such as season. The probability of occupancy (the probability that a species was actually present at a site) is therefore explicitly estimated in models that combine probabilities of detection and occupancy allowing for unbiased estimates of occupancy.

We fitted two such models for each individual bird taxon: one for each of the two atlas periods. In each model we considered only observations from complete sheets. This means that absences should reflect a true failure to detect a bird, which is a prerequisite for estimating detection probabilities in occupancy models. We also rely on complete sheets as a consistent indicator of effort and ignore other effort indicators (days between start and finish of measurement, which was recorded inconsistently between atlases, and number of full days of survey undertaken, recorded only in Atlas 2). We allowed probability of detection in each model to vary seasonally by including season (spring, summer, autumn, or winter) as a covariate.

Each model was fitted using Bayesian inference with three Markov chain Monte Carlo (MCMC) chains. Once the chains had converged, we drew 1,000 fitted estimates of occupancy probability from each chain for each grid square with data (i.e. squares with at least one complete sheet returned). These fitted estimates are of the probability that a bird was actually present in each grid square (i.e. between 0.0 and 1.0).

Specifically, for each taxon in each measurement period (Atlas 1 and Atlas 2) we modelled the i^{th} occupancy observation (Y_{ijkm}) recorded in each of j grid squares, in k seasons, on m islands, as a finite mixture model comprising a probability process that described the occupancy state and another describing the observation process. The Y_{ijkm} were 1 for positive observations (sight or by sound) of a species and 0 otherwise.

We modelled the Y_{ijkm} as:

$Y_{ijkm} \sim \text{Bernoulli}(p_k \times z_{jm})$ (1)

where p_k is the probability of detecting the taxon in season k and z_{jm} is a random variable describing the occupancy for the j^{th} square on island m (1 = occupied, 0 = not occupied). We accounted for seasonal differences in observability by including a separate fixed effect intercept for each of the k seasons (γ_{1k}), such that:

$\text{logit}(p_k) = \gamma_0 + \gamma_{1k}$ (2)

The occupancy state process was modelled as:

$z_{jm} \sim \text{Bernoulli}(q_{jm})$ (3)

where q_{jm} is the probability of occupancy of the j^{th} square on island m. We included a separate intercept for each island (β_{1m}) to allow the probability of occupancy to vary at this scale, and captured the variation in occupancy between grid squares using a random intercept for each square (α_{jm}), so that:

$\text{logit}(q_{jm}) = \beta_0 + \beta_{1m} + \alpha_{jm}$ (4)

Island was coded at two levels: 'North Island' and 'South Island'. While this grouping was at the level of the main islands of New Zealand, each classification also included any nearby offshore islands. Stewart Island/Rakiura was included with the South Island.

We assume diffuse priors throughout. For the β and γ terms we assume ~N(0, 10^3). The priors on the α_{jm} were assumed ~N(0, σ_m), with the island specific standard deviation σ_m assumed to be ~U(0, 100).

We fitted separate models for each taxon in each of the two measurement periods. For taxa that occur exclusively in only one island (whitehead (*Mohoua albicilla*), North Island kōkako (*Callaeas wilsoni*), New Zealand dabchick (*Poliocephalus rufopectus*), and brown teal (*Anas chlorotis*) in the North Island, and kea (*Nestor notabilis*), brown creeper (*Mohoua novaeseelandiae*), mohua (*Mohoua ochrocephala*), rock wren (*Xenicus gilviventris*), black stilt (*Himantopus novaezelandiae*), Australasian crested grebe (*Podiceps cristatus australis*), and Stewart Island shag (*Leucocarbo chalconotus*) in the South Island), we modified the above model such that only squares from the one island were considered. We excluded the separate island intercept, such that the random intercept to capture variation in occupancy between grid squares became α_j, and Eq 4 became:

$\text{logit}(q_j) = \beta_0 + \alpha_{1j}$ (5)

with the prior on the estimated standard deviation of the grid square-level random effects σ_{Grid} assumed to be ~U(0, 100).

For all other taxa, a single national model was fitted. Hence a single national model was fitted for the different species, subspecies and/or recognised forms of kiwi (*Apteryx* species, excluding little spotted kiwi *A. owenii*), falcon (*Falco novaeseelandiae*), weka (*Gallirallus australis australis*), rifleman (*Acanthisitta chloris*), blue duck/whio (*Hymenolaimus malacorhynchos*), tomtit (*Petroica macrocephala*), fantail (*Rhipidura fuliginosa fuliginosa*), robin (*Petroica longipes* and *P. australis*), fernbird (*Bowdleria punctata*), and New Zealand dotterel (*Charadrius obscurus*) that are recognised within and between islands.

The models were fitted using the Hamiltonian MCMC sampler Stan, accessed through the R (R Development Core Team 2018) package rstan (Stan 2.0; Stan Development Team 2015, 2016). Convergence was deemed to have been obtained when the Gelman-Rubin statistic R-hat was less than 1.05 for all parameter estimates (Gelman *et al*. 2004). All inference was based on 1,000 observations of the parameter posterior distributions for each of three MCMC chains.

Stage 2: Interpolating estimates to a common grid

In stage 2 we addressed differences in the spatial location of observations.

The geospatial grid squares used for survey in the two national bird atlases differed. Square sides were 10,000 yards in Atlas 1 and 10,000 metres (i.e. 10 × 10 km) in Atlas 2, and different geospatial projections were used. Occupancy estimates derived from stage 1 were assigned the New Zealand Map Grid (NZMG) projection geographic coordinates of the centre of the relevant grid square and measurement period. We assumed that the areal extents of the grid squares (about 83.6 km^2 in 1969–1979 vs 100 km^2 in 1999–2004) were not materially different enough to affect either detection or occupancy probabilities, and therefore we did not apply any adjustments for square size.

To enable comparison of occupancy estimates between the two measurement periods at the same places, we created a common grid of 10 × 10 km squares in the NZMG projection, with centres marginally offset (100 metres north and east) from the centres of the grid used for the surveys for Atlas 2. To avoid prediction beyond the geographic range of our data, the common grid excluded any squares that were not sampled with at least one full sheet in the second measurement period, so that it included only 2,632 of the 3,111 10 × 10 km squares potentially surveyed.

We used simple kriging to produce smoothed surfaces of occupancy (q_{jm} and q_j described in Eqs 4 and 5 respectively) for each bird taxon across all grid squares used in each measurement period, and then sampled these smoothed surfaces at the centres of the squares of the common grid. This process ensured that estimates from both Atlases were smoothed and resampled using an identical method, which can be replicated using different spatial grids or coordinate systems as may be necessary or more convenient in the future. We used functions in the R libraries gstat (Pebesma & Graeler 2015) were used for geostatistical analysis and libraries sp (Pebesma *et al*. 2015) and raster (Hijmans & van Etten 2015) for spatial data manipulation.

Kriging is based on the spatial variance of a variable, modelled using a variogram representing semi-variances with distance across multiple pairs of points (Cressie 1993). Semi-variances were modelled with simple models describing how variance increases with distance from the centroids of the original squares. Different variogram models can be used, but we achieved best fits using Stein's parameterisation of the Matern model (Stein 1999) for most taxa. These models each had four parameters (nugget, sill, range and kappa, defined in accordance with Cressie 1993, pp. 59, 67–68, 130–131) which were derived for each bird taxon across the points on each main island in each measurement period. When kriging our estimates of occupancy values to the common grid, we estimated 1,000 conditional simulations drawn from the normal distribution of parameters in the applicable variogram model (Bivand *et al*. 2013), and retained the median value from simulations (Dungan 1999) at each common square centre as our estimate of occupancy for the square.

Finally, so as not to compare probabilities of occupancy outside the range of the original data, we also excluded all points on the common grid that represent squares not sampled by complete sheets in both atlases. In the case of Atlas 1 squares, 'not sampled' meant that less than 50% of the land area was overlain by a square that was sampled. We also excluded squares overlying more than 75% water (i.e. some coastal grids overlying areas of sea and large lakes). These exclusions mean that our standardised data do not include all of the areas sampled in the atlases, but only the areas for which we can make robust comparisons between measurement periods. In total, 2,155 10 × 10 km grid squares fitted these criteria.

Bird taxa included and excluded

We fitted occupancy models for as many of New Zealand's native land bird species as possible (Table 1).

We did not fit occupancy models for seabirds because coverage of the seas around New Zealand by the atlases was limited. Specifically, we omitted penguins (Sphenisciformes), albatrosses, fulmars, petrels, prions and shearwaters, storm petrels, and diving petrels (Procellariformes), and tropicbirds (Phaethontiformes). We also omitted pelicans (Pelacidae), gannets and boobies (Sulidae), darters (Anhingidae), and frigate birds (Fregatidae), but included the cormorants and shags (Phalacrocoradicae) because a number of species occur inland.

Some of New Zealand's extant native land bird species were recorded too infrequently in the atlases for occupancy to be estimated successfully. We were obliged to omit the following extant species or subspecies from our study: little-spotted kiwi (*Apteryx owenii*, in the order Apterygiformes); kākāpō (*Strigops habroptilus*, in the family Strigopidae); stitchbird (*Notiomystis cincta*, in the endemic family Notiomystidae; Driskell *et al*. 2007); and North Island saddleback and South Island saddleback (*Philesturnus carunculatus rufusater* and *P. c. carunculatus,* both in the endemic family Callaeidae). We also excluded two species of New Zealand wrens (Ericson *et al*. 2002) that inhabited forest (North and South Island bush wrens *Xenicus longipes stokesii* and *X. longipes longipes*, in the family Acanthisittidae), which were extant and recorded in Atlas 1 (Bull *et al*. 1985), but are now considered to be globally extinct (Robertson *et al*. 2013). We excluded South Island kōkako (*Callaeas cinereus*), of which there has been only one accepted sighting since 1967 (in 2007; Miskelly *et al*. 2013). All the above taxa were recorded in fewer than 10 mainland squares in one or both atlases, and all are endemic to New Zealand at the order or family level.

Observations were too few for us to fit models for the cryptic freshwater wetland species marsh crake (*Porzana pusilla affinis*), spotless crake (*Porzana tabuensis tabuensis*), and banded rail (*Gallirallus philippensis assimilis*), and for brown teal (*Anas chlorotis*) in the South Island. We also omitted the grey duck (*Anas superciliosa*), which hybridises widely with exotic mallard and cannot reliably be distinguished from it in field observations.

We had to combine records of three species of parakeet (yellow-crowned (*Cyanoramphus auriceps*), red-crowned (*C. novaezelandiae*), and orange-fronted (*C. malherbi*) into a single taxon, and all forms of weka (*Gallirallus australis*) into a single taxon, because a substantial proportion of atlas records were of unidentified species. Different 'kinds' of South Island kiwi (Innes *et al*. 2015) were not distinguished in Atlas 1 (Bull *et al*. 1985), so we treat all South Island kiwi (other than little spotted kiwi, *Apteryx owenii*, which was excluded) as a single taxon, which combines all subspecies of tokoeka (*A. australis*; i.e. Haast, Fiordland, and Rakiura tokoeka), rowi (*A. rowi*), and great spotted kiwi (*A. haastii*).

Table 1. The 64 native taxa included in our models and analyses. In the 'Islands' column, NI/SI means that different species or subspecies are recognised on the North and South Islands; NI means occurs only in the North Island; SI means occurs only on the South Island (including Stewart Island/Rakiura); and Both means the taxon occurs on both islands. Asterisks indicate that a single combined national model was fitted for all species or subspecies because of difficulty in distinguishing them from records in the atlases (e.g. all weka, and brown, tokoeka and great spotted kiwi were combined, all falcon 'forms', all robin species). Nomenclature follows Gill (2010). Within each habitat group (subheadings), bird taxa are arranged in order of level of endemism, and then in alphabetical order of order, family and Latin name. (Native-Rec means naturalised since 1840).

Common name	Latin name	Family	Order	Endemism	Islands
Forest birds					
Kiwi species*	*Apteryx* species	Apterygidae	Apterygiformes	Order	NI/SI
Rifleman*	*Acanthisitta chloris chloris* (SI) or *A. c. granti* (NI)	Acanthisittidae	Passeriformes	Family	NI/SI
North Island kōkako	*Callaeas wilsoni*	Callaeidae	Passeriformes	Family	NI
Kākā*	*Nestor meridionalis*	Nestoridae	Psittaciformes	Family	NI/SI
Kea	*Nestor notabilis*	Nestoridae	Psittaciformes	Family	SI
Whitehead	*Mohoua albicilla*	Pachycephalidae	Passeriformes	Family	NI
Brown creeper	*Mohoua novaeseelandiae*	Pachycephalidae	Passeriformes	Family	SI
Mōhua/yellowhead	*Mohoua ochrocephala*	Pachycephalidae	Passeriformes	Family	SI
Blue duck/whio	*Hymenolaimus malacorhynchos*	Anatidae	Anseriformes	Subfamily	NI/SI
Kererū	*Hemiphaga novaeseelandiae*	Columbidae	Columbiformes	Genus	Both
Bellbird	*Anthornis melanura melanura*	Meliphagidae	Passeriformes	Genus	Both
Tūī	*Prosthemadera novaeseelandiae novaeseelandiae*	Meliphagidae	Passeriformes	Genus	Both
Grey warbler	*Gerygone igata*	Acanthizidae	Passeriformes	Species	Both
Long-tailed cuckoo	*Eudynamys taitensis*	Cuculidae	Cuculiformes	Species	Both
New Zealand falcon*	*Falco novaeseelandiae*	Falconidae	Falconiformes	Species	Both
New Zealand robin*	*Petroica longipes* (NI) or *P. australis* (SI)	Petroicidae	Passeriformes	Species	NI/SI
New Zealand tomtit*	*Petroica macrocephala*	Petroicidae	Passeriformes	Species	NI/SI
Parakeet/kākāriki species*	*Cyanoramphus* spp.	Psittacidae	Psittaciformes	Species	Both

Table 1. cont.

Common name	Latin name	Family	Order	Endemism	Islands
Weka species*	*Gallirallus australis australis*	Rallidae	Gruiformes	Species	Both
New Zealand fantail*	*Rhipidura fuliginosa*	Rhipiduridae	Passeriformes	Species	NI/SI
Shining cuckoo	*Chrysococcyx lucidus lucidus*	Cuculidae	Cuculiformes	Native	Both
Morepork	*Ninox novaeseelandiae novaeseelandiae*	Strigidae	Strigiformes	Native	Both
Silvereye	*Zosterops lateralis lateralis*	Zosteropidae	Passeriformes	Native-Rec	Both
Coastal-breeding wading birds					
New Zealand dotterel	*Charadrius obscurus aquilonius* (NI) or *C. o. obscurus* (SI)	Charadriidae	Charadriiformes	Species	Both
Variable oystercatcher	*Haematopus unicolor*	Haematopodidae	Charadriiformes	Native	Both
Southern black-backed gull	*Larus dominicanus dominicanus*	Laridae	Charadriiformes	Native	Both
Red-billed gull	*Larus novaehollandiae scopulinus*	Laridae	Charadriiformes	Native	Both
Caspian tern	*Hydroprogne caspia*	Sternidae	Charadriiformes	Native	Both
White-fronted tern	*Sterna striata*	Sternidae	Charadriiformes	Native	Both
Inland-breeding wading birds,					
Wrybill	*Anarhynchus frontalis*	Charadriidae	Charadriiformes	Genus	Both
Banded dotterel	*Charadrius bicinctus bicinctus*	Charadriidae	Charadriiformes	Species	Both
South Island pied oystercatcher	*Haematopus finschi*	Haematopodidae	Charadriiformes	Species	Both
Black-billed gull	*Larus bulleri*	Laridae	Charadriiformes	Species	Both
Black stilt	*Himantopus novaezelandiae*	Recurvirostridae	Charadriiformes	Species	Both
Black-fronted tern	*Childonias albostriata*	Sternidae	Charadriiformes	Species	Both
Australasian pied stilt	*Himantopus himantopus leucocephalus*	Recurvirostridae	Charadriiformes	Native	Both
Coastal wetlands and shores					
Stewart Island shag	*Leucocarbo chalconotus*	Phalacrocoracidae	Pelecaniformes	Species	SI
Spotted shag	*Stictocarbo punctatus punctatus*	Phalacrocoracidae	Pelecaniformes	Species	Both
Reef heron	*Egretta sacra sacra*	Ardeidae	Ciconiiformes	Native	Both
Pied shag	*Phalacrocorax varius varius*	Phalacrocoracidae	Pelecaniformes	Native	Both
Royal spoonbill	*Platalea regia*	Threskiornithidae	Ciconiiformes	Native-Rec	Both
Freshwater wetlands					
Brown teal	*Anas chlorotis*	Anatidae	Anseriformes	Species	Both
New Zealand scaup	*Aythya novaeseelandiae*	Anatidae	Anseriformes	Species	Both
Fernbird	*Bowdleria punctata punctata*	Megaluridae	Passeriformes	Species	Both

Table 1. cont.

Common name	Latin name	Family	Order	Endemism	Islands
Little shag	*Phalacrocorax melanoleucos brevirostris*	Phalacrocoracidae	Pelecaniformes	Species	Both
New Zealand dabchick	*Poliocephalus rufopectus*	Podicipedidae	Podicipediformes	Species	NI
New Zealand shoveller	*Anas rhynchotis*	Anatidae	Anseriformes	Native	Both
Black swan	*Cygnus atratus*	Anatidae	Anseriformes	Native	Both
White heron	*Ardea modesta*	Ardeidae	Ciconiiformes	Native	Both
Australasian bittern	*Botaurus poiciloptilus*	Ardeidae	Ciconiiformes	Native	Both
New Zealand kingfisher	*Todiramphus sanctus vagans*	Halcyonidae	Coraciiformes	Native	Both
Black shag	*Phalacrocorax carbo novaehollandiae*	Phalacrocoracidae	Pelecaniformes	Native	Both
Little black shag	*Phalacrocorax sulcirostris*	Phalacrocoracidae	Pelecaniformes	Native	Both
Australasian crested grebe	*Podiceps cristatus australis*	Podicipedidae	Podicipediformes	Native	SI
Pūkeko	*Porphyrio melanotus melanotus*	Rallidae	Gruiformes	Native	Both
Grey teal	*Anas gracilis*	Anatidae	Anseriformes	Native-Rec	Both
White-faced heron	*Egretta novaehollandiae novaehollandiae*	Ardeidae	Ciconiiformes	Native-Rec	Both
Australian coot	*Fulica atra australis*	Rallidae	Gruiformes	Native-Rec	Both
Birds of other open habitats					
Rock wren	*Xenicus gilviventris*	Acanthisittidae	Passeriformes	Family	SI
Paradise shelduck	*Tadorna variegata*	Anatidae	Anseriformes	Species	Both
New Zealand pipit	*Anthus novaeseelandiae novaeseelandiae*	Motacillidae	Passeriformes	Species	Both
Australasian harrier	*Circus approximans*	Accipitridae	Falconiformes	Native-Rec	Both
Spur-winged plover	*Vanellus miles novaehollandiae*	Charadriidae	Charadriiformes	Native-Rec	Both
Welcome swallow	*Hirundo neoxena neoxena*	Hirundinidae	Passeriformes	Native-Rec	Both

Table 2. Average local occupancy probability [and upper and lower bounds of 95% intervals] in each Atlas on each island, from 1,000 kriged posterior estimates. South Island includes Stewart Island/Rakiura. Asterisks indicate that a single combined national model was fitted for all mainland species or subspecies because of difficulty in distinguishing them from records in the atlases (e.g. all weka, and brown, tokoeka and great spotted kiwi were combined, all falcon 'forms', both robin species). As in Table 1 of the paper, within each habitat group (subheadings), birds are arranged in order of level of endemism, and then in alphabetical order of order, family and Latin name.

	North Island		South Island	
Common name	**Atlas 1**	**Atlas 2**	**Atlas 1**	**Atlas 2**
Forest birds				
Kiwi species*	0.11 [0.07, 0.17]	0.04 [0.03, 0.04]	0.07 [0.05, 0.11]	0.05 [0.04, 0.05]
Rifleman*	0.09 [0.08, 0.11]	0.05 [0.04, 0.05]	0.29 [0.26, 0.33]	0.22 [0.20, 0.25]
North island kōkako	0.02 [0.02, 0.03]	0.01 [0.01, 0.01]	-	-
Kākā*	0.07 [0.07, 0.08]	0.06 [0.05, 0.06]	0.14 [0.13, 0.16]	0.09 [0.09, 0.11]
Kea	-	-	0.16 [0.15, 0.17]	0.14 [0.13, 0.16]
Whitehead	0.14 [0.12, 0.20]	0.17 [0.14, 0.18]	-	-
Brown creeper	-	-	0.25 [0.22, 0.32]	0.24 [0.23, 0.28]
Mōhua/yellowhead	-	-	0.04 [0.03, 0.04]	0.04 [0.03, 0.05]
Blue duck/whio	0.06 [0.04, 0.07]	0.01 [0.01, 0.02]	0.08 [0.05, 0.12]	0.02 [0.01, 0.02]
Kererū	0.37 [0.34, 0.40]	0.40 [0.38, 0.41]	0.36 [0.34, 0.39]	0.27 [0.26, 0.29]
Bellbird	0.31 [0.29, 0.32]	0.38 [0.37, 0.40]	0.61 [0.59, 0.63]	0.63 [0.61, 0.65]
Tūī	0.52 [0.50, 0.55]	0.65 [0.63, 0.66]	0.30 [0.28, 0.32]	0.25 [0.24, 0.26]
Grey warbler	0.68 [0.66, 0.69]	0.86 [0.84, 0.87]	0.63 [0.62, 0.64]	0.74 [0.72, 0.76]
Long-tailed cuckoo	0.19 [0.15, 0.22]	0.13 [0.10, 0.16]	0.16 [0.13, 0.20]	0.13 [0.10, 0.16]
New Zealand robin*	0.11 [0.09, 0.12]	0.08 [0.07, 0.11]	0.16 [0.15, 0.18]	0.14 [0.13, 0.18]
New Zealand tomtit*	0.22 [0.21, 0.24]	0.21 [0.19, 0.22]	0.48 [0.45, 0.50]	0.41 [0.39, 0.43]
Parakeet/kākāriki species*	0.05 [0.05, 0.06]	0.04 [0.04, 0.05]	0.13 [0.12, 0.14]	0.14 [0.12, 0.17]
Weka species*	0.04 [0.03, 0.05]	0.01 [0.00, 0.01]	0.14 [0.12, 0.16]	0.09 [0.08, 0.10]
New Zealand fantail*	0.78 [0.76, 0.80]	0.88 [0.88, 0.89]	0.58 [0.56, 0.60]	0.59 [0.58, 0.61]
Shining cuckoo	0.31 [0.29, 0.36]	0.43 [0.41, 0.46]	0.15 [0.14, 0.18]	0.20 [0.18, 0.22]
Morepork	0.29 [0.22, 0.36]	0.25 [0.23, 0.28]	0.20 [0.15, 0.24]	0.15 [0.14, 0.17]
Silvereye	0.69 [0.67, 0.72]	0.77 [0.76, 0.79]	0.63 [0.61, 0.65]	0.65 [0.63, 0.66]

Table 2. cont.

Common name	North Island		South Island	
	Atlas 1	Atlas 2	Atlas 1	Atlas 2
Coastal wading birds, terns and gulls				
New Zealand dotterel	0.05 [0.05, 0.09]	0.06 [0.06, 0.07]	0.00 [0.00, 0.01]	0.00 [0.00, 0.01]
Variable oystercatcher	0.12 [0.10, 0.13]	0.20 [0.19, 0.21]	0.11 [0.10, 0.12]	0.15 [0.14, 0.16]
Southern black-backed gull	0.46 [0.44, 0.47]	0.52 [0.51, 0.53]	0.61 [0.59, 0.62]	0.62 [0.60, 0.63]
Red-billed gull	0.26 [0.24, 0.27]	0.30 [0.29, 0.31]	0.15 [0.14, 0.16]	0.18 [0.17, 0.19]
Caspian tern	0.16 [0.14, 0.18]	0.20 [0.20, 0.22]	0.07 [0.06, 0.08]	0.10 [0.09, 0.11]
White-fronted tern	0.16 [0.15, 0.18]	0.20 [0.18, 0.21]	0.13 [0.12, 0.15]	0.15 [0.14, 0.17]
Inland–breeding wading birds, terns and gulls				
Wrybill	0.02 [0.01, 0.02]	0.02 [0.02, 0.02]	0.02 [0.01, 0.02]	0.02 [0.01, 0.02]
Banded dotterel	0.06 [0.06, 0.07]	0.07 [0.07, 0.08]	0.17 [0.16, 0.18]	0.14 [0.12, 0.15]
South Island pied oystercatcher	0.04 [0.04, 0.05]	0.11 [0.10, 0.11]	0.35 [0.33, 0.39]	0.34 [0.32, 0.35]
Black-billed gull	0.03 [0.02, 0.03]	0.05 [0.04, 0.05]	0.22 [0.21, 0.23]	0.17 [0.16, 0.19]
Black stilt	-	-	0.01 [0.01, 0.02]	0.01 [0.01, 0.02]
Black-fronted tern	0.00 [0.00, 0.01]	0.00 [0.00, 0.01]	0.15 [0.14, 0.16]	0.17 [0.15, 0.19]
Australasian pied stilt	0.26 [0.25, 0.27]	0.28 [0.27, 0.29]	0.19 [0.18, 0.20]	0.18 [0.17, 0.19]
Coastal wetlands and shores				
Stewart Island shag	-	-	0.01 [0.01, 0.02]	0.02 [0.01, 0.02]
Spotted shag	0.01 [0.01, 0.01]	0.01 [0.01, 0.01]	0.06 [0.05, 0.08]	0.11 [0.10, 0.12]
Reef heron	0.09 [0.05, 0.12]	0.06 [0.06, 0.07]	0.03 [0.02, 0.04]	0.01 [0.01, 0.01]
Pied shag	0.11 [0.10, 0.15]	0.22 [0.21, 0.23]	0.06 [0.05, 0.08]	0.11 [0.10, 0.11]
Royal spoonbill	0.00 [0.00, 0.00]	0.03 [0.03, 0.03]	0.01 [0.00, 0.01]	0.04 [0.03, 0.04]

Table 2. cont.

Common name	North Island		South Island	
	Atlas 1	Atlas 2	Atlas 1	Atlas 2
Freshwater wetlands				
Brown teal	0.01 [0.01, 0.01]	0.01 [0.01, 0.02]	-	-
New Zealand scaup	0.03 [0.03, 0.03]	0.07 [0.06, 0.08]	0.05 [0.04, 0.05]	0.12 [0.11, 0.13]
Fernbird	0.06 [0.05, 0.11]	0.10 [0.09, 0.11]	0.05 [0.04, 0.09]	0.05 [0.05, 0.06]
Little shag	0.25 [0.24, 0.27]	0.42 [0.41, 0.44]	0.18 [0.17, 0.20]	0.25 [0.23, 0.26]
New Zealand dabchick	0.04 [0.03, 0.05]	0.09 [0.08, 0.09]	-	-
New Zealand shoveller	0.06 [0.05, 0.07]	0.10 [0.09, 0.11]	0.07 [0.06, 0.08]	0.11 [0.10, 0.12]
Black swan	0.10 [0.09, 0.11]	0.21 [0.20, 0.22]	0.10 [0.09, 0.11]	0.14 [0.13, 0.15]
White heron	0.02 [0.01, 0.02]	0.01 [0.01, 0.02]	0.04 [0.03, 0.05]	0.04 [0.03, 0.05]
Australasian bittern	0.05 [0.05, 0.06]	0.06 [0.05, 0.07]	0.02 [0.02, 0.02]	0.01 [0.01, 0.02]
New Zealand kingfisher	0.62 [0.60, 0.63]	0.80 [0.78, 0.81]	0.16 [0.15, 0.17]	0.21 [0.19, 0.22]
Black shag	0.27 [0.26, 0.29]	0.38 [0.37, 0.39]	0.26 [0.25, 0.27]	0.28 [0.27, 0.29]
Little black shag	0.08 [0.07, 0.09]	0.15 [0.13, 0.17]	0.00 [0.00, 0.01]	0.02 [0.02, 0.03]
Australasian crested grebe	-	-	0.01 [0.01, 0.02]	0.02 [0.02, 0.03]
Pūkeko	0.47 [0.43, 0.51]	0.66 [0.64, 0.68]	0.22 [0.20, 0.25]	0.24 [0.23, 0.25]
Grey teal	0.02 [0.01, 0.02]	0.09 [0.08, 0.09]	0.03 [0.02, 0.03]	0.12 [0.11, 0.12]
White-faced heron	0.37 [0.36, 0.39]	0.52 [0.51, 0.53]	0.27 [0.26, 0.29]	0.32 [0.30, 0.33]
Australian coot	0.01 [0.01, 0.01]	0.02 [0.02, 0.03]	0.01 [0.00, 0.01]	0.02 [0.01, 0.02]
Birds of other open habitats				
Rock wren	-	-	0.02 [0.02, 0.03]	0.01 [0.01, 0.02]
Paradise shelduck	0.22 [0.21, 0.25]	0.75 [0.74, 0.77]	0.43 [0.42, 0.48]	0.67 [0.65, 0.69]
New Zealand falcon*	0.04 [0.04, 0.05]	0.05 [0.04, 0.06]	0.07 [0.07, 0.08]	0.13 [0.12, 0.15]
New Zealand pipit	0.29 [0.28, 0.31]	0.32 [0.30, 0.33]	0.36 [0.34, 0.37]	0.28 [0.27, 0.29]
Australasian harrier	0.65 [0.63, 0.66]	0.86 [0.85, 0.87]	0.55 [0.53, 0.56]	0.67 [0.66, 0.68]
Spur-winged plover	0.01 [0.01, 0.02]	0.81 [0.80, 0.83]	0.34 [0.32, 0.37]	0.60 [0.58, 0.62]
Welcome swallow	0.35 [0.33, 0.38]	0.90 [0.89, 0.91]	0.08 [0.07, 0.08]	0.47 [0.45, 0.48]

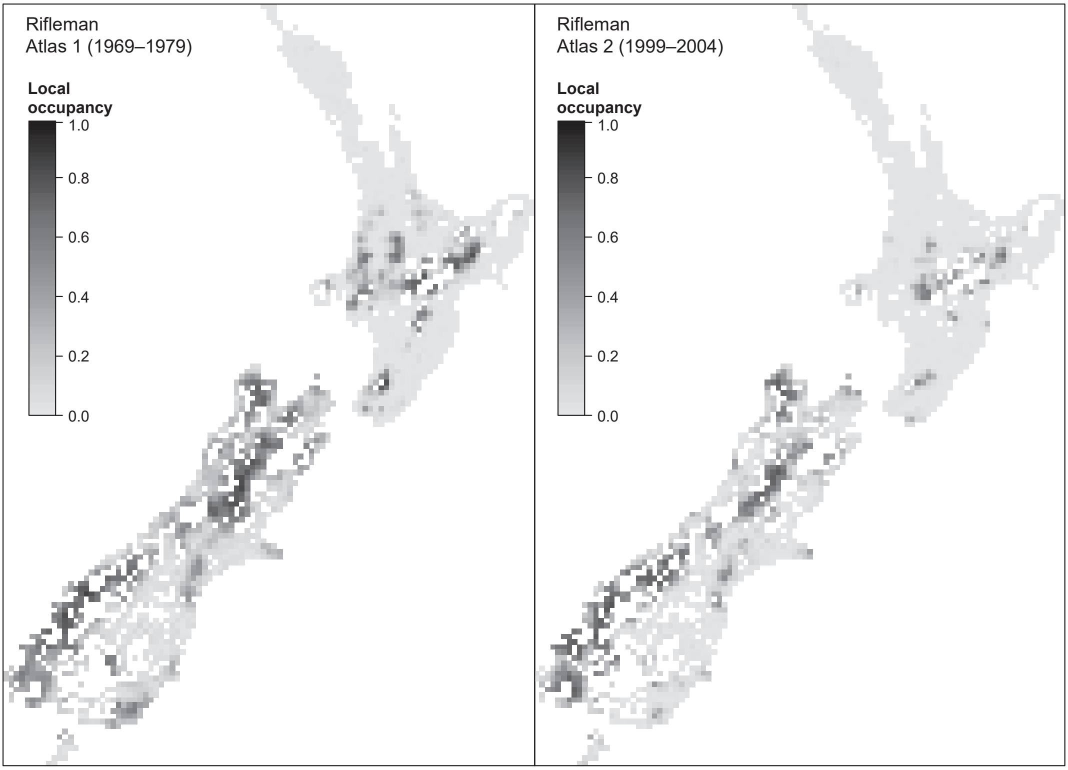

Figure 1. Median local occupancy estimates for rifleman (*Acanthisitta chloris chloris* in the South Island and *A. c. granti* in the North Island, modelled as a single taxon) in 2,155 squares on our common grid across New Zealand, showing status in 1969–1979 and 1999–2004. Gaps (white squares) in each map indicate squares that were not sampled in both Atlases and are therefore excluded from our dataset.

RESULTS

The dataset produced by the two-stage process described above contains estimates of the probability of occupancy for each of 64 modelled native bird taxa, in each of 2,155 unique 10 × 10 km grid squares, in each of two measurement periods (1969–1979 and 1999–2004). There are 1,083 North Island squares and 1,072 squares on South Island and Stewart Island together, covering similar areas of land on each island (99,510 and 99,630 km^2, respectively). The data cover 88% of the land on the North Island and 66% of the land on the South Island and Stewart Island combined.

Variability in estimates of occupancy (Stage 1) and in the estimates from kriging (Stage 2) was preserved so that this can be incorporated in future analyses. Table 2 provides the average local occupancy probability [and upper and lower bounds of 95% intervals] in each Atlas on each island, derived from 1,000 kriged posterior estimates. We have also produced a dataset of median estimates of probabilities of occupancy, and the spatial centres of each grid square. These median estimates can be mapped, as shown in Fig. 1.

The original datasets, derived local occupancy data for 64 native bird taxa, and a collation of maps have been deposited in the Manaaki Whenua – Landcare Research permanent repository (https://datastore.landcareresearch.co.nz/organization/osnz-atlas-data). The original data may be accessed and used through a request to the OSNZ, and the derived data through requests to OSNZ and the authors.

DISCUSSION

Our process has produced unbiased estimates of probabilities of local occupancy derived on an identical basis for each atlas measurement period and each of 64 bird taxa. Estimates for a particular taxon at the same location can be compared between the two measurement periods, and estimates can also be compared between and among different taxa. For example, median occupancy probabilities can be summed across taxa within squares to estimate the number of taxa likely to occupy a square ('local richness'), and change in local richness can be derived by subtracting local richness estimates for squares in 1969–1979 (Atlas 1) from those in 1999–2004 (Atlas 2). We first used our estimates of local occupancy to provide technical advice to the Parliamentary Commissioner for the Environment on state and change in New Zealand land birds (Walker & Monks 2017; Walker *et al*. 2017).

Covariates can be included in occupancy models in order to refine estimates (Bailey *et al*. 2014). However, to ensure that our estimates were produced on an identical basis in each atlas measurement period, we retained only season and island as covariates in our process. In early experimental runs of the models, we allowed probability of detection in each model to vary with observer, but found that these models fitted poorly and produced spatially biased estimates of occupancy. We concluded that observer-specific detection probabilities were sensitive to the number of observers and their distribution across space for any species. Observer covariate terms were therefore excluded from all final models. We assumed that all complete sheets represented sufficient effort by an observer to cover a square and record all species seen or heard. Other potential indicators of observer effort that might influence detection probability (i.e. days spent searching per sheet or card, or survey start and end date) were not included in our models because they were estimated and recorded differently in the two Atlases. We also did not include any environmental covariates in our models, both because comparable environmental information is not available for the two measurement periods, and because doing so would introduce different assumptions into occupancy estimates for different measurement periods, confounding attempts to later test for differences in responses to environmental variables between atlas measurement periods.

Ability to compare data collated in any future Atlas with the first two atlases will depend on the use of similar sampling methods. The most critical of these is use of a similar spatial scale of sampling unit (c. 10 × 10 km squares). It is also desirable for observers to return full lists ('complete sheets') which therefore record the absence as well as the presence of bird species in each square. Incorporating presence-only data into occupancy models is challenging, and we did not attempt it.

Users of our standardised estimates of local occupancy should be aware that median estimates (e.g. Fig. 1) do not consider variability in the estimates from our two-stage process. To take account of this variability, analyses must sample from the range of different posterior estimates of local occupancy produced for each species by our Bayesian process (e.g. by bootstrapping). The need to bootstrap analyses to take account of variation adds complexity and time, but we have produced code for the software R (R Development Core Team 2018) which achieves this, and have provided a starter script in the data repository. We have also undertaken exploratory analyses in which we bootstrap the fitting of models to consider variability in local occupancy estimates. These analyses have produced generally similar results to models run on median estimates only (e.g. the approach used in the reports of Walker & Monks 2017 and Walker *et al*. 2017).

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APPENDIX 1

Glossary of technical terms

Bootstrapping: methods that rely on random sampling with replacement to produce metrics or undertake statistical tests. Bootstrapping allows measures of accuracy and confidence to be estimated based on samples from a distribution, such as the posterior estimates derived from Bayesian statistics.

Detection probability (or probability of detection): the probability that a taxon will be detected at a site, if it is present. Detection probabilities are usually less than 1, so not accounting for detection probabilities will usually lead to occupancy probabilities being underestimated.

Grid square or square: a square on the national grid. For our estimates of occupancy probability we use a common grid of 10,000 m (10 × 10 km) squares defined in the metric New Zealand Map Grid (NZMG) coordinate system.

Kriging: a method of interpolating between measures in space, used here to interpolate estimates of local occupancy probability from the centres of the two different spatial grids used in the two measurement periods to the centres of a common 10 × 10 km grid.

Local occupancy probability: the probability that a taxon is present in a particular grid square.

Measurement period: the period of field survey for a national atlas of bird distribution compiled by the Ornithological Society of New Zealand (OSNZ; Bull *et al*. 1985; Robertson *et al*. 2007). Field surveys for the first atlas (the 'first measurement period') ran from September 1969 to December 1979 and for the second atlas (the 'second measurement period') from December 1999 to November 2004.

Native: occurring naturally in New Zealand, having either been present at the time of human settlement, or become established without human assistance since that time.

Occupancy: presence at a site.

Occupancy model: a model that combines estimates of probabilities of detection and occupancy at a site to estimate the probability that a taxon is actually present.

Occupancy probability (or probability of occupancy): the probability that a taxon uses, or is present at, a site. Occupancy probability is expressed as a proportion (i.e. between 0.0 and 1.0).

Taxon (plural taxa): a species or a combination of species, subspecies, forms or varieties for which we fitted an occupancy model. For example, the taxon 'kiwi' on the North Island refers to all recognised forms of *Apteryx mantellii* ('North Island kiwi taxa') and on the South Island it refers to *A. rowi*, *A. haastii* and all recognised forms of *Apteryx australis* ('South Island kiwi taxa') together.

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SHORT NOTE

A rare vocalisation from an adult female tui (*Prosthemadera novaeseelandiae*)

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Vocal communication between adult birds and nestlings must be conspicuous if it is to maximise effective transmission (Magrath *et al*. 2010). There is often however a trade-off within this communication because calls between parents and young must be unlocatable to eavesdropping predators or rival conspecifics by their subtlety. Yet, they must also be noticeable enough for the nestlings and/or other adult birds to hear and successfully perceive the sound and respond in a behaviourally appropriate way (Anderson *et al*. 2010). Parent calls directed towards nestlings can induce silence (Marques *et al*. 2011), and may also induce other behaviours in nestlings (Anderson *et al*. 2010). A key behavioural response that parent signals can induce in nestlings is the begging posture (Anderson *et al*. 2010; Caro *et al*. 2016; Ryser *et al*. 2016; Searcy & Yasukawa 2017) which chicks adopt when requesting food.

In November 2012, at an active nest site at Wenderholm Regional Park, Auckland, a rare vocalisation was produced by a female tui (*Prosthemadera novaeseelandiae*) (identified by its size compared to her male partner that was also observed) in a possible communication with nestlings. It was not established whether males also produce the vocalisation. Although tui have an extensive range of vocal signals within their repertoire (e.g. Hill *et al*. 2018), this vocalisation has, to my knowledge and despite extensive observation (~300 hours of field observations), not been documented. Although it must be added that the predominant field observations have been of male tui. The vocalisation was recorded during a nest observation session that lasted approximately 2 hours. They were recorded from approximately 2 metres below the bird using a Sennheiser ME67 long-range directional microphone (Sennheiser, Old Lyme, CT) attached to a Marantz PMD620 digital recorder (Marantz, Kanagawa, Japan). The nest was situated within a manuka tree (*Leptospermum scoparium*) with a large adjacent puriri (*Vitex lucens*).

This vocalisation could potentially be categorised as a solicitation signal as it was produced when the female parent was arriving at the nest with food. The vocalisation consisted of a short note (mean of 0.071 ± (SE) 0.005 sec) with a mean minimum frequency of 0.75 ± 0.006 kHz, and harmonics (up to 4.89 kHz) (Fig. 1). The notes had a mean peak frequency, the frequency at which the maximum power is produced, of 2.07 kHz ± 0.04 sec. According to my observations the vocalisation was produced once on 3 occasions when approximately 1–2 metres from the nest on arrival.

Although further observations are needed for confirmation, this vocalisation may prime the nestlings to adopt a begging posture that will facilitate rapid transfer of food and removal of faecal sacs. However, the rarity of this call may mean that the parents only produce the vocalisation under certain conditions such as when the nestlings are at a particular development stage or even in the presence of a potential predator or even a human observer. Furthermore, there is a possibility that this vocalisation was unique to this individual and indeed may have been an alarm call towards nestlings due to human presence, despite this specific call not being heard at other locations

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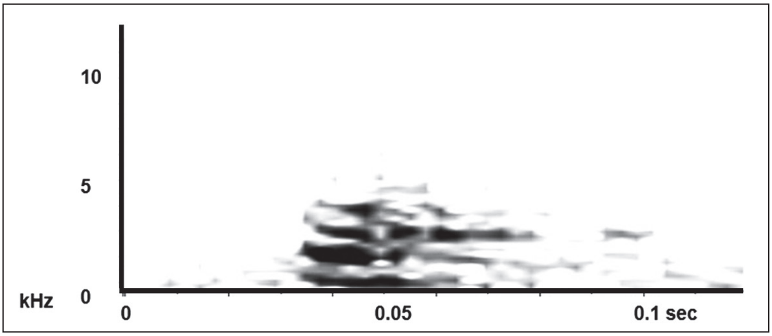

Figure 1. A sound spectrogram of a rare female tui (*Prosthemadera novaeseelandiae*) call from Wenderholm Regional Park, Auckland. The sound spectrogram was produced using Raven Pro 1.4 Beta Version software (Cornell Lab of Ornithology, Ithaca, NY, USA).

in human presence. There is also the possibility that this call may have limited broader biological relevance. Nevertheless, these aspects need further clarification.

To elucidate the function of this and other vocalisations within the tui repertoire, playback experiments would be ideal. Furthermore, whether nestlings exhibit sound-based discrimination of parents' solicitation calls (see Charrier *et al*. 2001) or whether these are generic calls across the species such are alarm calls should also be future foci. Using equipment such as fixed cameras (*e.g*. GoPro, San Mateo, California) above nests would help us obtain a full, real-time view of nests. This would be ideal in order to observe and document nestling response to playbacks. Future work could also focus on potential structural changes in tui nestling begging calls in response to different parent calls such as alarm calls. Moreover, documenting visual signals would be useful in ascertaining whether they work in concert with vocal cues to act as honest signals of offspring hunger (reviewed in Mock *et al*. 2011). Furthermore, the advent of automated bird call identification technology (Priyadarshani *et al*. 2018) could be important in detecting rarer calls from multiple species.

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Keywords: nestling, tui, *Prosthemadera novaeseelandiae*, vocalisation.

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SHORT NOTE

Dispersal of translocated endemic passerines to nearby islands in Chalky and Preservation Inlets, southern Fiordland, New Zealand

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Most of New Zealand's endemic passerines have poor dispersal ability, which is one of the reasons why they are the focus of much conservation translocation effort (Diamond 1984; Miskelly & Powlesland 2013). It is self-evident that species with poor dispersal ability will require translocation over large distances following their local extirpation, in order to achieve ecological restoration objectives. However, their subsequent dispersal from translocation release sites will be influenced by many factors including species-specific flying ability, inter-specific competition at the release site, habitat fragmentation, and physical barriers to dispersal (Diamond 1984; Empson & Fastier 2013; Miskelly *et al*. 2017).

A recent survey of the dispersal ability of three species of endemic passerines by Miskelly *et al*. (2017) found that South Island robins *Petroica australis* readily crossed water-gaps of at least 1.4 km, while South Island saddlebacks *Philesturnus carunculatus* and mohua *Mohoua ochrocephala* rarely crossed gaps of more than 100 metres (although mohua are apparently capable of crossing gaps up to 860 m). An additional robin example from Fiordland was a bird seen on a northern peak of Resolution Island in early 2007, a few months before they were released on Pigeon Island off the south coast of Resolution Island (Pete Kirkman pers. comm. to CMM, 26 November 2017). This bird is likely to have come from either Breaksea Island or nearby Hawea Island, requiring a minimum water-crossing of 1.2 km.

The impetus for the 2017 paper was a survey of 56 islands in Dusky Sound, Fiordland, undertaken in November 2016. We here report observations from a November 2017 survey of 70 islands in Chalky Inlet and Preservation Inlet and adjacent waterways in southern Fiordland, and additional data from June 2018. These same three passerine species had each been released at two sites in Chalky and Preservation Inlets following predator eradication campaigns on the Passage Islands, Chalky and Coal Islands (Department of Conservation 2017).

Ecological restoration of islands in Chalky and Preservation Inlets began with eradication of stoats *Mustela erminea* from Chalky Island (514 ha) and the Passage Islands (177 ha) in 1999, followed by stoat eradication on Coal Island (1,163 ha) in 2005, and mouse *Mus musculus* eradication there in 2008 (further information and maps in Department of Conservation 2017). Limited information is

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available on predator distribution on adjacent islands in Chalky and Preservation Inlets; however, traps targeting stoats and rats (*Rattus* spp.) are maintained on most of the smaller islands referred to here, including 'North' Passage Island, Steep-to Island, and the Cording Islands (CRB unpublished data).

South Island saddlebacks were released on the larger ('South') Passage Island in 2001 and on Chalky Island in 2008 (Miskelly & Powlesland 2013). Mohua were released on Chalky Island in 2002 and Coal Island in 2015, and South Island robins were released on Chalky Island in 2010 and Coal Island in 2015 (Miskelly & Powlesland 2013; Department of Conservation 2017). All three species were thriving on Chalky Island on 23 November 2017, plus we observed many South Island saddlebacks on South Passage Island on 24 November (Coal Island was not included in our survey).

In addition to these sites, in November 2017 and June 2018 South Island robins were observed on three islands where they had not been released, and South Island saddlebacks on two islands (Table 1). The 160 m minimum water gap between the two Passage Islands equals the previous maximum water crossing recorded for South Island saddleback (Taylor & Jamieson 2007). Mohua were not recorded at any sites where they had not been released in Chalky and Preservation Inlets, supporting the suggestion that this species has a fear of flying over water (Diamond 1981, 1984; Miskelly *et al*. 2017).

Two of the islands where we recorded robins are large enough to hold substantial populations, and we suspect that we witnessed the very earliest stages of colonisation. A single robin was heard singing on Steep-to Island, and the only robins recorded on South Passage Island were a pair feeding three fledglings on the south-west headland. If robins become established on Steep-to and South Passage Islands, and effective predator control is maintained on adjacent islands, these two islands are likely to provide source populations for colonisation of several further islands. Islands within 1.4 km of either Steep-to Island or South Passage Island include Round Island, Weka (Long) Island and the Cording Islands in Preservation Inlet, and North Passage Island and Great Island in Chalky Inlet.

South Island robins have apparently displaced congeneric tomtits (*Petroica macrocephala*) on numerous small islands in Dusky Sound (Miskelly *et al*. 2017). Robins were translocated to three islands in Dusky Sound between 2002 and 2013, and have subsequently spread to at least 33 further islands (Miskelly & Powlesland 2013; Miskelly *et al*. 2017). The smallest island where both species were recorded in 2016 was Parrot Island (40 ha), and tomtits were no longer present on 9 smaller (1–21 ha) islands where they were found during 1979–84 which now have robins. Robins (but not tomtits) were also recorded from 19 additional small islands (0.2–20 ha) in Dusky Sound in 2016 for which there was no 'pre-robin' data (Miskelly *et al*. 2017).

We recorded tomtits on 16 islands in southern Fiordland in November 2017, including South Passage Island, Weka Island (110 ha), Steep-to Island, 4 of the Cording Islands (1.6–24.5 ha) and North Passage Island (8.7 ha) (full species lists for all sites are entered in eBird). Based on the minimum island size where robins and tomtits were found to co-exist in Dusky Sound, we predict that tomtits will disappear from North Passage and the Cording Islands, concurrent with the establishment of robin populations there. However, tomtits may persist on the larger South Passage, Weka and Steep-to Islands regardless of the presence of robins.

Table 1. Endemic passerines recorded away from translocation release sites in southern Fiordland, South Island, New Zealand, in November 2017 and June 2018. *Pair with 3 fledglings.

Species	Island	Date	Island size (ha)	No. of birds	Nearest source population	Minimum distance flown (m)
South Island saddleback	Largest stack off south-west coast of South Passage Island	23 Nov 17	0.2	2	South Passage Island	50
South Island saddleback	North Passage Island	16 Jun 18	8.6	1	South Passage Island	160
South Island robin	Steep-to Island	22 Nov 17	57.6	1	Coal Island	550
South Island robin	Zero Nugget	23 Nov 17	0.1	2	Chalky Island	370
South Island robin	South Passage Island	24 Nov 17	167.9	5*	Chalky Island	870

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Keywords: saddleback, South Island robin, translocation

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SHORT NOTE

Vertebrate prey in the diets of free-ranging kiwi (*Apteryx* spp.)

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Kiwi (*Apteryx* spp.) are a monotypic order (Apterygiformes) of flightless birds endemic to New Zealand. Most palaeognath lineages are diurnal including the extant ostrich (*Struthio* spp.), rhea (*Rhea* spp.), and emu (*Dromaius novaehollandiae*), while the majority of tinamous (family: Tinamidae) and kiwi are nocturnal (Mitchell *et al*. 2014). Due to their secretive nature and nocturnal lifestyle, it is challenging to study kiwi life history. They use their sensitive bill and olfactory system to identify and select food items on the ground or buried in the substrate (Wenzel 1968). Historically, kiwi – including the North Island brown kiwi (*Apteryx mantelli*) – have been considered invertebrate specialists (Buller 1888; Gurr 1952; Bull 1959; Reid *et al*. 1982). One diet study found >75% of the North Island brown kiwi diet to consist of cicada nymphs, scarabaeid beetle larvae, and annelid worms (Kleinpaste & Colbourne 1983). In other studies, earthworms were the main prey of *A. mantelli*, consisting of 80% and 94% of the total diet respectively (Reid *et al.* 1982; Colbourne & Powlesland 1988). Plant material is consumed to a lesser extent and typically consists of 10-15% of the total diet, with seeds and fruits preferred over greens (Reid *et al.* 1982). While kiwi consume a variety of invertebrates and plant material, published reviews of kiwi diets provides no mention of them ingesting vertebrate prey in the wild (Marchant & Higgins 1990; Heather & Robertson 2005; Sales 2005; Robertson 2013). Here, we summarise evidence of kiwi ingesting vertebrate prey and present the first photographic documentation of a kiwi (*A. mantelli*) ingesting vertebrate prey in the wild.

While there are no records in the peer-reviewed literature, there are anecdotal reports of vertebrate prey in the diets of free-ranging kiwi. In one instance, a little spotted kiwi (*Apteryx owenii*) was filmed attempting to consume a New Zealand common gecko (*Woodworthia maculatus*) on Kapiti Island, but the gecko escaped before the kiwi could ingest it (R. Hitchmough *pers. comm.*). In the mid 1980s small skink bones were found in the droppings of a little spotted kiwi on Red Mercury Island (R. Colbourne *unpubl. data*). The skink consumed was most likely a moko skink (*Oligosoma moco*), though this was unable to be verified with certainty (D. Towns *pers. comm.*). Another report noted that a little spotted kiwi destroyed a New Zealand robin (*Petroica longipes*) nest, which included probing the nestlings with its bill thus resulting in the death

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of the nestlings; however, the nestlings were not consumed and this behaviour was concluded to be misdirected territorial aggression (Shaw & Mackinlay 2016).

Despite being the most abundant species of kiwi, records of North Island brown kiwi consuming vertebrate prey are also scarce. A New Zealand Forest Service report documented bones of green and golden bell frog (*Litoria aurea*) in kiwi faeces on two occasions in the Waitangi Forest, Northland (Colbourne 1982). This has not been previously reported in the peer-reviewed literature. However, ingestion of these frogs is presumed to be rare at least in part because the frog's parotid glands led to gastric distress for the kiwi that consumed them (Colbourne 1982). Beyond this, we were unable to locate any other examples of *A. mantelli* ingesting vertebrate prey.

On Little Barrier Island (Hauturu-o-toi) there is a stable population of brown kiwi numbering approximately 1,000 individuals (BirdLife International 2016). After nightfall, these kiwi can be easily seen on flat open habitat on the southwest edge of the island. On the night of 6 March 2017 between 2315 h and 2345 h an adult kiwi was observed and photographed feeding in the short grass. Upon reviewing the images it became clear that the kiwi had been photographed consuming at least two different skinks (*Oligosoma* spp.; Fig. 1A, B, C). The skinks consumed were most likely copper skinks (*Oligosoma aeneum*), though this could not be confirmed since the diagnostic characteristics were not clearly visible in the photographs (G. Patterson *pers. comm.*).

In compiling this and other aforementioned observations, we believe kiwi may have broader diets in certain regions than originally reported. In locations such as Little Barrier Island where there are several common terrestrial and fossorial reptile species, it is possible that this behaviour is not unusual. For example, skinks are known to live in the soil, occasionally utilize worm burrows, and are likely to be sluggish at night in colder temperatures (G. Patterson *pers. comm.*), thus making them potential prey for kiwi. Furthermore, there are several species of skink – including *O. aeneum* – that are abundant on Little Barrier Island (McCallum & Harker 1982). Though likely not a common

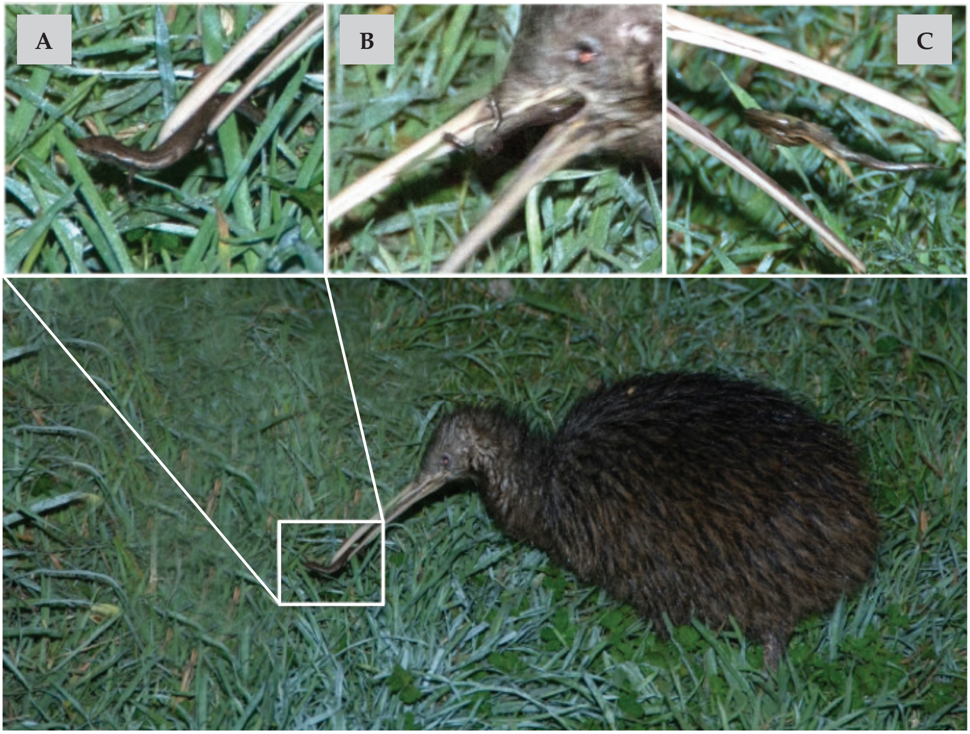

Figure 1: (a) A North Island brown kiwi (*Apteryx mantelli*) selects the first of two skinks (*Oligosoma* spp.) seen consumed that night. Photo taken on Little Barrier Island at 2317 h on 6 March 2017. (b) The kiwi ingests the first of two skinks it consumed that night. Photo taken on Little Barrier Island at 2317 h on 6 March 2017. (c) The same kiwi ingests the second of two skinks (*Oligosoma* spp.) seen consumed that night. Photo taken on Little Barrier Island at 2325 h on 6 March 2017.

diet item, on islands such as Little Barrier, skinks may be regularly encountered and occasionally consumed. Our findings suggest that kiwi diet may be more reflective of opportunistic foraging and consequently, vertebrates may be consumed by kiwi more commonly than previously thought.

There are few locations where there are both high densities of kiwi and small terrestrial vertebrates co-occurring, which may account for the lack of previous observations. Lizards can clearly co-exist in large numbers with kiwi, as is the case on Little Barrier Island, therefore our finding does not raise any obvious species conservation management implications at present. However, on many island reserves such as Little Barrier, the Kiore (Pacific Rat, *Rattus exulans*) have been successfully eradicated, which leads to higher densities of native fauna (Rayner *et al.* 2007), such as skinks and kiwi, and hence, the possibility of more encounters over time. As Reid *et al.* (1982) asserts, a 'typical' *A. mantelli* diet probably does not exist and diet composition likely reflects prey availability rather than choice. In that case, we expect an increase in skinks in kiwi diets on island reserves like Little Barrier as lizard populations recover following mammal eradication campaigns. Furthermore, as invasive herpetofauna (e.g. *Lampropholis delicata* and *Ichthyosaura alpestris*) increase on the mainland, they many interact with kiwi in areas where kiwi persist.

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