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Distribution of great spotted kiwi (*Apteryx maxima*), 2012–2021

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Abstract: Conservation management requires knowledge of the distribution of species and how this changes over time. Great spotted kiwi (roroa, *Apteryx maxima*) is classified as globally threatened, 'Vulnerable' by the IUCN. It occurs only in the northwest of the South Island of New Zealand, is nocturnal and occurs at low density in mainly remote, mountainous terrain. To determine its distribution, we deployed acoustic recorders at 1,215 locations across 1,400,000 ha between 2012 and 2021. We analysed 3,356 nights of recordings to determine presence and call rates at each location. Roroa were distributed across 848,000 ha, but we identified a core area in northwest Nelson representing just 12% of the distribution (101,000 ha). Within the core, call rates exceeded 3 calls/h at many locations. Call rates provide only a relative indication of abundance but, outside the core, call rates fewer than 0.3 calls/h are common, suggesting that roroa are relatively sparse over much of their distribution. We used a static occupancy model with climatic, topographic and land-cover class variables to better understand the distribution. Eighty percent of recorder-nights had a detection probability exceeding 50%. At this probability, 73% of 5 x 5 km cells surveyed were sampled sufficiently to exceed 90% probability of detection if roroa were present. Annual rainfall and land-cover class appear most important for modelling occupancy. However, comparison of probability of occupancy and actual distribution suggests that variables not included in the modelling, which might include predation, also affect the distribution.

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Key words: Great spotted kiwi, roroa, *Apteryx maxima*, *Apteryx haastii*, distribution, acoustic recorder, call rate, occupancy modelling, detection probability

INTRODUCTION

Kiwi (family Apterygidae) are endemic to New Zealand. The great spotted kiwi (roroa, *Apteryx maxima* [Potts 1872], formerly *A. haastii* (Shepherd *et al.* 2021), and henceforth referred to as roroa) is classified as globally threatened, 'Vulnerable' by the International Union for the Conservation of Nature (BirdLife International 2020). It is classified as 'Nationally Vulnerable' in New Zealand based on a moderate to large population (5,000–20,000) and predicted decline of 30–70% over three generations, with qualifiers of 'data poor' and 'recruitment failure' (Robertson *et al*. 2017). In

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2015, the area occupied by roroa was estimated to be 800,000 ha, and populations without predator control were estimated to be declining at 2% a year (Innes *et al*. 2015). The Kiwi Recovery Plan (Germano *et al.* 2018) and the Roroa Species Plan (Department of Conservation 2021) aim to reverse this decline by restoring the former distribution, growing the population of the species by at least 2% per year, and maintaining genetic diversity. The plans acknowledge uncertainty around the population estimate and distribution, and have objectives to use accurate survey and monitoring data to inform kiwi recovery priorities and management requirements.

Restoring former distribution requires an understanding of past distribution. Unfortunately, sub-fossil remains of roroa and 'brown' kiwi species cannot be morphologically distinguished because they overlap in size (Worthy & Holdaway 2002). However, ancient DNA indicates the pre-human range of roroa was restricted to the northwest quadrant of the South Island (Shepherd & Lambert 2008). In the 19th century, roroa were recorded in Westland, western Canterbury, and northwestern Nelson (Heather & Robertson 2015), but syntype specimens from southern Westland are hybrids between rowi (*A. rowi*) and little spotted kiwi (*A. owenii*) (Shepherd *et al.* 2021). Since 1900, roroa are reported to have disappeared from apparently suitable habitat in the Grey Valley to the east of the Paparoa Range, and northern Westland (Heather & Robertson 2015). Approximate locations of places named in the text are shown in Figure 1 or Appendix 1.

Heather & Robertson (2015) describe the range shown in the Kiwi Recovery Plan (Germano *et al.* 2018), as three recently isolated, extant populations: from northwestern Nelson to the Buller River and east to the Arthur and Matiri Ranges; in the Paparoa Range; and in the Southern Alps from about the Nina Valley near Lewis Pass to the Taipo River (Fig. 1). There are also translocated populations at Rotoiti (Heather & Robertson 2015), in the Flora Valley (Toy & Toy 2020) and the Nina Valley (S. Yong *unpubl. data*).

The current distribution of roroa may reflect historic conditions that are no longer prevalent. Roroa may not occur in areas of suitable habitat due to past adult mortality, lack of recruitment, and immigration. Given that roroa have a life expectancy of 57 years and low productivity (Department of Conservation 2021), such mortality may have been many years ago. Dogs (*Canis familiaris*) and the use of leg-hold traps for possums (*Trichosurus vulpecula*), along with habitat modification, are likely to have been the main causes of adult roroa mortality in more accessible parts of the range (McLennan & McCann 1991; McLennan & McCann 2002), for example, the coastal fringe of the Paparoa Range (Jolly & Roderick 1983). Restrictions on dog access and use of leg-hold traps should now have reduced these threats over large parts of the roroa range. Stoat (*Mustela erminea*) control is key to addressing lack of recruitment (Germano *et al.* 2018) as young kiwi and kiwi eggs are vulnerable to predation by stoats (McLennan *et al.* 1996). Effective mustelid control results in roroa population increase (Department of Conservation 2021). However, while much of the roroa range is on public conservation land (Fig. 1), prior to the commencement of the aerial 1080 (sodium fluoroacetate) programme, Tiakina nga manu (Battle for our Birds) in 2014, there was little landscape-scale predator control (Elliott & Kemp 2016). Less than 10% of the roroa distribution has had sustained predator control (Department of Conservation 2021).

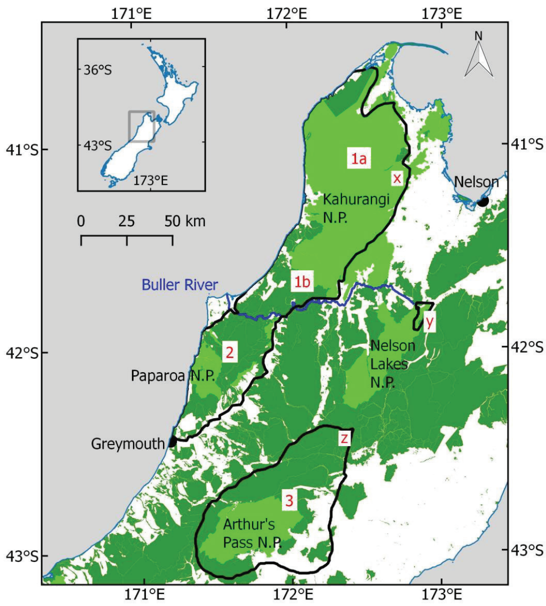

Figure 1. Range of great spotted kiwi (roroa, *Apteryx maxima*) as shown in the Kiwi Recovery Plan (2018) outlined in black, and conservation status of public land reproduced from LINZ (pale green, National Park; dark green, other public conservation land), although not all parts of the conservation estate have had predator control. Regions surveyed are labelled: 1a, NW Nelson; 1b, Westport; 2, Paparoa Range; 3, Arthur's Pass-Hurunui. Translocated populations: x, Flora Valley; y, Rotoiti; z, Nina Valley.

Predation will not be the only factor determining the distribution. Roroa feed primarily on invertebrates, especially earthworms, but also on berries and leaves (McLennan & McCann 1991). They roost during the day in natural cavities or under vegetation, and nest in similar cavities (McLennan & McCann 1991; Toy & Toy 2021a; Toy & Toy 2021b). Climatic, edaphic and topographic factors, together with vegetation type are likely to determine the availability of these basic requirements for food and shelter. Other factors such as competition with non-native rodents for food, habitat modification by ungulates, and effects of disease or parasites may also influence roroa distribution; all are poorly understood (Department of Conservation 2021).

Roroa pose survey challenges as their population is spread over 800,000 ha (Innes *et al.* 2015), and they are nocturnal and live in mainly remote, mountainous terrain (McLennan & McCann 2002). Much of the current understanding of roroa distribution is derived from the Kiwi Call Scheme (McClennan & McCann, 2002; Department of Conservation *unpubl. data*) which involves people listening for kiwi calls for two hours starting 30 minutes after sunset. Most of the records from this scheme are from the early 1990s. Roroa calls are distinctive and can carry over distances of more than 1 km (McLennan & McCann 1991; Colbourne *et al*. 2020; Toy & Toy 2020). Nevertheless, there are many reasons why roroa may not be detected even though they are present in an area. For example, roroa have large home ranges (McLennan & McCann 1991; Keye *et al*. 2011; Jahn *et al*. 2013; Toy & Toy 2020), and may be a long distance from a listening location for much of the night; calls may carry much less than 1 km in rugged habitat; and incubating roroa may not call at certain times of the night (Colbourne *et al*. 2020). Distribution mapping without taking account of imperfect detection can thus be misleading (MacKenzie *et al*. 2018).

The use of light-weight acoustic recorders enables a greater sampling effort than human listening. They can be left in remote locations for comparatively long periods, several recorders can be installed by a single person over a large area in one day, and they can be programmed to record all night. An additional advantage is the ability to store recordings and to check the identification of uncertain calls (Digby *et al*. 2013; Castro *et al*. 2019; Colbourne *et al*. 2020), thus minimising the chance of false positive detections. Critically, recorders provide verifiable records of non-detection as well as detection, enabling detection probability to be determined. Detection probability, in conjunction with variables describing habitat, can be used to model the occupancy probability of areas that were not directly sampled.

Call rates can be determined from acoustic recordings and may provide a measure of relative abundance. Use of such indirect measures assumes that the index correlates, and ideally is directly proportional, to true population size (Allen & Engeman 2015), and remains relatively stable temporally and spatially (Greene 2012). These assumptions are rarely tested; indeed, it is often impossible to obtain absolute numbers in free-ranging populations with which to validate indirect indices of abundance (Allen & Engeman 2015). For kiwi, call rates are assumed to reflect relative abundance although there is a need to identify the relationship (Innes *et al.* 2015; Germano *et al*. 2018). Colbourne & Digby (2016) conclude that due to the inherent natural variation in call rates, and the fact that chicks and juveniles rarely call, call rates should be used as a relative indicator of abundance, rather than to determine an accurate density of a kiwi population. The Nationwide Kiwi Call Count Monitoring Scheme has been used in this way since 1993, with changes in call rate being considered a surrogate measure of temporal changes in populations at specific sites (Colbourne *et al*. 2020).

This study aimed to update knowledge of the distribution of roroa, and determine relative abundance across its range. Occupancy modelling was used to take account of imperfect detection and identify factors that might help interpret the distribution. Knowledge of where roroa occur with some indication of abundance, will inform where management intervention will have greatest benefit for the recovery of the species, and will provide a verifiable basis against which to determine future changes in distribution.

METHODS

Study design

We aimed to survey the Kiwi Recovery Plan range (Fig. 1), but excluded areas of dry pasture which we deemed poor habitat for kiwi. We focused on identifying the edges of the distribution. We also surveyed some outlying areas from which there had been recent reports of kiwi. The extent of the roroa range and funding available necessitated an opportunistic approach to recorder deployment; locations were selected to fit in with planned routes of volunteers and Department of Conservation (DOC) staff accessing the back-country for other reasons. In areas not covered opportunistically, and to define the edge of the distribution, we undertook specific recorder deployment trips.

Acoustic recorder survey

Acoustic recorders were the primary survey tool; units (AR models 2–4) designed by the New

Zealand DOC Electronics Laboratory, Wellington, were used. These were set to record at 8 kHz sampling frequency and generate 16-bit resolution WAV files, saved to a 16 GB SD card. Recorders were fixed to a small tree about 1.5 m above the ground, away from vegetation that might rustle. Their locations were determined by handheld Garmin GPS. Locations were selected to maximize listening coverage, wherever possible on spurs, rises or ridges and away from running water. Recorders were deployed at any time of year, with 95% of recorder-nights between September and May.

Between 2012 and 2021, but primarily 2017–2019 (Fig. 2), recorders were deployed at 1,215 locations (Table 1) over 1,400,000 ha. Recorders were deployed for at least one night and we analysed an average of 2.8 nights/location (*sd* = 2.2).

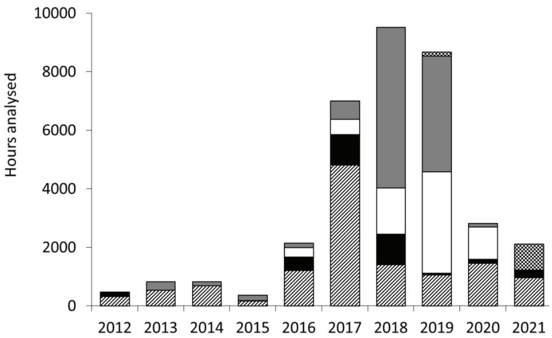

Figure 2. Survey effort analysed by region per annum, as indicated by number of nocturnal acoustic recording hours: diagonal shading, NW Nelson; black, Westport region; white, Paparoa Range; grey, Arthur's Pass-Hurunui; chequered, Rotoiti.

Analysis of records

Recordings were analysed by the authors using Freebird bird call analysis software (version 1.4.4.0). This generates spectrograms from the recordings and allows audio playback. Detection was primarily conducted from visual inspection of the spectrograms, but very faint or unusual calls were confirmed aurally. The time of each call, the sex of the roroa calling and whether the call was part of a 'duet' involving both sexes, were recorded. Nights, or portions of nights, with strong interference from wind, rain or other noise were not analysed. Calls outside the period 30 minutes after sunset to 30 minutes before sunrise (determined for the nearest city) were not used for call rate determination.

We estimated the area occupied by roroa by calculating minimum concave polygons around detections, using a 2,500 m buffer zone and a 0.25 edge restriction around the points (Ranges 9 Lite v2.02, www.anatrak.com). Where the estimated distribution overlapped the coast or the Buller River, we adjusted it to follow these features.

To enable comparison of relative abundance, call rates were categorized into subjective classes: ≥3 calls/h , 0.3 to 3 calls/h, or ≤0.3 calls/h.

Incidental records of occupancy

Additional records of occupancy were collated and used for determining distribution, but not for occupancy modelling or call rate determination. These included detections from acoustic recorders from DOC's Tier 1 monitoring programme (Mortimer & Greene 2017). Tier 1 recordings from 2011–2018 in which roroa calls were detected were made available and calls were verified by the authors. Tier 1 recorders are located on grid intersections which are not selected to optimise listening coverage. By inference, probability of detection may be lower than for recorders we deployed, so locations with roroa detected were treated as incidental records, and non-detect Tier 1 records were not used. Acoustic recorder records from the Nina Valley were also treated as incidental records, as the number of calls was determined using automated recognition software rather than by visual inspection of the spectrograms.

Additional non-acoustic recorder records of kiwi presence covering the period 2010–2020 were reviewed. Human call-counts, territory mapping studies and records of calls from observers known by the authors to be familiar with roroa calls were treated as incidental presence records. Records based on probe marks, footprints and faeces were not accepted due to potential confusion with other species. A few reliable records were found on the online, citizen-science record repositories, eBird and iNaturalist.

Occupancy analysis

Occupancy analysis takes account of imperfect detection and was used to estimate the probability of roroa occupancy and the variables most likely to affect that probability. For this analysis, a grid with 5 x 5 km cells was overlaid across the South Island, north of latitude 43.51°S and west of longitude 173.61°E. The probability of roroa detection and occurrence within each cell was based on the acoustic recordings made between 2012 and August 2020. This dataset contains both detections and non-detections.

Table 1. Acoustic recorder sampling effort and number of incidental great spotted kiwi (roroa, *Apteryx maxima*) records in each of the regions identified in Fig. 1.

Region	Acoustic recorder			Number of locations with incidental records
	Locations	Recorder-nights analysed	Hours analysed	
NW Nelson	463	1,250	12,560	123
Westport	150	323	3,174	65
Paparoa Range	154	635	6,987	83
Arthur's Pass-Hurunui	405	1,058	10,979	103
Rotoiti	43	90	1,009	12
Total	1,215	3,356	34,712	386

During the survey, effort varied (Fig. 2). Since roroa have an estimated life expectancy of 57 years (Department of Conservation 2021), and our interest was the distribution of roroa during the survey period, rather than any change within the period, the static occupancy model of MacKenzie *et al*. (2002) was used. This model explicitly accounts for imperfect detection (i.e. roroa may be present in a cell, but not detected by an acoustic recorder).

Nightly detection/non-detection data were assigned to the grid cell in which the acoustic recorder was located. A 'survey', *sensu* MacKenzie *et al*. (2002), was a 'recorder-night'; each acoustic recorder operating within a cell during a single night. If multiple acoustic recorders operated within the same cell on the same night, or a single device recorded for more than one night, these were regarded as separate recorder-nights for the analysis. The number of recorder-nights analysed per surveyed grid cell ranged between one and 128. Seventy-three percent of cells had more than four recorder-nights, 31% more than 10. Of the 343 grid cells surveyed, 11 had more than 30 recorder-nights, but to reduce computation time, only the first 30 recorder-nights in a cell were used for the analysis. This truncation lost no occupancy information, since any cell in which roroa were detected after the 30th recorder-night, had had a detection during the first 30 recorder-nights.

Land-cover, topography and climate are considered the factors most relevant to roroa ecological requirements for food and shelter and were used as covariates in the roroa occupancy and detection analysis (Table 2). At the order and group

Table 2. Variables used in analysis of great spotted kiwi (roroa, *Apteryx maxima*) occupancy and detection probability.

Application	Category	Name	Description
Grid cell (probability of occupancy and probability of detection)	Climatic	Rain	Mean annual rainfall
		Temp0	Mean annual ground level temperature
		Temp10	Mean annual temperature, 10 cm below ground level
		SMD	Mean annual soil moisture deficit
	Elevation	EleM	Mean elevation
		EleSD	Standard deviation of elevation, an indicator or ruggedness
	Land-cover	BareGround	Proportion of bare ground land-cover type
		ExoticWoody	Proportion of exotic woody land-cover types
		FarmedGrass	Proportion of farmed grass land-cover types
		SubAlpineScrub	Proportion of sub alpine scrub land-cover types
		TallTussock	Proportion of tall tussock land-cover types
		Other	Proportion of other land-cover types
		NativeWoody	Proportion of native woody land-cover types
Recorder-night (probability of detection only)		Proportion night	Proportion of night surveyed
		Location-topography	Location topography
		Survey	Survey year

levels of the New Zealand Soil Classification, the brown and podzol types found throughout the roroa range are predominantly influenced by climate rather than rock type (Hewitt 2013), and so neither geology nor soil type were included as covariates in the occupancy analysis. For detection probability, recorder-night specific variables of location-topography, year, and proportion of night analysed were also considered as potential covariates. The raster input layers for the variables that appear most important for modelling occupancy are shown in Appendix 2.

Occupancy and detection probabilities were modelled as functions of potential covariates using the logit link function (Appendix 3). There are a very large number of models that could be fitted to the data if all possible combinations of predictor variables are considered simultaneously for both occupancy and detection components, so a 2-stage model selection strategy was used. In Stage 1, a set of variables was identified which appeared to be most important for each of the components while maintaining a general model structure (or structures) for the other component. Variable importance was identified on the basis of summed AIC (Akaike Information Criterion) model weights (Anderson 2008). In Stage 2, all combinations of the most important variables identified in Stage 1 were considered for both components simultaneously. A total of 165 combinations of variables for both occupancy and detection were considered in Stage 2 model selection. AIC was again used as the model selection metric (Appendix 3).

The probability of roroa occupancy in both surveyed and unsurveyed grid cells was predicted using the Stage 2 models and mapped. 95% confidence intervals for the estimated occupancy probabilities were calculated using model-averaged values. Univariate plots were drawn to show the relationship between each variable considered in Stage 2 of model selection and model-averaged estimated detection probability and occupancy probability.

RESULTS

A total of 20,505 roroa calls were identified, 63% of them male. The number of calls by both males and females is similar throughout the night, other than the last decile before dawn (Fig. 3).

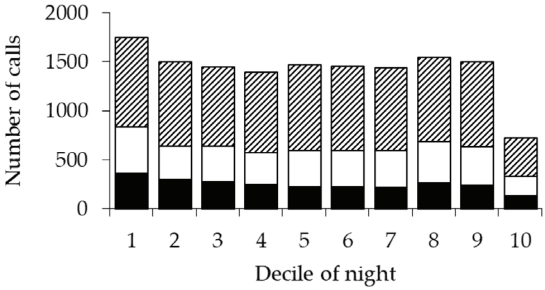

Figure 3. The timing of great spotted kiwi (roroa, *Apteryx maxima*) calls (n = 16,728) throughout the night as determined by acoustic recorders in this survey. Black bars show the number of duets involving both sexes, white the number of female only calls, diagonal stripes the number of male only calls. Over the year, night length (from 30 minutes after sunset to 30 minutes before sunrise) varies from 7 h 54 mins to 13 h 50 mins; to account for this seasonal variation, nights were divided into deciles, so each decile varied by about 35 minutes between season extremes. Only nights in which recordings were made for the entire night were included in this analysis.

Roroa distribution and call rates

We found roroa in six discrete areas. The total area occupied by roroa was 848,000 ha consisting of: i) 300,000 ha in NW Nelson, which included 10,000 ha occupied by the kiwi reintroduced to the Flora Valley area; ii) 112,000 ha in the Westport region; iii) 194,000 ha in the Paparoa Range; iv) 222,000 ha in the Arthur's Pass-Hurunui region; v) 8,400 ha in the Nina Valley (translocated population) and vi) 11,200 ha at Rotoiti (translocated population) (Fig. 4). Over most of this distribution, call rates were less than 3 calls/h, but in NW Nelson there was a 'core' area of 101,000 ha (12%) with call rates exceeding 3 calls/h at many locations. This 'core' extended from the west coast, through Gouland Downs to Boulder Lake in the east and from Kahurangi Point in the north to the Grindley Range in the south. Call rates exceeding 3 calls/h were rarely recorded in other regions (Fig. 4). There were large areas within the range shown in the Kiwi Recovery Plan (Fig. 1), in which roroa were not detected.

Probability of roroa occupancy and detection

The predicted probability of roroa occupancy and the width of the 95% confidence interval on that estimate were mapped for each 5 x 5 km grid cell and compared to locations at which we had placed recorders used in the analysis (Fig. 5). The probability of occupancy was highest in NW Nelson with narrow confidence intervals (i.e. less uncertainty) on those estimates. Roroa were found through much of this region, but to the south and east of this region, detection was more patchy. In parts of the Kiwi Recovery Plan's NW Nelson range (Fig. 1), the predicted probability of occupancy was lower and roroa were not found.

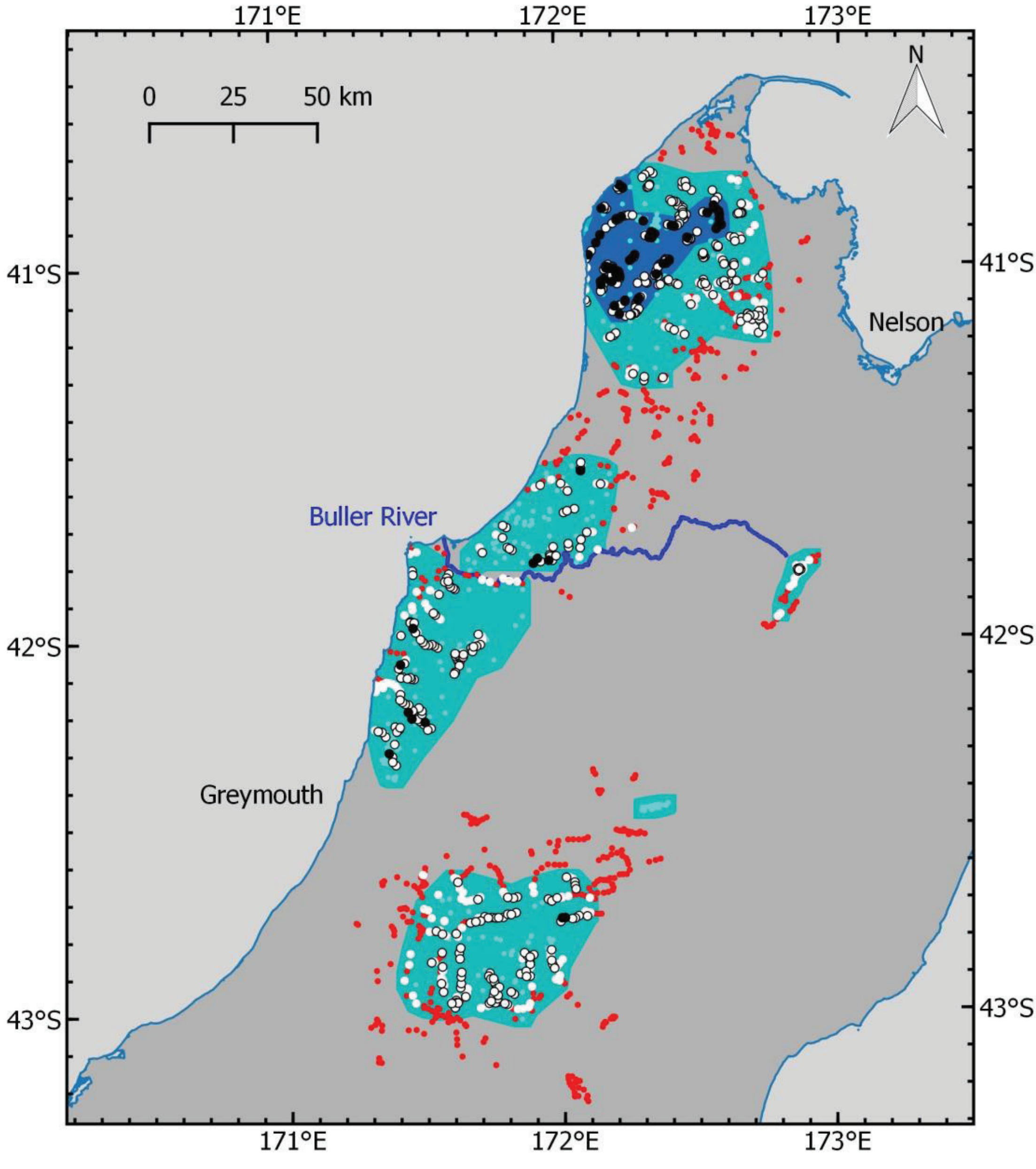

Figure 4. Locations of acoustic recorders and incidental records (2012–2021) used to determine the great spotted kiwi (roroa, *Apteryx maxima*) distribution. Black spots, call rates exceeding 3.0 calls/h; white spots bordered black, call rates of 0.3–3.0 calls/h; white spots, call rates less than 0.3 calls/h. Red spots show acoustic recorder locations at which roroa were not detected. Pale blue spots show locations with presence records treated as incidental; these were not used to calculate call rates. The core area in which many acoustic recorder locations had call rates exceeding 3 calls/h is shown by dark blue shading; the area in which call rates were lower, or roroa were detected but without call rates, is shaded turquoise.

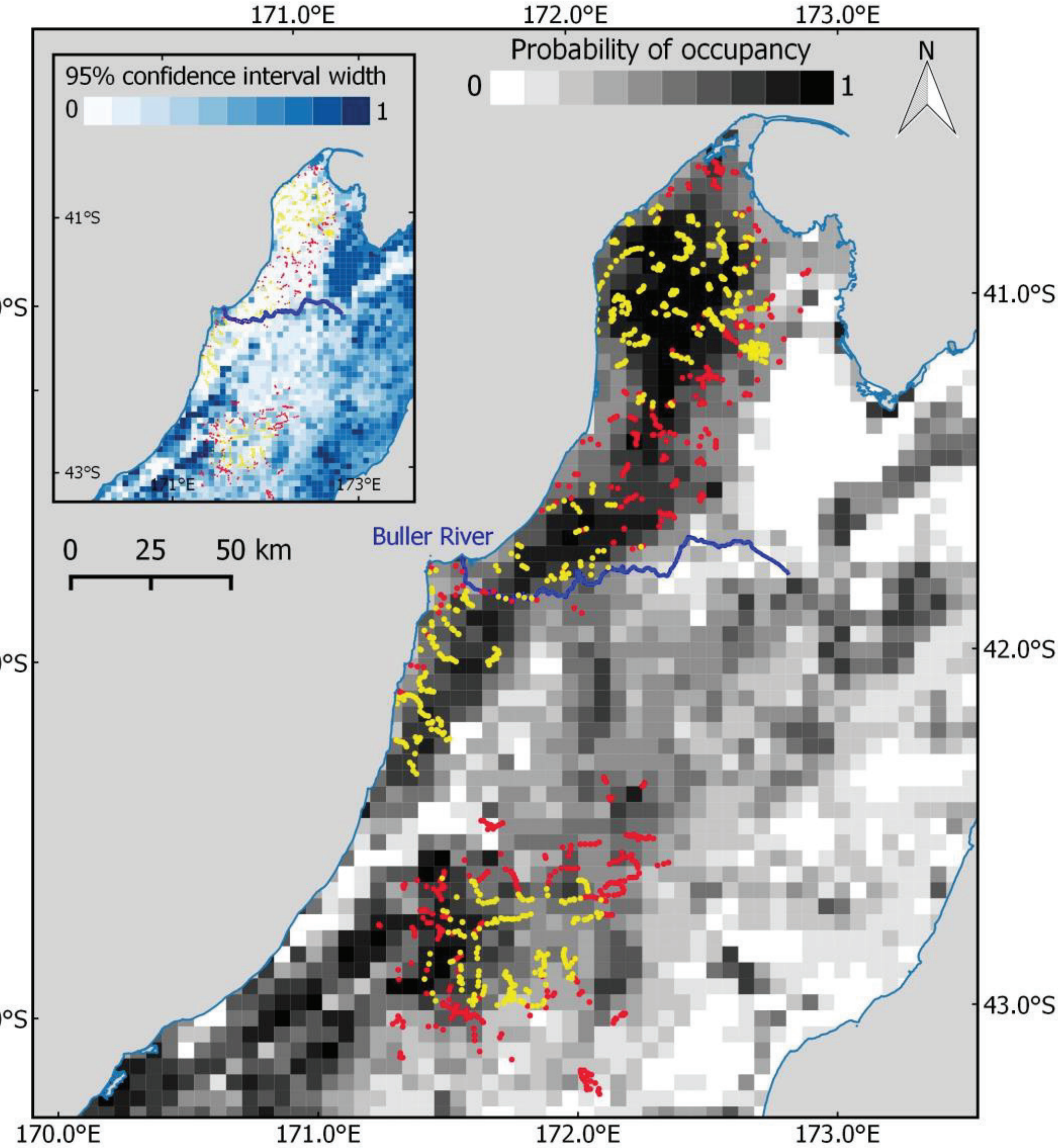

Figure 5. Predicted probability of great spotted kiwi (roroa, *Apteryx maxima*) occupancy of 5 x 5 km cells (main map), with width of 95% confidence interval for predicted values (inset). The locations of acoustic recorders used for occupancy modelling are also shown; roroa were detected at yellow spot locations, but not at red spot locations. Incidental detection records and acoustic recorder results analysed after August 2020 were not used for occupancy modelling, and are not shown.

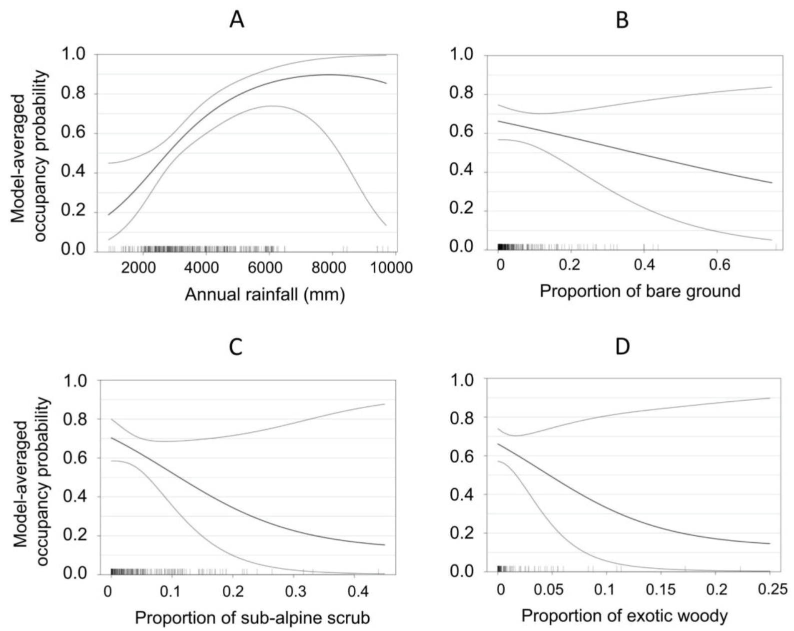

Figure 6. Univariate plots with 95% confidence intervals of relationship between model-average great spotted kiwi (roroa, *Apteryx maxima*) occupancy probabilities and (A) annual rainfall, (B) bare ground, (C) sub-alpine scrub and (D) exotic woody vegetation, with all other variables set to observed mean. Tick marks on the x-axis indicate the observed values for each variable.

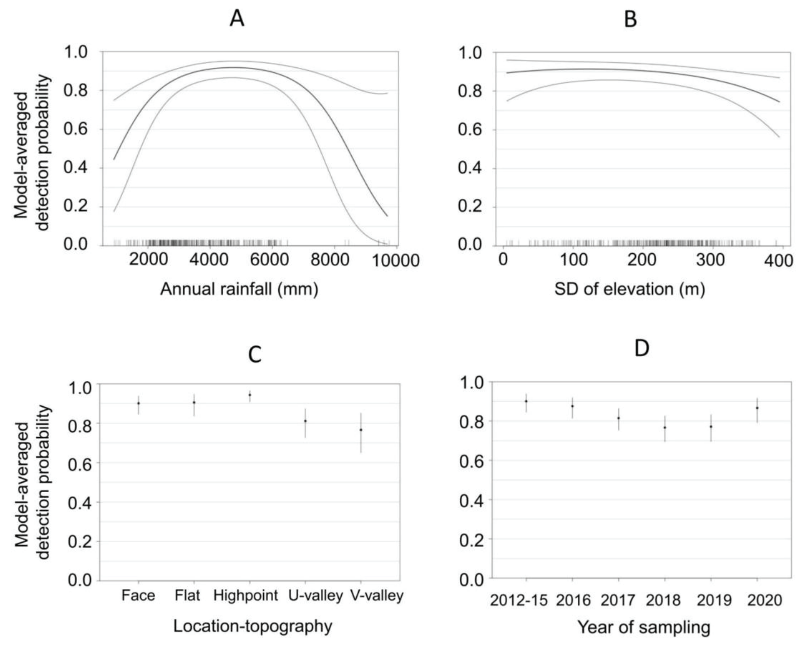

Figure 7. Univariate plots with 95% confidence intervals of relationship between model-average great spotted kiwi (roroa, *Apteryx maxima*) detection probabilities and (A) annual rainfall, (B) standard deviation (*sd*) of elevation, an indicator of ruggedness (C) location-topography, and (D) year of sampling. Tick marks on the x-axis indicate the observed values for continuous variables.

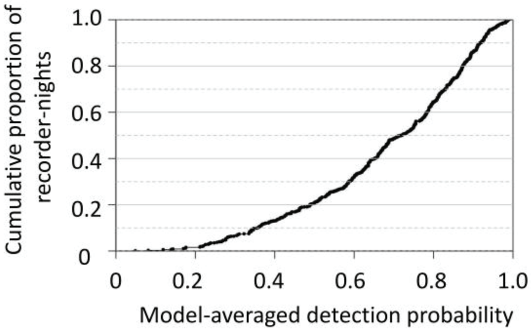

Figure 8. Great spotted kiwi (roroa, *Apteryx maxima*) detection probability is calculated for each acoustic recorder-night and is shown as a plot of the cumulative proportion of recorder-nights against model-averaged detection probability.

For example, around Karamea Bend, roroa were not detected despite 31 recorder-nights analysed. However, there is a band between approximately latitude 41.35°S (north of the Little Wanganui River) and latitude 41.53°S (the Mokihinui River) in which roroa were not detected although the modelling suggests a relatively high probability of occupancy. This gap, which is about 25 km wide, apparently separates the NW Nelson roroa from those in the Westport region. The Westport region north of the Buller River has a high probability of occupancy with narrow confidence intervals for the prediction. Roroa were detected west of 172.18°E but not, with one isolated exception, east of this longitude. In the Paparoa Range, probability of occupancy is highest in the middle, decreasing towards the coast and inland, mostly with narrow confidence intervals. Roroa were detected throughout this region. In the Arthur's Pass-Hurunui region, probability of occupancy declines from west to east and is more variable than other regions, and confidence interval widths are more variable, generally wider. However, roroa were detected extensively, including in areas with lower probability of occupancy.

In some places that we did not survey because they are outside the range shown in Fig. 1, the modelling predicts high occupancy probabilities for roroa: i) parts of the Richmond Range; ii) the Victoria Range; iii) the mountains north of the Awatere River; and iv) south through the western Southern Alps in northern Westland (Fig. 5).

Univariate plots of the variables that appear most important for modelling occupancy show that roroa occurrence in a cell appears to increase with increasing mean annual rainfall (Fig. 6A) and decrease as the proportion of the cell covered in bare ground, sub-alpine scrub or exotic woody vegetation increases (Fig. 6B–D). Other variables, including elevation, appeared to have relatively little effect on roroa occupancy.

Univariate plots of the variables that appear most important for probability of detection show detection probability: is highest in occupied cells with annual rainfall around 4,000 mm (Fig. 7A); decreases as elevation standard deviation, a measure of topographic ruggedness, increases (Fig. 7B); and is lower when acoustic recorders are deployed towards valley bottoms compared to sites classified as highpoints, faces or flat land (Fig. 7C). In addition, detection probability appears to be lower in 2018 and 2019 (Fig. 7D), which may reflect greater sampling in the more rugged terrain of the Arthur's Pass-Hurunui region in those years (Fig. 2). Other variables considered individually appeared to have little effect on detection probability.

Eighty percent of recorder-nights had model-averaged, single-night detection probabilities greater than 0.5 (Fig. 8). When detection probability is 0.5, 3.3 nights recording are needed to be 90% confident that if roroa are present they will be detected ($0.5^{3.3} = 0.1$). Overall, 73% of sampled cells had more than 3.3 recorder-nights. Cells with fewer than 3.3 recorder-nights were scattered throughout the range. Only 5% of recorder-nights had a detection probability less than 0.28. At this detection probability, seven nights of recording will give 90% certainty of detecting roroa if they are present. Overall, 45% of surveyed cells had more than seven recorder-nights. These analyses give high confidence in the broad pattern of the roroa distribution. Nevertheless, sampling effort was not uniform and some cells were not sampled either because of practicalities of access or because they were outside the regions in which roroa had been reported. This could have affected detection probability.

DISCUSSION

Roroa distribution

This survey indicates a roroa distribution of 848,000 ha. Roroa were not detected in several areas within the Kiwi Recovery Plan range shown in Fig. 1. We have high confidence in the roroa distribution derived from acoustic recorders (Fig. 4), because of the high probability of detection. This was achieved by placing recorders for good listening coverage, and sampling intensively where roroa density is likely to be low around the edge of the distribution.

The 848,000 ha distribution we determined is larger than the 800,000 ha estimated in 2015 (Innes *et al*. 2015). Since the 2015 estimate excluded areas where the population was thought to be extremely sparse and non-viable, we think it unlikely that there has been an increase in area occupied. Indeed, there is evidence that the distribution has contracted in the last 30 years. Between latitudes

41.53°S and 41.35°S (the Mokihinui River and north of the Little Wanganui River) there was 45 h recording at 26 locations as part of the Kiwi Call Scheme. Roroa were detected at four sites, all west of the Radiant Range within 10 km of the sea. These detections were made by six different people in 1992–1993 (Department of Conservation *unpubl. data*). Between these latitudes we placed acoustic recorders at 71 locations, analysed 1,300 h of recordings and detected no roroa. It appears roroa have been absent between the NW Nelson and Westport regions to the east of the Radiant Range area for many years, and in the last 30-40 years this gap in the distribution has expanded west to the sea. Between 1993 and 1996, roroa were recorded at ten locations in the Hope, Kiwi, and Doubtful Valleys (Arthur's Pass-Hurunui region) as part of the Kiwi Call Scheme (Department of Conservation *unpubl. data*). In 833 hours of recordings analysed from 30 locations in these valleys, we detected no calls. Given our effort and probability of detection (Fig. 8), it seems unlikely that differences in methodology would be the explanation. Furthermore, a 2008 intensive survey in the Hope and Kiwi River valleys, using certified kiwi dogs during the day and passive and solicited call surveys at night, found no evidence of roroa (J. Fraser & C. Rickard *pers. comm.*). Our modelling shows the area has a moderate probability of occupancy. Elsewhere, a pair of kiwi were recorded in the Puketeraki Range in 1993 (Department of Conservation *unpubl. data*), but we did not detect any calls in 184 hours analysed. This area also has a predicted moderate probability of occupancy. Conversely, in the 'Goldfields' gullies flowing north into the Aorere River, and in the mid reaches of the Crooked River we detected roroa where they have not been reported previously, but there was little listening in these areas in the past and our finds probably reflect greater sampling effort.

Rainfall was consistently important in the occupancy modelling, with lower predicted probability of occupancy in cells with lower annual rainfall (Fig. 6A). McLennan & McCann (2002) considered that the abundance of stoats and possums was higher in areas with lower rainfall, which impacted on roroa abundance and consequently, the distribution of roroa had contracted into areas of higher rainfall. However, given that stoats occur in extremely wet (>6,000 mm rain/year) conditions in parts of Westland and Fiordland (King & Murphy 2005), the impact of rainfall may be different, for example on food availability as soil invertebrates are likely to be scarce and difficult to obtain in dry areas. Food availability is also likely to be limited in areas of bare ground and rock, and in sub-alpine scrub where the ground will be frozen for long periods, land-cover classes identified to be important in the occupancy modelling.

Two areas of difference between the observed distribution and the probability of occupancy map are notable (Fig. 5). The reason why roroa were not found between NW Nelson and Westport regions (Fig. 4), despite a high modelled probability of occurrence, is unexplained. Rock types (Rattenbury *et al.* 1998) and soil groups (Hewitt 2013) within this area are also found either side of it, and there are no obvious physical barriers to roroa movement. Predation is another factor not included in our modelling, but spatially-defined predator numbers or indices are not available. The distribution of roroa in the Arthur's Pass-Hurunui region also appears anomalous, with roroa widespread to the east of the main divide despite rainfall and modelled probability of occurrence being comparatively low (Fig 5). This may reflect the greater effort invested in predator control in some of the eastern valleys compared with those in the west (Department of Conservation 2021), and we heard anecdotal historic reports of roroa mortality in leg-hold traps set for possums on the more accessible western edge of the range.

NW Nelson core area

Call rates commonly exceeded 3 calls/h in a 101,000 ha area in NW Nelson, comprising only 12% of the roroa distribution. The maximum call rate in this area was 13.8 calls/h. Call rates provide only a relative indication of abundance, but call rates less than 0.3 calls/h were found through much of the rest of the distribution (Fig. 4), suggesting that roroa are relatively sparse over much of their distribution. McLennan & McCann (2002) also found higher call rates in northern NW Nelson than elsewhere and concluded that this area is the stronghold of the species, supporting about 55% of the total roroa population.

Theory suggests that population size and viability of edge-sensitive species are driven by the area and shape of 'core' habitat fragments, and modelling indicates that irregularly-shaped fragments consistently reduce the population size of core-dwelling species (Ewers & Didham 2007). Indeed, habitat loss and fragmentation are considered to be the main cause of extinction and population decline of many threatened species globally (Wilson *et al.* 2016; Herse *et al.* 2018). Maximizing core habitat area rather than total habitat area may be key to achieving conservation goals (Herse *et al.* 2018). The higher roroa population density in NW Nelson may reflect that the habitat is less fragmented than elsewhere and is largely surrounded by unmodified habitat. The Arthur's Pass–Hurunui region differs in that it is dissected by grassy valleys, the habitat of ferrets (*Mustela furo*) (Clapperton & Byrom 2005), and high mountain ranges. These create a high edge-to-area ratio which will increase vulnerability to localised extinction (McLennan & McCann 2002). The Paparoa Range and Westport regions are less fragmented and lack the high peaks of the Arthur's Pass–Hurunui region but have a higher edge-to-area ratio than NW Nelson. All regions, except the NW Nelson core, are surrounded by modified habitats which generally provide little cover for roosting and, at least historically, posed risks from dogs and leg-hold traps.

Management implications

Given the extent and the high probability of detection in this survey, it can be used with confidence to guide roroa management. The identification of core and fringe areas provides information to help prioritise predator control. Focusing predator control on the high call rate core of NW Nelson is likely to benefit the most kiwi per hectare, and if high predicted probability of occurrence indicates better conditions for roroa, this population may also be more resilient. However, management is required across all the regions to maintain genetic diversity (Taylor *et al*. 2021) particularly as roroa have relatively high genetic diversity compared to other kiwi species (Ramstad *et al.* 2010). Management of areas with lower call rates that have not had predator control is particularly urgent, as these populations will contain a higher proportion of old kiwi due to low recruitment. These areas may also have greater potential for population increase than areas with higher call rates which may be closer to carrying capacity. Restoring connectivity between the NW Nelson and Westport populations, which has high probability of occupancy, is desirable to maintain gene flow, particularly as evidence of isolation by distance in roroa has been identified. To avoid disrupting genetic patterns arising from isolation by distance, predator control that allows natural expansion is the preferred management tool to re-establish roroa populations (Taylor *et al*. 2021). In addition, the alternatives of translocation or ex-situ management are challenging and costly (Toy & Toy 2020; Toy & Toy 2021a; Department of Conservation 2021).

Additional survey should focus on areas that were little sampled and in which roroa were not found such as parts of the eastern Paparoa Range and Westport regions. We did not survey inland of Ross and parts of the Victoria Range because they are outside the presumed roroa range (Fig. 1) but they have high predicted probability of occurrence. Any roroa in these areas would be isolated remnant populations, likely with unique genetic diversity. Shepherd & Lambert (2008) indicate that the historical range of roroa was restricted to the northwest of the South Island. This does not include the Richmond Range or the mountains north of the Awatere River, so these areas are not a priority for survey despite a high predicted probability of occurrence.

The results of this study can be used in the design of future roroa surveys. For example, topography affects probability of detection (Fig. 7B) and should be taken into account in selecting recorder locations, a result also found by Castro *et al.* (2019) in less rugged terrain. Locations with low probability of detection require greater recording effort (MacKenzie *et al*. 2018), for example, low density populations. Since call rate is similar throughout the night (Fig. 3), probability of detection will be the same recording all night as for selected hours over several nights.

Existing roroa monitoring consists of two long-term territory mapping projects (Robertson *et al*. 2005) and the Nationwide Kiwi Call Count Monitoring Scheme which counts at six sites (Colbourne *et al*. 2020). Neither approach is sufficiently widespread to identify changes in roroa distribution. Such changes are most likely in fringe areas with low call rates, as these are likely to be most susceptible to stochastic local extinction. An additional wider network of acoustic recording focused on these fringe areas and using a subset of the locations used in this study could address this.

Progress with the study was communicated to roroa managers developing the roroa species plan (Department of Conservation 2021). Our results provide a reliable description of roroa distribution and relative abundance to use as a basis for delivering the Kiwi Recovery Plan and against which to compare future distribution and relative abundance patterns.

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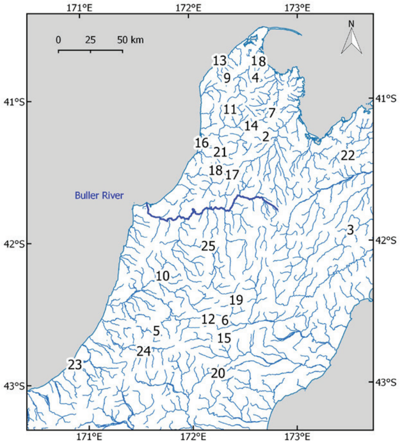
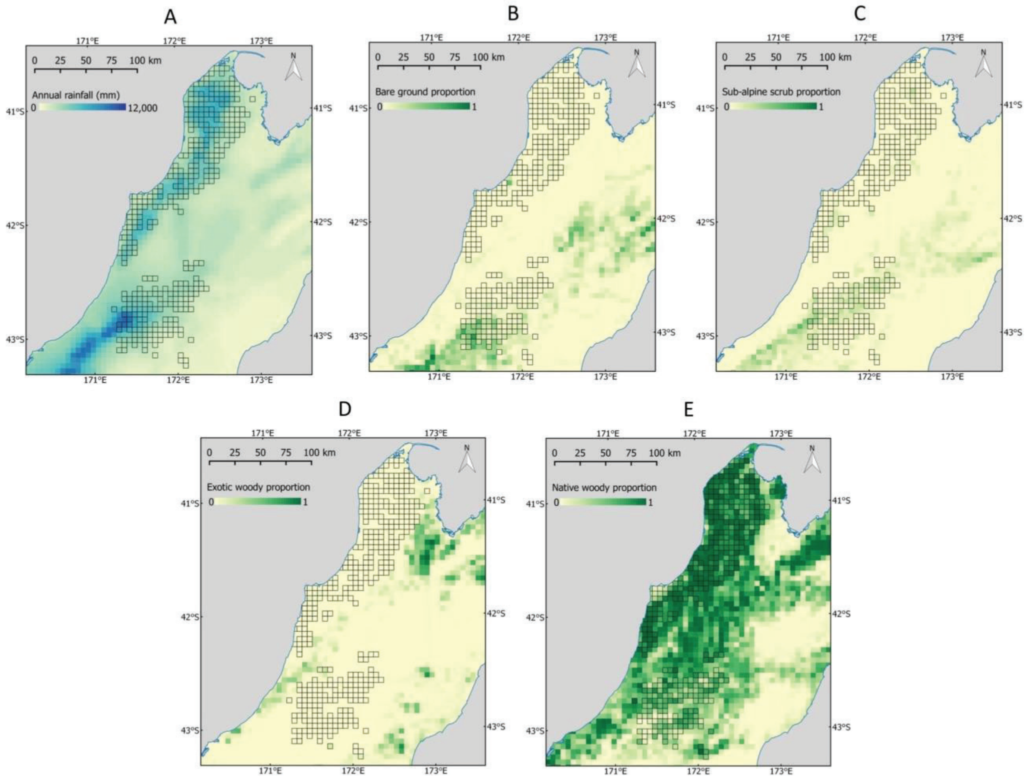
APPENDIX 1. Approximate locations of places referred to in text. 1, Aorere River; 2, Arthur Range; 3, Awatere River; 4, Boulder Lake; 5, Crooked River; 6, Doubtful River; 7, Flora Valley; 8, Goldfields gulleys; 9, Gouland Downs; 10, Grey Valley; 11, Grindley Range; 12, Hope River; 13, Kahurangi Point; 14, Karamea Bend; 15, Kiwi River; 16, Little Wanganui River; 17, Matiri Range; 18, Mokihinui River; 19, Nina Valley; 20, Puketeraki Range; 21, Radiant Range; 22, Richmond Range; 23, Ross (township); 24, Taipo River; 25, Victoria Range.



APPENDIX 2. Raster input layers for variables used in great spotted kiwi (roroa, *Apteryx maxima*) occupancy modelling. A, annual rainfall; B, bare ground; C, sub-alpine scrub; D, exotic woody land cover classes. Native woody (E) is the reference land cover class (Appendix 3). Cells with black borders had acoustic recorder-nights used in the analysis.



APPENDIX 3. Details of occupancy modelling

Variables: Climatic, elevation and land-cover variables were considered as potential covariates for great spotted kiwi (roroa, *Apteryx maxima*) occupancy and detection. Climatic information covering the period 1981–2010 was obtained from the National Institute of Water and Atmospheric Science (NIWA) at 500 m resolution. This information is interpolated from an irregularly spaced network of climate stations using methods described in Wratt *et al*. (2006). The information was aggregated to the defined grid resolution (5 km) by taking mean values. Seasonal climatic variables were available, but were highly correlated with the annual variable, so the annual values were used. Elevation was extracted from the New Zealand Digital Elevation Model (South Island) projected at 25 m resolution. For each grid cell, the mean and standard deviation (SD) of the elevation values were calculated for use in the analysis. The SD of elevation was interpreted as a measure of ruggedness. Land-cover information was obtained from the Landcare Research New Zealand land-cover database v5.0. We amalgamated the 34 land-cover classes used in the database, into seven classes (Table 2), and calculated the proportion of each cell in each category so that the sum of the proportions equalled 1.0. Thus, land-cover variables were treated as a single predictor variable for each cell. This was necessary as considering each variable separately would have greatly increased the number of possible models that could be fitted to the data. As the land-cover proportions sum to 1.0, they are not independent, and therefore the Native Woody variable was not used in any analyses, essentially treating it as the reference land-cover category. Thus, when all of the other land-cover variables equal zero, the model results should be interpreted as being applicable to a cell with 100% Native Woody land-cover. Estimated effect sizes for the other land-cover classes were interpreted as the difference between a cell with 100% land-cover of that class compared to a cell with 100% Native Woody land-cover.

Location-topography, year, and proportion of night were considered as additional potential covariates for detection probability. Location-topography was assessed manually from topographic maps using the categories: *highpoint*, representing spurs, ridges, peaks more than 100 m above surrounding land; *face*, representing slopes; *valley*, representing points within 100 vertical metres of a V-shaped valley floor; *bottom of slope*, representing points within 100 vertical metres of the bottom of a slope in a U-shaped valley or foot of a range; *flat*, representing land without major slopes or gullies. Location-topography and year were both used as categorical covariates, while proportion of night was a continuous variable (with values between 0–1). Year of survey was included because different parts of the range, probably with different population densities, were surveyed in different years, and roroa abundance is expected to affect detection probability. Because of the low survey effort in 2012–2015, these years were combined into a single category (i.e. the levels of the year of survey variable are 2012–2015, 2016, 2017, 2018, 2019, and 2020).

Modelling: Climatic and elevation variables were checked for correlation. Annual values for Temp0 and Temp10 were highly correlated to each other, and both were highly correlated with mean elevation. Therefore, three base models for detection and occupancy probability were considered, each containing just one of these three variables in addition to rain, soil moisture deficit (SMD), elevation SD and land-cover.

Occupancy and detection probabilities were modelled as functions of potential covariates using the logit link function (e.g. logistic regression):

$$logit(\theta_i) = \beta_0 + \beta_1 x_{1,i} + \beta_2 x_{2,i}$$

where θi is the probability of interest at cell or recorder-night i, x_1 and x_2 are predictor variables and β_0, β_1 and β_2 and are the regression coefficients or parameters to be estimated. For any given model, the number of predictor variables and regression coefficients may vary, and will not always equal two.

Inclusion of continuous-valued variables in a model assumes a linear relationship, on the scale of the logit link function, between the variable and parameter of interest. However, a parabolic, or quadratic, relationship may be more appropriate for species with ecological preference for certain climatic or elevation conditions, such as a particular elevation band. Therefore, some models were considered that included as covariates both the variable values, and the square of the variable values (i.e. x and x^2). Squared-variable values were only included in a component if the corresponding unsquared values were also included.

A 2-stage model selection strategy was used. In Stage 1, variable importance was identified on the basis of summed AIC (Akaike Information Criterion) model weights (Anderson 2008). For models that included the square of a variable, a correction was made to enforce inclusion of a linear term for a predictor variable if a quadratic relationship was used. If S_L and S_Q are the summed AIC weights for the linear and quadratic terms respectively, then, because the linear term always must be included with the quadratic term, S_L must be $\geq S_Q$. If $S_Q > 0.5$, then a quadratic relationship for that variable was included in Stage 2 of the model selection. If $S_Q < 0.5$, the adjusted value of S_L, S_L^* was considered, where:

$$S_L^* = \frac{S_L - S_Q}{1 - S_Q}$$

If $S_L^* > 0.5$, a linear relationship for the variable is used in Stage 2, and if $S_L^* < 0.5$, that variable was not considered in Stage 2 of the model selection.

Summed AIC model weights for roroa occupancy probability were consistent across all three detection probability base models (Table A3-1). Linear and quadratic terms for rainfall, linear SMD, and land-cover variables were identified as variables to consider for occupancy in Stage 2 modelling. Results for the detection probability component were also consistent across the three occupancy probability base models (Table A3-1). Linear and quadratic terms for rainfall, SMD and the standard deviation of elevation, land-cover, location-topography and year were identified as variables for detection probability in Stage 2 modelling.

In Stage 2 of the occupancy model selection procedure, the 165 models were ranked based on ΔAIC (Table A3-2). The eight models highest-ranked on the basis of AIC, all had the same structure for detection probability:

logit(p)=Rain+Rain²+SMD+SMD²+EleSD+EleSD²+Land-cover+location_topography+Year

but varied in the combination of variables included for occupancy probability (Table A3-2). Rain, Rain^2 and Land-cover appear the most important for modelling occupancy, but given there is uncertainty regarding the most appropriate combination of variables, model-averaging was used to make final inferences about roroa occupancy.

The relationship between each variable considered in Stage 2 of model selection and model-averaged estimated occupancy probability and detection probability was examined using univariate plots (Fig. 6 & 7). In this analysis, values for the predictor variables that were not the subject of the plots were set to 0, or a reference category in the case of a categorical variable (e.g. 'face' for location-topography and '2012–2015' for the year variables). Use of different reference categories may change absolute values but has little effect on the shape of the curves.

All analyses were conducted using the RPresence package for fitting occupancy models in R.

Table A3-1. Occupancy modelling, Stage 1, in which variables for use in Stage 2 were selected. The table shows summed model weights for each variable: for great spotted kiwi (roroa, *Apteryx maxima*) detection probability, using three different base models for occupancy probability; and for occupancy probability, using three base models for detection probability. Summed model weights have been adjusted for linear terms (i.e. S_L^*). Variables selected for use in the Stage 2 models are indicated by a X.

	Focal probability							
	Detection				Occupancy			
	Occupancy model			Stage 2	Detection model			Stage 2
Variable	**Base 1**	**Base 2**	**Base 3**		**Base 1**	**Base 2**	**Base 3**	
Rain	0.28	0.27	0.29	X	1.00	1.00	1.00	X
Rain^2	0.98	0.97	0.99	X	0.76	0.74	0.73	X
Temp0	0.28	0.20	0.31	-	0.51	0.49	0.50	-
Temp0^2	0.16	0.11	0.19	-	0.47	0.39	0.58	-
Temp10	0.17	0.18	0.17	-	0.07	0.09	0.05	-
Temp10^2	0.43	0.55	0.37	-	0.03	0.04	0.03	-
SMD	0.63	0.58	0.66	X	0.68	0.63	0.70	X
SMD^2	0.93	0.94	0.92	X	0.30	0.26	0.34	-
Ele	0.04	0.04	0.04	-	0.06	0.08	0.05	-
Ele^2	0.02	0.01	0.02	-	0.06	0.06	0.06	-
Ele SD	0.92	0.94	0.91	X	0.31	0.30	0.32	-
Ele SD^2	0.94	0.93	0.95	X	0.18	0.19	0.17	-
Land-cover	1.00	1.00	1.00	X	0.93	0.92	0.93	X
Proportion night	0.31	0.31	0.31	-	-	-	-	-
Location-topography	1.00	1.00	1.00	X	-	-	-	-
Year	1.00	1.00	1.00	X	-	-	-	-

Table A3-2: Summary of Stage 2 of the occupancy modelling, model selection procedure, showing the eight models ranked highest on basis of ΔAIC. Column headings are the relative difference in AIC (ΔAIC), AIC model weight (*w*), number of parameters (*K*) and twice the negative log-likelihood (-2*l*). The detection component of the models included Rain, $Rain^2$, SMD, SMD^2, Ele SD, Ele SD^2, land-cover, location-topography and year as predictor variables.

Occupancy	**ΔAIC**	***w***	***K***	**-2*l***
Rain+$Rain^2$+Land-cover	0.00	0.32	31	2,571.22
Rain+Land-cover	0.96	0.20	30	2,574.18
Rain+$Rain^2$+SMD+Land-cover	1.03	0.19	32	2,570.24
Rain	2.25	0.10	24	2,587.47
Rain+SMD+Land-cover	2.95	0.07	31	2,574.16
Rain+$Rain^2$	4.19	0.04	25	2,587.4
Rain+SMD	4.25	0.04	25	2,587.47
Rain+$Rain^2$+SMD+SMD^2	6.04	0.02	26	2,587.26