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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 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]

Table 2. cont.

Common name	Atlas 1	Atlas 2	Atlas 1	Atlas 2
Forest birds				
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]
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]
Freshwater wetlands				

Table 2. cont.

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]

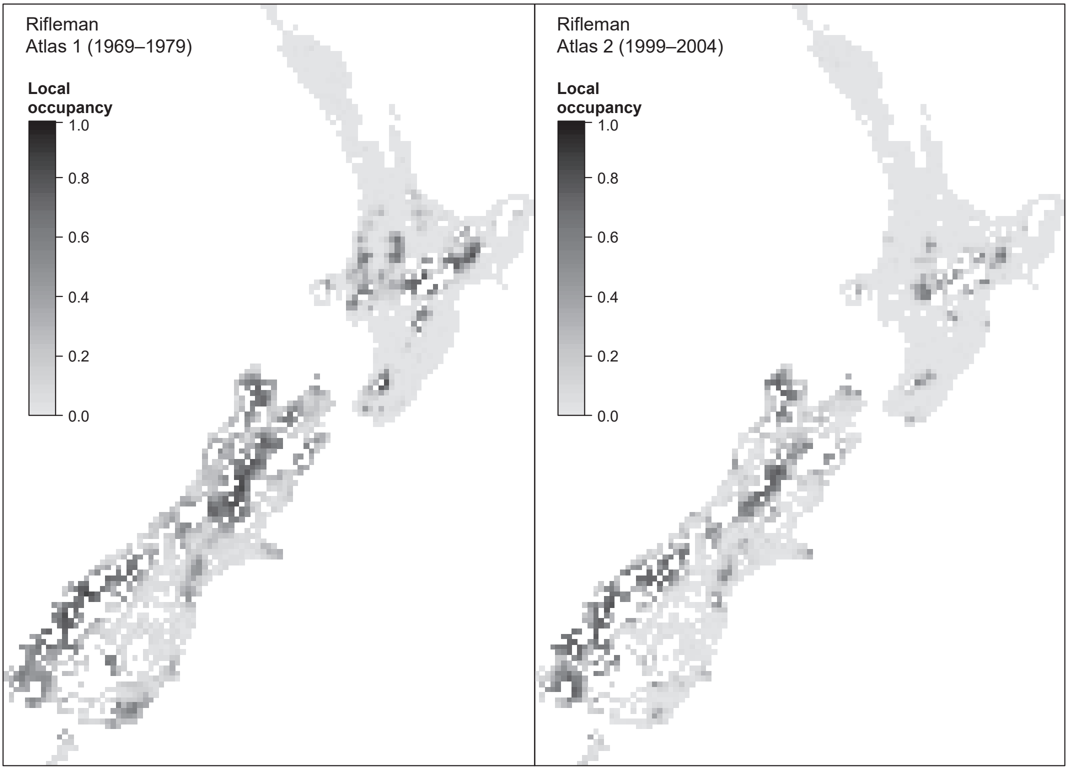

Figure 1. Median local occupancy estimates for rifleman (*Acanthisitta chloris chloris* in the South Island and *A. c. granti* in the North Island, modelled as a single taxon) in 2,155 squares on our common grid across New Zealand, showing status in 1969–1979 and 1999–2004. Gaps (white squares) in each 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.