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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 habetween 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 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 prehuman 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: \geq 3 calls/h, 0.3 to 3 calls/h, or \leq 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.

Region		Acoustic recorde	Number of		
	Locations	Recorder-nights analysed	Hours analysed	locations with incidental records	
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	

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.

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

Application	Category	Name	Description				
Grid cell Climatic (probability of occupancy and probability of	Climatic	Rain	Mean annual rainfall				
		Temp0	Mean annual ground level temperature				
		Temp10	Mean annual temperature, 10 cm below ground level				
detection)		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				

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

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).

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



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.

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 modelaveraged, 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 edgeto-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-toarea 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 reestablish 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 landcover database v5.0. We amalgamated the 34 landcover 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. Locationtopography 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 θ_i 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.

Å 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 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:

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

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 Δ AIC (Table A3-2). The eight models highest-ranked on the basis of AIC, all had the same structure for detection probability:

$logit(p) = Rain+Rain^2+SMD+SMD^2+EleSD+$ EleSD²+Land-cover+location_topography+Year

but varied in the combination of variables included for occupancy probability (Table A3-2). Rain, Rain² 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								
		Detec	tion			Occup	ancy		
	Occupancy model			Stage 2	Dete	Detection model			
Variable	Base 1	Base 2	Base 3		Base 1	Base 2	Base 3		
Rain	0.28	0.27	0.29	Х	1.00	1.00	1.00	Х	
Rain ²	0.98	0.97	0.99	Х	0.76	0.74	0.73	Х	
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	Х	0.68	0.63	0.70	Х	
SMD^2	0.93	0.94	0.92	Х	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	Х	0.31	0.30	0.32	-	
Ele SD ²	0.94	0.93	0.95	Х	0.18	0.19	0.17	-	
Land-cover	1.00	1.00	1.00	Х	0.93	0.92	0.93	Х	
Proportion night	0.31	0.31	0.31	-	-	-	-	-	
Location-topography	1.00	1.00	1.00	Х	-	-	-	-	
Year	1.00	1.00	1.00	Х	-	-	-	-	

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Table A3-2: Summary of Stage 2 of the occupancy modelling, model selection procedure, showing the eight models ranked highest on basis of \triangle AIC. Column headings are the relative difference in AIC (\triangle AIC), AIC model weight (*w*), number of parameters (*K*) and twice the negative log-likelihood (-2*l*). The detection component of the models included Rain, Rain², SMD, SMD², Ele SD, Ele SD², land-cover, location-topography and year as predictor variables.

Occupancy	ΔΑΙΟ	w	K	-21
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

When the lonely goose? Implications of a revised history of the lake and its surrounding vegetation for a radiocarbon age for the only South Island goose (*Cnemiornis calcitrans*) from the Pyramid Valley lake bed deposit, New Zealand

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Abstract: A high resolution chronology of deep water charophyte algal remains in the Pyramid Valley lake deposit, North Canterbury, South Island, New Zealand, records the presence and drainage of a previously unsuspected much larger (*c*. 50 ha) lake. The larger lake occupied the surrounding basin and the present lake (1 ha) was a semi-isolated embayment at its south-western margin. Fluctuating lake levels and its final drainage drove changes in the vegetation and hence in the habitats available for the avifauna recorded in the rich fossil record. A high precision radiocarbon age on the only South Island goose (*Cnemiornis calcitrans*) in the fauna coincided with the presence of lowland forest and not with the brief period when sedges and grassland colonised the newly exposed former lake bed. This suggests that the South Island goose was able to survive in different habitats through successive glacial-interglacial vegetation cycles. Information from other disciplines can be essential to interpreting both a fossil site and the circumstances surrounding the presence of a particular species in it.

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INTRODUCTION

The extinct flightless South Island goose (*Cnemiornis calcitrans*) is related to the Cape Barren goose (*Cereopsis novaehollandiae*) of southern Australia

(Oliver 1955; Worthy *et al.* 1997; Gill *et al.* 2010). Based on this relationship, the New Zealand bird has been assumed (Holdaway & Worthy 1997; Worthy *et al.* 1997; Worthy & Holdaway 2002) to have required the same short grass swards as its Australian relative, which avoids scrub and forest (Marchant & Higgins 1990). Worthy & Holdaway

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(2002) also assumed, based on the inferred habitat, that it shared the Australian bird's diet of grass and herbs (Marchant & Higgins 1990).

phylogenetic analogies Such can be inappropriate, however, especially when one of the taxa has colonised a different area, with different environments and different suites of potential predators, competitors, and food resources. Local examples are the extinct New Zealand harriers (*Circus* spp.), which had evolved the wing proportions of forest-dwelling, bird-eating, goshawks (Accipiter spp.). Despite their different proportions, habitat, and diet, the New Zealand harriers were undoubtedly harriers and not goshawks (Holdaway, in Worthy & Holdaway 2002). Similarly, there is no *a priori* reason why *Cnemiornis* geese should behave in the same way as Cereopsis does in its own environment. The relationship between the Australian and New Zealand geese is at generic level or above, not sister species like the harriers, and *Cnemiornis* confronted completely different suites of competitors and predators.

In addition to potential clues from phylogenetic relationships, evidence for the habitats of extinct taxa can be gained by secure association between species' presence and the contemporary а local palaeoenvironment. A glacial climate has prevailed for most of the past million years (Petit et al. 1999; Ehlers & Gibbard 2007), interspersed with relatively brief warm interglacials such as the present Holocene. Climatically driven changes in the New Zealand vegetation have been routinely (Worthy & Mildenhall 1989; Worthy & Holdaway 1993, 1994, 1995, 1996, 2000, 2002; Worthy 1994, 1997, 1998a, b, 2000; Worthy & Swabey 2002; Worthy & Grant-Mackie 2003) taken into account in discussions of fossil avifauna.

In broad terms, the Quaternary history of New Zealand's vegetation is regarded as well known, but there are still issues, and local details are sparse. Pollen-based models of the glacial vegetation include extensive grasslands and little forest in the South Island (Newnham et al. 2013), despite the diversity of forest birds endemic to the South Island (Gill et al. 2010). The prevailing views on past vegetation patterns means that much of the discussion on former habitats in the South Island has been predicated on an implied paucity of forest for most of the past million years. Fleming's (1962, 1979) reconstruction, with its extensive grasslands and ice caps, has become – with recent refinements (e.g. Newnham *et al.* 2013) – canonical. The goose is therefore seen as a relict, glacial grassland species confined to tiny areas of suitable habitat in the forest-dominated Holocene landscape, as has been proposed for the South Island takahe (Porphyrio hochstetteri), based on the tiny relict population's Fiordland habitat (Mills et al. 1984).

During the Holocene, grassland in New Zealand was limited to riparian strips and river beds, alpine meadows, and drought-prone areas of central Otago (McGlone 1988). If the South Island goose required short grasslands, its fossil remains should be found both where and, importantly, when there were grasslands in an area. However, their fossils are present in areas, such as North and South Canterbury, when and where the dominant Holocene vegetation was forest (Molloy *et al.* 1963; Burrows 1989; Holdaway & Worthy 1997; Wood et al. 2017). One such site is the Pyramid Valley lake bed deposit in North Canterbury (42° 58' 22.54" S, 172° 35′ 50.12″ E) (Fig. 1), whose rich fossil avifauna includes just a single South Island goose (Holdaway & Worthy 1997; Holdaway 2015).

To put its rarity at Pyramid Valley in context, a brief survey of published records of the South Island goose yielded a total of 14 individuals from north of South Canterbury, including the West Coast and Takaka areas (Worthy & Holdaway 1993, 1994, 1995, 1997). There was none among the 137 waterfowl individuals in the large (a total of 770 individuals) natural and archaeological avifaunas at Marfells Beach in Marlborough (Worthy 1998c). Twentyone have been recorded from South Canterbury (Worthy 1997), 43 from Otago (Worthy 1998b), and only two from Southland (Worthy 1998a).

The presence of a grassland goose at Pyramid Valley is anomalous because the site contains a diverse forest bird fauna (Holdaway 1990; Holdaway & Worthy 1997). Indeed, Holdaway & Worthy (1997) appealed to the unlikely and unsubstantiated presence of grassland and shrubland on the surrounding hills to explain the presence of a known grassland species, the New Zealand quail (Coturnix novaezelandiae), in the lake bed. The goose was one of eight species of waterfowl recorded from the deposit (Holdaway & Worthy 1997), including both aquatic and terrestrial species, but of these only the extant New Zealand shelduck (Tadorna variegata) is a grazer, known to require grassland (Williams 1971). Its remains from Pyramid Valley have not been radiocarbon dated.

Local events can, while being usually much more difficult to identify, modify the vegetation around a particular site on much shorter time glacial-interglacial cycles. scales than The possibility of significant local changes during the relatively brief history (Gregg 1972; Johnston 2014) of Pyramid Valley has never been considered. The environment around the lake over the past 5,000 years is thought to be one of the best known in New Zealand as a result of decades of analysis of the microfossils in the lake bed sediments (Deevey 1955; Harris 1955; Moar 1970; Gregg 1972; Burrows 1989) and interpretation of the avifauna preserved there (Holdaway & Worthy 1997).



Figure 1. Locations of sites for which radiocarbon ages on New Zealand geese (*Cnemiornis* spp.) are available. *Cnemiornis gracilis*: Zw, Zweiholen Passage, Gardners' Gut Cave. *Cnemiornis calcitrans*: MC, Metro Cave; OS, Omihi Stream cutting, State Highway 1; PV, Pyramid Valley; FF, Finsch's Folly pitfall cave.

Results of these studies supported a model in which Pyramid Valley was surrounded by lowland forest, growing to the water's edge (Eyles 1955), throughout the late Holocene (Burrows 1989) before the forest was destroyed by Polynesian fires (Moar 1970). As the 1 ha lake lacks an inlet stream, its maximum depth of *c*. 1 m is sustained by rainfall runoff from the surrounding hills and a few springs at its southern periphery. The springs depend on the local water table, and the outlet stream is small, intermittent, and deeply incised. There was no space for peripheral or riparian grassland. The lake bed now supports a vegetation of pasture grasses during long dry periods.

The lake has always been assumed to have been shallow and confined to its present basin. Moar (1970) suggested that the charophyte algae (Plantae: Charophyceae: Charales) that Deevey (1955) identified by their oospores in distorted cores from Pyramid Valley are typical of shallow, calcareous lakes such as that at Pyramid Valley, but could not provide a chronology because of the core distortion. However, New Zealand charophytes have since been shown to have narrow ecological ranges within a water body (Schwarz *et al.* 2002). All species require a water depth of at least 1 m over them and are usually found at water depths of 2–12 m (Schwarz *et al.* 2002). These depth requirements pose a problem for current interpretations of how the deposit developed and of its surrounding environment. Investigating the implications of this re-interpretation of the habitat of charophytes, with its attendant requirement for deep water, is important in interpreting the environmental history of the lake basin, and hence of the habitats of birds living there.

The lone Pyramid Valley goose represents a local source population of geese which seems, on the basis of the otherwise abundant large birds in the deposit, to have been small. If it was present at a time when there was grassland in the catchment, then that would support the hypothesis that the South Island goose was restricted to grassland and that "forest was not its preferred habitat" (Holdaway & Worthy 1997). To determine whether the goose's presence coincided with grassland, we developed a new detailed chronology of the lake's history and hence of changes in the surrounding vegetation. We also re-evaluated the local ecosystem in the context of the local topography and its tectonic and seismic history, and obtained a high precision radiocarbon date for the goose to align it with its contemporary habitat.

MATERIALS and METHODS Radiocarbon ages

Goose

The radiocarbon age for the goose (Canterbury Museum Av5406) was measured at the 14Chrono Laboratory, Queen's University, Belfast, UK, and the conventional age calibrated to calendar years using OxCal4.4 software (Bronk Ramsey 1995, 2001) referenced to the SHCal20 curve (Hogg *et al.* 2020). Bone collagen was extracted using a method based on that of Brown *et al.* (1988), but using a Vivaspin® filter cleaning method introduced by Bronk Ramsey *et al.* (2004).

Deposit age-depth model

AGJ obtained five ¹⁴C ages in addition to ages measured for the excavation in 2008 (Holdaway 2015) and four presented by Gregg (1972) for a total of 14. Using PAST Version 3.26b® (Hammer *et al.* 2001), mean calibrated (SHCal20) calendar dates were regressed against depth (cm) of the sample in the stratigraphy to relate subsurface features with the geologic age. In addition, a Bayesian age-depth model was generated using the same radiocarbon ages via the Deposition option in OxCal4.4 (Bronk Ramsey 2009), as a comparison to the regression models.

Palaeolimnology

Sediment cores

The Pyramid Valley site is protected under a Queen Elizabeth II National Trust Covenant. Permission was obtained from the covenant management committee and the landowners (the Hodgen family) for a 4×4 m excavation, which was undertaken in February 2008 (Holdaway 2015). Cores were obtained from the northern and western walls of the excavation pit (Holdaway 2015). The cores were taken by embedding two 100 × 100 mm aluminium angle extrusions into the sediment walls, one overlapping the other so that an almost square section of the sediment column was contained. The cores were cut free using monofilament nylon, depths marked and labelled, then wrapped in two layers of self-adhesive plastic vapour barrier, a layer of aluminium foil and a final outer layer of selfadhesive plastic. Both excisions yielded unbroken 1,500 mm cores with minimum distortion of the stratigraphy. Two supplementary "cores" were cut in the same way, with aluminium angle extrusions sized to make a final 1-cm square section. The cores were wrapped and frozen at -18°C until processing.

Charophyte sampling and analysis

Charophyte oospores in successive 1-cm³ blocks cut from main core were counted in water suspension. The gel-like nature of the sediment made it impossible to sieve the microfossils from the organic lake sediment. Each block was disaggregated in a few drops of distilled water in a Petri dish under a binocular microscope, with the sediment being stirred gently with a paint brush.

The oospores sometimes had to be separated from the remaining amorphous organic matter (AOM) using size 00 and 000 brushes. Identifiable specimens were counted once the disaggregated sediment had dried in the dishes as the AOM tended to obscure some of the oospores. Most samples contained only 5–10% inorganic material, mainly as individual quartz grains. Three 1-cm³ samples were taken for each lineal centimetre of the core, and the individual totals of oospores of *Chara globularis* and *C. australis* were recorded and averaged.

Each species was counted by dividing the sediment in the Petri dish into pie-segments with a brush and rotating the dish under the microscope until each section had been counted and the totals recorded. The larger charophyte oospores floated and were relatively straightforward to count. The much smaller *Nitella* oospores were difficult to remove from the sediment gel and were not included in the analyses. Totals for the two species were plotted against depth in the core and against the age-depth model dates for each sample.

Topography

A digital elevation model (DEM) at 5-cm resolution was generated from high resolution aerial photogrammetry, collected using a DJI Phantom Pro® quadcopter. The photogrammetry survey was flown by M. Cockcroft and A. Wandres, Department of Geology (now School of Earth and Environment), University of Canterbury, and the DEM was generated by Dr Wandres using Agisoft Photoscan[®] (now Metashape[®]). Ground control points for the photogrammetry survey were collected with a real-time-kinematic (RTK) GPS survey (Trimble R8 GNSS®) relative to a site benchmark at northern end of the present lake. The DEM was further cross-checked against an earlier roving RTK survey of the site collected by BD using the same RTK equipment. The site's lack of forest cover provided a relatively favourable GPS environment and horizontal accuracies are likely to be entirely within 2 cm, with minor variation depending on the detailed satellite geometry during the surveys.

Tectonic setting

An appreciation of the tectonic setting is fundamental to understanding the history of the Pyramid Valley lake site. The North Canterbury Fault and Fold Belt (NCFFB) is an area of intense deformation within the Pacific Plate of the New Zealand Plate Boundary, south of the Hope Fault (Pettinga et al. 2001; Litchfield et al. 2003). A key feature of the NCFFB is the Culverden Basin. which is appressed between the Hurunui Bluff Fault and the foothill ranges of the Southern Alps (Fig. 2). Pyramid Valley lies in an area of, generally, north and northwest-trending faults that mark the southwestern end of the Culverden Basin and where shortening rates may reach 3–5 m / 1,000 years (Nicol 1991; Nicol et al. 1994). Pettinga et al. (2001) referred to the westernmost, range front elements of this north-striking fault system as the West Culverden Fault Zone. At the southern end of the West Culverden Fault Zone, the Culverden Basin terminates at the Doctor's Dome, a domal uplift that exhumes basement greywackes of the Pahau subterrane of the Torlesse Supergroup (Nicol 1991; Nicol & Campbell 2001; Campbell et al. 2003; Rattenbury *et al.* 2006).

Along the western edge of Doctor's Dome, the Early Cenozoic rocks of the Eyre Group are partially truncated by westward thrusting on the Karetu thrust, forming the MacDonald Syncline. The Karetu Fault probably ruptured most recently 350 ± 60 yrs B.P., near simultaneously with linked faults further south, and as part of a centuries-long episode of uplift of the dome (Nicol & Campbell 2001).



Figure 2. Geology of the study area based on the Kaikoura and Christchurch 1:50,000 geological map sheets (Rattenbury *et al.* 2006; Forsyth *et al.* 2008). Inset shows the regional context of the study area at the southwest end of the Culverden Basin (CB).

North of Pyramid Valley, the left-lateral reverse Mason's Flat Fault forms as a footwall splay of the West Culverden Fault Zone. A Holocene earthquake on the Mason's Flat Fault has thrust Late Pleistocene and Holocene gravel fans eastward along a complex NW-striking fault trace. The timing of that earthquake is unknown (Barrell & Townsend 2012). The northward change from westward thrusting on the Karetu Fault to eastward thrusting on the Mason's Flat Fault is probably at least partially accommodated by the un-named east-west fault that truncates the Cenozoic stratigraphy on the northern edge of the Doctor's Dome and which is analogous to multiple east-west faults further south, including the Birch Fault (Campbell *et al.* 2012). East of Pyramid Valley, north-striking faults and folds repeat much of the Cenozoic stratigraphy, forming prominent ridges of the Weka Pass limestone and resulting in eastward thrusting on the Horsley Down Fault system. The southward extension of this fault system south of Hawarden is unclear (Barrell & Townsend 2012). North Canterbury is an active seismic area and the complex tectonic system, with its several known faults, has controlled the drainage patterns and the development of basins such as that which formerly contained Pyramid Lake. Individual earthquakes on the local fault lines may therefore have controlled the distribution of local vegetation by determining the presence and fates of impoundments, and hence of habitats for moa and other birds.

Pyramid Valley geology

Within all this complexity, Pyramid Valley is a lithologically controlled, north-trending valley on the western limb of a north-trending anticline, referred to here informally as the North Doctor's Anticline. The valley is developed between strike ridges of the Oligocene Weka Pass Formation to the east and the Miocene Mount Brown Formation of the Motanau Group to the west (Rattenbury *et al.* 2006). Although relatively simple at first glance, several aspects of the geomorphology are remarkable.

The Motunau Group underlying the Mt Brown Formation limestone doubles in thickness between the southern and northern parts of the study area at a location that coincides with a possible northside-upthrown, northeast-striking, thrust fault. The fault bounds the northern edge of Pyramid Valley lake and is so interpreted because its trace displaces a small, northwest-plunging valley and ridge a few tens of metres northeast of the lake. The trace is parallel to the Weka Pass Limestone and thus may represent bedding-parallel slip. The divergence of the Motunau group from the Weka Pass stone may be caused by depositional thickening against a presently west-dipping unconformity, which is locally reactivated as a bedding-plane fault. Alternatively, it may represent localised thickening of the Motunau Group to accommodate the variable wavelength of folding between weaker and stronger elements of the Cenozoic stratigraphy. Either way, the Pyramid Lake scarp, which is parallel to bedding in the Weka Pass Limestone, probably developed by faulting parallel to the bedding.

Another possible tectonic feature is suggested by the presence of a NW-striking, cross-valley scarp of indeterminate origin that aligns with the course of the stream that now drains the valley through the gap in the Mt Brown limestone. The elevated area is mapped as alluvium (Rattenbury et al. 2006). However, the Mt Brown Limestone south of the river dips much less steeply than it does north of the river and is apparently displaced westwards on the north side of the river by several meters, consistent with the expected effect of south-westward thrusting on a northeast dipping fault. If this feature is a fault, it does not appear to displace the Weka Pass Limestone and thus may merge with the same bedding plane that forms the Pyramid Lake Scarp.

RESULTS

Radiocarbon ages *Goose*

The Pyramid Valley goose's conventional radiocarbon age (UBA42951) of 928 \pm 34 years B.P. (Before Present, Present = 1950 CE) is equivalent to a calendar date 1 σ range of 1062 \pm 23 CE. This age is listed, along with other radiocarbon ages available for *Cnemiornis* spp., in Table 1.

Table 1. Radiocarbon ages for New Zealand geese (*Cnemiornis* spp.). Calibrated dates and date ranges from OxCal4.4, using the SHCal20 curve (Hogg *et al.* 2020). Sources: 1, this paper; 2, Wood *et al.* (2017); 3, Worthy & Holdaway (2002); 4, Worthy & Swabey (2002). Locations are shown in Fig. 1. The South Island birds constitute 5% of the recorded individuals (see text). Museum accession codes: Av, Canterbury Museum, Christchurch; AU, Auckland University Department of Geology; WO, Caves Museum, Waitomo. The Omihi Stream specimen will be lodged with the Museum of New Zealand Te Papa Tongarewa.

					Calibrated dates B.P.				
Site	Museum	Lab. no.	CRA	SD	$\delta^{13}C$	Mean	SD	Median	Source
Pyramid Valley	Av5406	UBA42951	1,062	23	-25.4	928	34	935	1
Omihi Stream, SH#1	RNH colln	NZA24925	18,954	75	-21.9	22,817	124	22,846	1
Finsch's Folly	2013.2	Wk33990	1,646	25	-24.09	1,486	38	1,488	2
Metro Cave	AU9789	NZA2141	15,260	140	?	18,507	152	18,493	3
Zweiholen	WO446	NZA9071	22,630	130	?	26,879	226	26,946	4



Figure 3. Quartic age-depth model for sediment deposition in the Pyramid Valley lake bed. Dotted lines indicate depth and date of the increase in grass and sedge pollen interpreted by Moar (1970) as marking Polynesian arrival. Equation is: Y (date) = $2.469E-6^{*}X$ (depth)⁴ – $0.002007 * X^3 + 0.4387 * X^2 - 2.886 * X + 1426; n = 14.$ Linear $R^2 = 0.98212$; quadratic $R^2 = 0.98438$; cubic $R^2 = 0.98963$; quartic $R^2 = 0.98964$. See Appendix for age-depth model analyses.

Age-depth model

Radiocarbon ages available for the development of a depth-age model for the Pyramid Valley deposit are shown in Appendix Table T1. The calibrated ages in Johnston (2014) were recalculated using the later SHCal20 Southern Hemisphere calibration curve (Hogg *et al.* 2020), via OxCal4.4 (Bronk Ramsey 2009).

After comparing polynomial regressions of mean dates against depth with the Bayesian model (Appendix Fig. A1), the quartic regression (Fig. 3) was chosen as the best model for the changes in the deposition rate through time and for the dates of significant events in lake history (Fig. 3). Modelled probability distributions for the calibrated calendar age ranges are shown in Appendix Fig. A2.

Charophytes

Proceeding upwards from the bottom, charophyte oospores were recorded first at 95 cm (*c*. 3,400 years B.P.) (Fig. 4), then again at 89 cm (*c*. 3,300 years B.P.) after which they were present in every sample up to 71 cm depth (*c*. 2,900 years B.P.). The absence of oospores near the bottom of the core is associated with the lowest levels being within a well-preserved *Carex* sedge vegetation indicating low water levels.

Highest oospore counts were from 57 to 49 cm (*c*. 2,450–2,250 B.P.), in which interval both *Chara australis* (which grows in deeper water) (Schwarz *et al.* 2002) and *C. globularis* were present. No oospores were recovered from the 70 or 69 cm samples (*c.* 280 years B.P.), and they were also absent from the 59 to 57 cm samples (*c.* 2,550–2,450 years B.P.). No oospores were recorded from samples above 51 cm depth (*c.* 2,100 years B.P.) (Fig. 4).



Figure 4. Counts of black (*Chara globularis*) and white (deep water) (*C. australis*) charophyte oospores in contiguous 1 cm samples of the Pyramid Valley sediment core in relation to revised model of lake history and surrounding vegetation. **A**, mean counts of charophyte oospores versus depth on core. **B**, mean counts versus modelled date for sample depth. Dates derived from age-depth model (relationship in Fig. 3).

Topography

The extent of flooding of the southern arm of Pyramid Valley with even a small (≥ 25 cm) increase in water depth in the present lake is shown in a contour map (Fig. 5) generated from the GPS data. Profiles across and along the southern arm of the valley are located on the Digital Elevation Model with contours drawn at 1 m intervals above mean sea level (Fig. 6).



Figure 5. Contour map of southern arm of Pyramid Valley *sensu lato.* Note that the present lake (PV) is an enclave offset from the rest of the valley, and that a minimal increase in water depth entails the lake extending throughout the valley (dark blue). Map generated from GPS traverse data. Traverses and mapping by BD. IT III is a survey tube just outside the north-eastern corner of the boundary fence of the Queen Elizabeth II Covenant (Plan LT43834, "Proposed Open Space Covenant over Lot 2 D.P. 4721, Block X, Waipara Survey District". It is 18.36 m south-east of the Bench Mark referred to in Topology section above).



Figure 6. Digital elevation model of the southern arm of Pyramid Valley *sensu lato*, with valley profiles and profile of breakout gap (A). Maximum water level in the present (1 ha) lake outlined at southern end of valley is shown as blue shading in profile panels. Tall "structures" in profiles A, B, F, G, and I are trees; pattern at northern end of present lake and "deep" point in profile E are artefacts of reflection from the lake in the photogrammetry. Grid in main image is New Zealand Transverse Mercator 2000. In the present lake, excavations have been concentrated along the northwestern shoreline and in the middle of the northern basin. Low cliffs at northern ends of lines of profiles A and I are shown in Fig. 7. Grey line enhanced by line with triangles indicating side of uplift passing diagonally southwest along north-western shore of lake is a fault trace: the present lake has been offset from the rest of the valley by oblique movement of this fault.



Figure 7. Southern arm of Pyramid Valley. **A**, View northwest from above northern end of present lake, showing breakout gap in ridge of Mt Brown sandy limestone (central distance) and dry outlet stream. **B**, Enlarged central section of view in A showing the near 90° turn in the outlet stream bed towards the northwest, deepening as it does so. **C**, Detail of cliffs on northern side of breakout gap. Strata of brittle Mt Brown limestone stand proud of the surface, where soft clay has been eroded from between them. The willow (*Salix* sp.) trees stand in a deeply cut channel at the entrance to a narrow valley leading to the Waipara River flats beyond.

DISCUSSION

In contrast to the present view of a static environment around Pyramid Valley, with forest surrounding a small, possibly ephemeral, lake, the charophyte fossil record shows that the present 1 ha lake is a small remnant, in a high level enclave, of a much larger and deeper water body. For 1,500 years, oospores of deep water algae were deposited in fluctuating numbers in the accumulating sediment. They were shed by plants both growing within the small enclave when the lake was deep enough and drifted in from plants in the larger lake when the water bodies were still linked. The enclave itself was too shallow to support charophyte growth (Schwarz *et al.* 2002).

Gaps in the deposition record when the level of the main lake was below the lip of the enclave. In the strongly seasonal North Canterbury climate (Worthy & Holdaway 1996; Holdaway & Worthy 1997), lake levels would have fluctuated seasonally as well, but for most of its existence the large lake was deep enough in summer for the charophytes to grow and reproduce.

Recognition of a larger lake in the valley encompassing the smaller water body and deposit known for many years as "Pyramid Valley" creates a problem of nomenclature to distinguish one from the other despite their being aspects of the same structure. Hereafter, to maintain continuity of usage, the 1 ha enclave that contains the fossil deposit is Pyramid Valley (PV) and the larger lake is Pyramid Valley Lake (PVL).

Pollen records (Harris 1955; Moar 1970) set against the new age-depth model shows that until *c*. 2,050 B.P. (50 BCE) the area supported a forest of hardwoods with emergent matai (*Prumnopitys taxifolia*) podocarps. The lake margins fluctuated, with emergent wetland vegetation (Moar 1970). Sometime around 2050 B.P. (50–100 BCE), the Mt Brown limestone ridge failed at a point on the line of a much earlier west-east drainage feature (Fig. 7) and the PVL avulsed westwards down the old dry valley across the adjacent plain and into the upper Waipara River.

Why the ridge collapsed is under investigation. The presently favoured mechanism is based on the underlying structure revealed in the still-eroding cliffs on the northern side of the ridge break. Here brittle limestone strata are separated by soft, mobile clays. High lake levels along the ridge could mobilise the clay (as it is still eroding on the western side) causing it to slump and cease to support the limestone plates. Those in turn could then break away under their own weight: once water was flowing through the gap, the flow would have shaken and flexed them until they failed and fragmented in turn as further supporting clay was washed away. A catastrophic rate of flow is supported by the presence of a 10-m deep gouge in the valley floor at the break, below the cliffs, and the absence of limestone blocks of the Mt Brown strata in or beyond the gap. The ridge failure may have been triggered by an intense rainfall event which overfilled the PVL, or by a major earthquake caused by the rupture of one or more faults, including the Mason's Flat Fault which lies along the western foot of the enclosing ridge (Fig. 2).

The deep gully of the lower outlet stream, cut in indurated sediment is far deeper than could be cut in those sediments by any stream outflow from the present lake. However, it could have been cut by base flow during a catastrophic breakout. The tectonic structure of the valley itself may itself be responsible for the partial isolation and raised position of Pyramid Valley, as it is bounded on the outlet side by a fault trace (Fig. 6).

Regardless of the mechanism of the ridge failure, its timing is clearly shown by both the permanent cessation of deposition of charophyte oospores and the sudden appearance of abundant sedge and grass pollen. Draining of PVL would have left nearly 50 ha of bare lake bed within the valley itself and perhaps several square kilometres of flattened forest in the outlet valley and on the plain beyond.

At the onset of the high grass and pollen at 40 cm depth, in a "transition layer", Harris (1955) recorded the terrestrial hounds tongue fern (listed as Microsorum, now Zealandia pustulata). Although it grows in forest, the fern also colonises open ground: it is drought tolerant and can be found in open, dry environments (New Zealand Plant Conservation Network 2021). Moar (1970) did not mention its presence, and the sudden abundance of hounds tongue fern may signal the appearance of bare ground near the lake as it was not a feature of the record before or for long after the lake drained. The fern would have been replaced rapidly by grasses, sedges, and bracken fern (Pteridium esculentum). Moar (1970) suggested that the increase in grasses and other seral vegetation at 40 cm resulted from deforestation by Polynesian fires, but his figure does not show any contemporary reduction in tree pollen.

Contrary to Moar's (1970) interpretation, the new age-depth model shows that the sudden increase in grass and sedge pollen at 40 cm depth occurred at *c*. 2,100 yrs B.P., predating by at least 1,400 years the removal of the local forest by Polynesian fires, but contemporary with the abrupt end of charophyte deposition in the PV sediments. Hence, the changes in the pollen profile can now be confidently attributed to the sequence of seral vegetation colonising the newly vacated bed of the PVL. The likely extent of that area is shown in Figures 6 & 8. The forest surrounding the PVL and its fauna was unaffected and over the next few centuries spread across the former lake bed.

For a brief period, perhaps less than a century, after the PVL drained, there was grassland near Pyramid Valley. Holdaway & Worthy (1997) appealed to the unlikely presence of shrubland on the surrounding hills to explain the presence of a New Zealand quail (*Coturnix novaezelandiae*) in the deposit. The presence of seral vegetation following the lake drainage now offers an alternative explanation. The quail bones were not located in the Canterbury Museum collections during an intensive search (Holdaway & Worthy 1997), but if they can be found an AMS radiocarbon age could resolve that issue.

The presence of grassland near the deposit for a significant period, if only for a few decades, means that the goose's assumed habitat was present, as was an avenue for its colonisation from the Waipara River plain via the newly cleared outwash valley. However, there is no evidence that South Island geese reached Pyramid Valley then. The lone goose died in the 11th century CE, 1,000 years after the PVL drained, more than enough time for forest to have spread right across the former lake bed. There is no corridor of open country where water could flow into the larger lake. It was and is a closed basin whose saddles are above the levels of adjacent valleys. Any drought that could have changed the vegetation to replace forest with grassland would have had to have been protracted and would have been clearly visible in the pollen record. There is no such record. The rarity of other grassland species in the deposit (Holdaway & Worthy 1997) supports the brevity of the presence of grassland at Pyramid Valley.

The radiocarbon age for the Pyramid Valley goose brings the number of ages available for the genus to five, four for the South Island goose and one for the North Island species. The sample is too small to reveal detailed trends in distribution, but some patterns are apparent. The North Island goose lived near Waitomo just before the Oruanui super eruption of Taupo Volcano (Vandergoes *et al.* 2013). The local vegetation at that time was probably lowland rain forest judging from the contemporary presence of the moa *Anomalopteryx didiformis* (Millener 1981), a rainforest indicator species (Worthy & Holdaway 2002).

In the South Island, forest birds were preserved with the geese in Finsch's Folly Cave (Wood *et al.* 2017). According to the environmental reconstruction developed here, the goose at Pyramid Valley co-existed with forest birds. However, the other two radiocarbon dated South Island geese are much older. The goose from Metro Cave on the Nile River near Charleston on the West Coast (Fig. 1) lived there as the climate was



Figure 8. Reconstruction of the former extent and breakout path of Pyramid Lake, in relation to the position and extent of the present lake. **A**, Extent of lake with depth of 8 m at present lake; faint shoreline terraces on slopes to west of present lake indicate a possible maximum depth of *c*. 16 m. **B**, Position of valley wall failure and breakout stream down old drainage valley to west, with approximate extent of newly exposed lake floor and that cleared of vegetation by breakout flow.

warming after the most recent (Otiran-Weichselian) glaciation so would have occupied glacial low forest and shrubland (Newnham *et al.* 2013). The Omihi Stream goose from North Canterbury, 18 km from Pyramid Valley, lived there during the coldest part of the glaciation. The dated bone, a well-preserved tarsometatarsus whose sharp edges had not been worn by post-mortem transport, was recovered from clean sands that had accumulated in a stream delta in a wetland at a time when the local vegetation was indeed dominated by grassland.

What emerges, therefore, is that, far from being an obligate inhabitant of short turf grassland like its Australian relative, the South Island goose was able to occupy different habitats. Far more so than *Cereopsis*, the New Zealand birds were confronted with a landscape dominated by woody vegetation throughout their post-colonisation evolutionary history. During that time they lost entirely the power of flight.

Like the harriers, they retained their ancestral bill form. It is easier for waterfowl (and rails) than for other birds to become flightless when there is no selection pressure from predators. Unlike other birds, duck and rail wings develop later than their legs, so any selection for flightlessness would not be compromised by development processes in which wings developed before the legs (Olson 1973; Slikas et al. 2002). Bills adapted to cropping vegetation can cope easily with tree leaves as well as grass. Similar-sized goose-like birds (moanalo, whose ancestors were Anas ducks) occupied forest in pre-human Hawaii (Olson & James 1991). One species, Thambetochen cauliodous, at least, was folivorous and perhaps even a pteridivore (James & Burney 1997). Even the Hawaiian goose Branta sandvichensis, a true goose, can, despite its "normal goose bill", browse tree foliage (Fig. 9).



Figure 9. Goose bills adapted to cropping grass can also be used to browse tree foliage. Juvenile Hawaiian geese (*Branta sandvichensis*) foraging on tree leaves while their parents graze the grass below. Note that some of the lower branches have already been stripped bare. Photo: RNH, Regent's Park (London) Zoological Gardens, May 1988.

Our results show that the habitat and biology of species in the rich fossil avifauna of Pyramid Valley must be interpreted in relation to a changing local environment. Access to the site, and hence possibility of being incorporated in the deposit, would have been governed by the lake level, as well as defining when a species was "made available" by the local presence of its habitat. The implications of the presence of any species in a fossil deposit must be assessed therefore on the basis of detailed chronologies of both that species and of the local environment. On that basis, the presence of the South Island goose at Pyramid Valley in the 11th century CE when the area was forested and not during the brief period when grassland and an avenue of approach were available provides further evidence of the adaptability of these flightless birds. One important conclusion from the study is that, to understand the dynamics of an extinct system and the biology of an extinct species, even to explain the presence of a single individual of a species in an otherwise rich fossil avifauna, it is necessary to employ information from other, apparently unrelated, disciplines.

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Table A1. Radiocarbon ages for organic materials from the Pyramid Valley lake bed: shaded, ages used in age-depth model. Sources: *AJG; ¹this study; ²Holdaway *et al.* (2014); ³Gregg (1972). Dated materials: G, gyttja; BG, bone gelatin; PM, unidentified fossil plant material; Peat, lower black peat; *Carex*, leaf of fossil *Carex secta* in erowth position at base of excavation. **samples from same depths dated independently**.

OxCal4.4						Unmod	lelled B	.P. (Befo	re 195() CE)				Unmod	elled B	CE/CE			
SHCal20				68.3	3% CI	95.4	% CI				Depth	68.3%	IJ	95.4%	CI				
Laboratory number	CRA	SD	$\delta^{13}C$	From	1 To	From	To	Mean	SD	Median	(cm)	From	To	From	To	Mean	ß	Median	Material
*Direct AMS-PV 31	1558	30	-11.9	1424	1 1352	1513	1314	1398	44	1393	31	526	598	438	637	552	44	557	G
*Direct AMS-PV 22	1572	27	-19.8	1455	3 1362	1518	1352	1416	44	1407	22	497	588	432	598	534	44	543	ŋ
¹ NZA29769	1824	25	-21.4	1730) 1619	1810	1610	1687	50	1700	21	220	332	140	340	263	50	250	BG
¹ NZA29766	1812	25	-19.0	1722	2 1615	1745	1590	1668	43	1657	23	229	336	206	361	282	43	294	BG
Direct AMS-PV 40	2137	29	-19.8	2095	5 2015	2288	2000	2067	53	2062	40	-146	-66	-339	-51	-118	53	-113	ŋ
Direct AMS-PV 63	2473	29	-15.4	2681	1 2364	2703	2353	2513	107	2485	63	-732	-415	-754	-404	-564	107	-536	G
619ZNE	2620	49	NA	2762	2522	2844	2488	2657	96	2700	70	-813	-573	-895	-539	-708	96	-751	ΡM
Direct AMS-PV 56	2714	23	-13.4	2844	1 2752	2851	2746	2792	33	2781	56	-895	-803	-902	797-	-843	33	-832	G
3NZ620	2930	63	NA	3151	1 2946	3227	2851	3035	66	3032	83	-1202	7997	-1278	-902	-1086	66	-1083	ΡM
¹ NZA29785	2954	25	-25.0	3146	5 2997	3171	2956	3063	61	3061	83	-1197	-1048	-1222	-1007	-1114	61	-1112	ΡM
3NZ621	3720	60	NA	4143	3 3922	4231	3840	4024	95	4023	120	-2194	-1973	-2282	-1891	-2075	95	-2074	ΡM
¹ NZA29791	3818	25	-27.3	4234	4091	4289	3993	4158	67	4157	120	-2285	-2142	-2340	-2044	-2209	67	-2208	Μd
3NZ622	4280	62	NA	4869	9 4628	4967	4573	4767	105	4758	165	-2920	-2679	-3018	-2624	-2818	105	-2809	Peat
¹ NZA29811	4293	20	-25.5	4858	3 4825	4870	4652	4819	51	4838	160	-2909	-2876	-2921	-2703	-2873	51	-2889	Carex
¹ NZA29765	3359	25	-21.0	357() 3487	3680	3456	3538	46	3531	D	-1621	-1538	-1731	-1507	-1589	46	-1582	BG
¹ NZA29819	3892	20	-23.1	4395	9 4159	4407	4155	4280	71	4278	D	-2450	-2210	-2458	-2206	-2331	71	-2329	Wood



Position

Figure A1. Bayesian age-depth model (OxCal 4.4, Deposition Model, SHCal20 curve (Hogg *et al.* 2020) for Pyramid Valley lake bed deposit.



Figure A2. Bayesian modelled calibrated date distributions (OxCal 4.4, Deposition Model, SHCal20 curve) (Hogg *et al.* 2020) for the radiocarbon ages used to generate the Pyramid Valley lake bed deposit age-depth model, with date probability distributions for the start and end of the sequence.

New Zealand falcons (*Falco novaeseelandiae*) hunting petrels at night and underground during the day

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Abstract: New Zealand falcons (*Falco novaeseelandiae*) routinely feed on burrow-nesting seabirds (petrels: Procellariiformes) at several sites. As petrels are rarely present on the colony surface during daylight, and falcons are considered to be diurnal hunters, there has been much speculation about how falcons are able to capture petrels. We present evidence that New Zealand falcons are able to hunt petrels in forest at night, and also enter burrows during the day to extract chicks. These are novel hunting behaviours for falcons, and further increase the broad range of hunting strategies documented for New Zealand falcons. While these hunting methods may be used by only a few individual birds, they can produce high prey-capture rates.

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INTRODUCTION

New Zealand falcons (kārearea, *Falco novaeseelandiae*) are versatile foragers compared to other falcon species (Seaton & Hyde 2021). Seven different aerial hunting techniques were described for them by Fox (1977, and in Marchant & Higgins 1993), combining methods used by short-winged forest hawks (Accipitridae: *Accipiter* spp.) and open-country falcons (Falconidae: *Falco* spp.) elsewhere

in the world. New Zealand falcons can also extract nestlings from tree-hole or crevice nests (Marchant & Higgins 1993), and they can hunt on the ground: they have been observed hunting for ground-level bellbird (*Anthornis melanura*) nests and chicks among tree roots on the subantarctic Auckland Islands (Miskelly *et al.* 2020a). New Zealand falcons on the ground have also been observed stalking and catching skinks (*Oligosoma* spp.) on mown grass on Takapourewa/Stephens Island in the outer Marlborough Sounds (AdG *pers. obs.*), and attempting to do so among sand dunes on Whenua

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Hou/Codfish Island (Jake Osborne *pers. comm.* to CMM, 10 September 2021).

Falcons worldwide are generally regarded as diurnal predators, relying on acute eyesight to locate prey, often from great distances (Brown & Amadon 1968; Marchant & Higgins 1993; del Hoyo et al. 1994). However, New Zealand falcons have frequently been reported as having consumed species of burrow-nesting petrels (Procellariiformes: Procellariidae, Hydrobatidae, and Pelecanoididae) that visit their breeding colonies only at night (Wilson 1959; Harrow 1976; Chance 1992; Worthy & Holdaway 1995; Worthy 1997; Worthy et al. 2002; Worthy & Zhao 2006; Hyde & Worthy 2010; Cuthbert 2017; Miskelly *et al.* 2019, 2020; Elliott et al. 2020). There has been much speculation on how falcons are able to capture these petrels, including suggestions that falcons are catching birds out at sea, or catching birds that arrive at the colony before it is fully dark, or birds that depart late, when there is sufficient light for falcons to begin hunting (Harrow 1976; Worthy & Zhao 2006; Hyde & Worthy 2010; Cuthbert 2017; Elliott et al. 2020). We document two previously unreported hunting methods used by New Zealand falcons to capture petrels: hunting at night under forest, and entering burrows during the day. These behaviours further extend the diverse repertoire of hunting behaviours recorded for New Zealand falcons.

STUDY SITES AND METHODS

All observations were serendipitous encounters or recordings made during other conservation research, management, or leisure activities. Evidence of New Zealand falcons hunting mottled petrels (korure, *Pterodroma inexpectata*) in the middle of the night was obtained at two widely separated colonies in Fiordland, and a falcon was observed catching fairy prion (tītī wainui, *Pachyptila turtur*) chicks inside burrows on Takapourewa/Stephens Island in the Marlborough Sounds. Observation and recording methods are described under each study site below.

Lake Hauroko

'Motukōrure' islet (0.3 ha) lies 500 m south of Mary Island in Lake Hauroko, eastern Fiordland. It is usually free of introduced mammals and had an estimated 530 mottled petrel burrows in December 2019 (Miskelly *et al.* 2021). Following evidence of stoats (*Mustela erminea*) and then mice (*Mus musculus*) reaching the islet in mid-2020, trail cameras were installed on the islet as part of a successful pest mammal incursion response. Three cameras were installed on 28 May 2020, and then replaced with a single 'permanent' camera (Browning Dark Ops Apex, model BTC-6HD-APX) on 12 August 2020. This was the last date that evidence of stoats was detected on the islet, with two stoat corpses found in traps.

The single camera in place from August 2020 monitored activity over about 30 m² of forest floor, with the branches of 4–5 trees also close enough for large birds in them to trigger the motion-sensor. The camera was set to record 10 seconds of video whenever the motion-sensor was triggered. The islet was visited again by Department of Conservation staff on 9 October, 19 November, and 14 December 2020, and 29 January, 18 February, 1 April, 7 May, 11 June, and 4 August 2021, with the SD card from the camera removed and replaced on each occasion. Mottled petrel corpses were searched for on the colony surface, and either photographed or the corpses retrieved to determine cause of death.

Any video clip with a falcon in it was classified as 'falcon activity'. Records of falcon activity within 30 minutes of each other were considered to be part of the same falcon visitation event. These were classified as 'day' if between sunrise and sunset, 'dusk' during the hour after sunset, and 'night' from then until an hour before sunrise. No falcons were detected in the hour before sunrise. All times are reported in New Zealand Standard Time. Percentage moon disc illumination was obtained from the website https://lunaf.com/ lunar-calendar, viewed 15 August 2021.

In February 2011, the first calls by mottled petrels flying over the colony were heard 27–38 minutes after sunset (average = 33 minutes, n = 7; Matt Rayner *pers. comm.* to CMM, 30 August 2021).

Anchor Island

An estimated 700 mottled petrel burrows were found on the largest islet in Anchor Island Harbour in Dusky Sound, Fiordland, in November 2016 (Miskelly *et al.* 2017). CMM camped on the islet on the night of 27–28 February 2021, as part of a fourperson research team collecting viral swab samples from mottled petrels and sooty shearwaters (*Ardenna grisea*). Direct observations of mottled petrels and a New Zealand falcon were made between 2145–0110 h and 0415–0635 h.

Takapourewa/Stephens Island

AdG and Polly Hall were the Department of Conservation rangers on Takapourewa/ Stephens Island at the northern tip of the Marlborough Sounds during 2012–15. A pair of falcons was resident on the island, and successfully fledged two chicks in each of the 2012–13 and 2013–14 breeding seasons.

Takapourewa holds the world's largest fairy prion (*Pachyptila turtur*) colony, with an estimated

Table 1. Details of five occasions when a New Zealand falcon was filmed being active at night, or feeding on or carrying a mottled petrel corpse. All footage was captured on a trail camera set within a mottled petrel colony on a 0.3 ha islet in Lake Hauroko, Fiordland, in 2021. Shading is used to highlight nocturnal activity by the falcon or falcons. All times have been converted to New Zealand Standard Time. Lunar disc illumination is given as "% moon" under Day/Night (see Methods).

Date	Time (h)	Day/Night	Description
4 Feb	0403	Night 49% moon	Falcon attacking petrel, flying from tree to ground; tussle for 3 seconds, then falcon on ground looking away from petrel (which is out of sight)
15 Feb	2010	Dusk	Falcon flies up to tree perch carrying petrel (windy conditions), then flies further along perch, still carrying petrel. Many feathers on ground and being blown about
19 Feb	2040	Dusk	Falcon drags petrel carcass in from left to front of camera, using one foot. It proceeds to pluck the carcass and then feed over the next 17 min
25 May	0028	Night 99% moon	Falcon on ground, walks towards camera, with feather stuck to beak then pecks at something (out of camera, in foreground); 6 min later falcon walks away from the camera, to edge of bank
7 June	1818	Night 8% moon	Falcon on ground, to the left near the camera. Moves off to left out of frame

1.4 million pairs (Craig 2010; Jamieson *et al.* 2016). Fairy prions breed synchronously, with chicks on Takapourewa fledging from late January to mid-February (Miskelly & Gummer 2013). Before mid-January, prion chicks were not seen outside of their natal burrows by day or night, unless their burrows were flooded by an extreme rain event.

AdG was reading a book on the veranda of the rangers' house, in late December 2013, when he made the direct observation of a New Zealand falcon catching fairy prion chicks described below.

RESULTS

New Zealand falcon predation on mottled petrels based on prey remains

Three beheaded mottled petrel corpses were found on Motukōrure islet on 18 February 2021. Based on images of these, Graeme Taylor, Chifuyu Horikoshi, and Noel Hyde considered that they had been killed by a falcon (*pers. comms* to LMcL). At least 10 petrel carcasses were seen on 1 April 2020, a fresh carcass was noted on 7 May, and 26 carcasses were recovered on 11 June 2021 (these may have included all the previous corpses recorded). Fourteen of the mottled petrel corpses that were removed from the islet in May and June were confirmed as likely to have been killed by falcons, either in the field or during necropsy and skeleton preparation at Te Papa (authors, *pers. obs.*). The corpses included both adults and pre-fledged chicks.

Three sites where a falcon had plucked mottled petrels were found on the islet in Anchor Island Harbour during the evening of 27 February 2021. However, the team was unaware of any falcons being present on the 0.3 ha islet before they retired to their tents at 0110 h.

Nocturnal hunting

Video evidence

Video footage of a falcon (possibly a single adult) on Motukōrure islet was captured in 75 video clips during 53 falcon visitation events on 37 dates between 22 January and 7 June 2021. Video evidence of the falcon or falcons being active at night, and/or interacting with live or dead petrels, is summarised in Table 1. These included sequences of a falcon attacking an adult mottled petrel at night (4 February; Figs 1A & B), a falcon flying to a perch carrying a petrel corpse (15 February), and a falcon plucking a mottled petrel corpse (19 February; Fig. 1C).

Most of the falcon activity was during the day (75%), with 19% at dusk, and five video clips (three events = 6%) at night. These clips showed the falcon (or falcons) as being active in the middle of the night: at 0403 h on 4 February 2021 (the attack sequence described below), at 0028 h, 0029 h, & 0034 h on 25 May 2021, and at 1818 h on 7 June 2021. This last event was 1 h 6 min after sunset.

On 25 May, an adult falcon walked towards the camera (Fig. 1D) and then pecked at an apparent prey item on the ground that was too close to be in the camera field of view. Six minutes later, the falcon walked away from the camera. This date was one day before full moon (and had 99% illumination); however, local cloud cover conditions were not recorded on any date.



Figure 1. A & B) Two frames from a video showing a New Zealand falcon attacking a mottled petrel on an islet in Lake Hauroko, Fiordland, filmed at 0403 h on 4 February 2021. The bright spots are the eye-shines of both birds. A link to the video clip is provided in Supplementary materials. C) A New Zealand falcon plucking a mottled petrel corpse on an islet in Lake Hauroko, Fiordland, filmed at 2046 h on 19 February 2021. D) A New Zealand falcon walking around at night at a mottled petrel colony on an islet in Lake Hauroko, Fiordland, filmed at 0028 h on 25 May 2021.

The moon was ³⁄₄ full on 4 February (49% illumination), when a falcon was recorded attacking a mottled petrel (Figs 1 & B).¹ The adult petrel was likely leaving the colony before dawn (it was 1 h 46 min before sunrise), and was moving rapidly downslope, partially obscured by the surface topography. The falcon bounded down a sloping tree trunk towards the petrel, and then attacked it largely out of camera view, below the crest of a low bank. Flailing wingtips were visible for about 3 seconds, before the falcon re-appeared facing away from where the petrel had apparently escaped downhill.

Direct observation

An adult New Zealand falcon was disturbed from a freshly killed (still warm) adult mottled petrel on the islet in Anchor Island Harbour at 0440 h on 28 February 2021. It was a still, clear night with a full moon (100% illumination), although it was dark under the dense *Olearia* canopy (sunrise was at 0628 h). The site where the kill occurred had been visited multiple times earlier in the night. The falcon scrambled up a sloping trunk in CMM's headlamp beam and flew out through the canopy.

Hunting underground

Direct observation

The falcons on Takapourewa used live prion chicks each year to teach their fledglings how to catch prey in mid-air, and how to kill prey. The adult female falcon was frequently observed from late December to February carrying downy prion chicks and calling to her fledglings, before dropping the live prion chick for them to attempt to catch. If they failed to catch the falling chick, it was not retrieved, and the female would fly off to catch another chick.

At *c*. 1500 h on an unrecorded date in late December 2013, an adult female New Zealand falcon landed near the rangers' house on Takapourewa, ran under a hedge, then emerged soon after with a prion chick. This was used for a training session with the two fledglings nearby, but was soon dropped and lost in the long grass. The adult female returned to the hedge on two further occasions, and each time she was observed entering a prion burrow and disappearing out of site, before emerging backwards 5–10 seconds later dragging a live prion chick with her beak. Once on the mown lawn by the house, the prion chick was transferred to one foot before an ungainly running take-off with the heavy load.

The two burrows that the falcon was seen to enter were close together (and near the site where the first of the three prion chicks was caught). One of these burrows was inspected by AdG. It had a wide entrance leading to multiple prion nest chambers, all of which were beyond the length of his arm.

On other occasions, the adult female was observed emerging with a prion chick from the same patch of forest several times in quick succession, without the method of prion chick capture being observed. However, the impression was that she routinely entered prion burrows, as there is no other way that she was likely to have been able to catch the concealed prion chicks so rapidly.

Video evidence

The trail camera on Motukōrure islet recorded a falcon walking on the ground on 45 occasions (85% of visitation events) between 22 January and 7 June 2021. No falcons were detected during the previous

eight months or the succeeding two months. Although the bird was not seen inspecting or entering a burrow, there were no burrow entrances within the field of view – the camera was focused on a bait lure (intended to attract stoats) above a patch of flat ground with little ground cover.

DISCUSSION

Falcons hunting at night

Nocturnal hunting by falcons away from artificial lights is rarely reported. The low incidence of falcons being recorded on video at night on Motukōrure Islet (plus the single observation from Anchor Island) indicate that nocturnal hunting may be a rare behaviour, with night activity focussed on bright moonlit nights. However, it is possible that the Motukōrure falcon had favoured nocturnal hunting sites (e.g. areas with a more open canopy) elsewhere on the island, where activity would not have been recorded by the single camera present.

The only other report of a New Zealand falcon hunting in the middle of the night that we are aware of was told to Noel Hyde by Mr Robin Bagge of Tauranga, on 28 March 2009 (Noel Hyde pers. comm. to CMM, 22 July 2021). Robin Bagge worked for the New Zealand Forest Service and was a keen hunter. In 1978, while deer hunting with Stan Lowe in the middle reaches of Horomanga Stream, Murupara, they heard the squawking of a bird at 0200 h. Robin shone his spotlight up a tree and saw a falcon (presumed to be a male, based on its size) holding a still alive, flapping sacred kingfisher (Todiramphus sanctus). When questioned as to how bright the night sky was, he replied that he never hunted on a full moon, suggesting that the kingfisher had been caught at much less than 100% lunar illumination.

Potts (1882: 44) reported that "On Banks Peninsula we have observed it [New Zealand falcon], in the wintry month of June, hawking by the light of the waning moon, ere the little owl [likely *Ninox novaeseelandiae*], warned by the coming of day, has retired to the dim obscurity of its roost in the decayed tree." However, the reference to an owl going to roost indicates that this observation was pre-dawn rather than during complete darkness.

Many falcon species hunt in dim light after sunset and before dawn (Brown & Amadon 1968; Ratcliffe 1980; del Hoyo *et al.* 1994); however, we have found limited evidence of falcons hunting by natural light in the middle of the night. The numerous accounts of peregrine falcons (*Falco peregrinus*) hunting at night were mainly of birds in urban settings using artificial light to locate their prey (e.g. Rejt 2004; DeCandido & Allen 2006; Kettel *et al.* 2016; Time 2016). Similar behaviour has been reported for common kestrels (*F. tinnunculus*), lesser kestrels (*F. naumanni*), sooty falcons (*F. concolor*), and Eleanora's falcons (*F. eleanorae*) (Sachslehner 1996; Negro *et al.* 2000; Gschweng 2013; Buij & Gschweng 2017).

Satellite-tracking or GPS data loggers have revealed some lesser kestrels and Eleanora's falcons to be active at night in areas away from artificial illumination, particularly when moon disc illumination was >60% (Gustin *et al.* 2014; Buij & Gschweng 2017). However, the nearest comparable accounts that we have found of falcons hunting at night under natural light (or at sites with little artificial illumination) were two studies of peregrine falcons hunting seabirds at their breeding colonies, and one account of a duck being taken.

Wynn *et al.* (2010) used infrared cameras to detect nocturnal predation of Balearic shearwaters (*Puffinus mauretanicus*) by a peregrine falcon on bare ground at a cave entrance on the island of Menorca. At least 18 shearwaters were killed over two breeding seasons, at a rate of about 0.5 kills per night over a 2-month period, with most attacks occurring on moonlit nights (Wynn *et al.* 2010). It is unclear whether the cave entrance received artificial illumination, although the authors mention a tourist development nearby, and that "Artificial lights from these developments may assist night hunting Peregrines" (Wynn *et al.* 2010).

Collins *et al.* (2014) also used infrared cameras, installed at a black-legged kittiwake (*Rissa tridactyla*) colony on a cliff on Puffin Island, Wales, and detected predation of kittiwake chicks by a peregrine falcon. The two predation events captured by the camera occurred 53 mins and 48 mins before sunrise, 2 days apart: "It would not have been completely dark during predation events, thus it is possible that the peregrine was using the low-light conditions to enhance its chance of predation success" (Collins *et al.* 2014).

Hirata *et al.* (2013) reported a peregrine falcon that killed a mallard (*Anas platyrhynchos*) 40 minutes before sunrise, in an area with minimal artificial lighting in Hokkaido, Japan (Hirata *et al.* 2013). The snow-covered open ground may have facilitated detection of the dark-plumaged prey in the low light conditions.

In all three situations described by Wynn *et al.* (2010), Hirata *et al.* (2013), and Collins *et al.* (2014), the peregrine falcons were hunting in open, uncluttered environments, and may have been utilising artificial light, or light from the sun in the hour before sunrise. These circumstances were unlike the complex environments under dense canopy where we recorded New Zealand falcons attacking or feeding on mottled petrels more than 100 minutes before sunrise.

Falcons entering burrows to catch seabird chicks Although a falcon was observed entering petrel burrows on a single date only, we interpret the regular presence of a falcon on the ground at a dense mottled petrel colony during daylight (as detected by video) as circumstantial evidence that the bird was searching for petrel chicks inside burrows. The falcon was recorded only during the nestling period for mottled petrels (Warham et al. 1977), and it spent much of this time walking over the colony surface. The high recording rate (a minimum of 37 days over 4 months) is noteworthy, given the tiny patch of forest floor in the camera field of view. The highest density recorded for falcons on mainland New Zealand is about one pair per 900 ha (Seaton & Hyde 2021), although the Takapourewa falcons probably confined their hunting to the 150 ha island while breeding. Falcons have never been recorded nesting on 0.3 ha Motukorure islet; however, at least one adult falcon visited the islet sufficiently often in 2021 to be detected on a single trail camera (viewing less than 1% of the islet) on at least 27% of days during the mottled petrel nestling period. When combined with the recovery of at least 26 mottled petrel corpses (including of pre-fledged chicks) during this time, and the apparent absence of stoats on the islet in 2021, we suspect that the falcon was routinely entering burrows during daylight to extract petrel chicks, as observed on Takapourewa.

We have not found any published accounts of falcons hunting underground. However, Noel Hyde (*pers. comm.* to CMM, 23 July 2021) described a trained New Zealand falcon entering a burrow when in pursuit of a rabbit (*Oryctolagus cuniculus*):

"Some years ago, a female bush falcon I was flying perched on a post. We noticed it started head bobbing and focussing intently on a rabbit about 200 m away. The falcon quickly launched into a direct flying attack, and as it closed in, at the last moment the rabbit bolted. The rabbit sprinted across the paddocks about 150 m with the falcon in hot pursuit about 3 m behind. The rabbit disappeared down a burrow, and to our amazement the falcon followed the rabbit into the burrow at speed. On running over and looking in, the falcon was nearly an arm-length down the burrow, with the young rabbit firmly in its clutches. I had to reach in and gently wriggle, and pull the falcon out with her still firmly attached to *the rabbit.*" This active pursuit of fleeing prev into a burrow differs from falcons hunting petrel chicks, which remain stationary in a nest chamber at the end of a long burrow during daylight, and only begin to emerge (at night) in the week or so before fledging (Warham 1996).

Falcon predation of petrels in Fiordland

Hunting of mottled petrels by falcons on Motukōrure islet has been sporadic, rather than

continuous, over the past 47 years, suggesting that it is self-acquired behaviour by perhaps only two individual birds. The first report of mottled petrels on the islet was by Tom Neave and his daughter Rosemary in May 1974 (Wynston Cooper *pers. comm.* to CMM, 28 August 2021). The 2–3 partial skeletons that Tom Neave forwarded to the National Museum via the Wildlife Service for identification were considered by curator Sandy Bartle to have been killed by a falcon (Wynston Cooper *ibid.*).

Wynston Cooper monitored the Motukōrure mottled petrel colony during 31 visits between 1982 and 1987, and never observed a falcon on the islet (Wynston Cooper *ibid.*). Similarly, no evidence of falcons, or falcon predation of petrels, was detected during at least annual visits to the islet between 2008 and 2020 (Colin Bishop and Jenny Rickett *pers. comm.* to CMM, 30 August 2021). Matt Rayner camped on the islet for 26 days between 2009 and 2011; he found no evidence of predation, but heard a falcon calling over the island on a single occasion (Matt Rayner *pers. comm.* to CMM, 30 August 2021).

Evidence of falcons having fed on at least ten broad-billed prions (Pachyptila vittata) was found at five colonies on the outer Fiordland coast during 2017 and 2019 (Miskelly et al. 2019, 2020b). This included an adult falcon that was disturbed from a freshly killed (and mostly consumed) adult prion on an islet off the south coast of Passage Island in Chalky Inlet at 1700 h on 23 November 2017 (CMM, pers. obs.; photograph in Te Papa blog 'Seabird discoveries in remote southern Fiordland', published 5 December 2017). We were unable to determine how these prions were captured. However, we did not encounter any on the surface or flying over any of the 28 Fiordland colonies surveyed during daylight in 2016–2020 (Miskelly et al. 2021; CMM pers. obs.).

While the multiple records of New Zealand falcons feeding on broad-billed prions at their breeding colonies in Fiordland indicate that falcons may be hunting at night or underground, there are other ways that they may have captured the petrels. These large-headed prions are prone to getting caught by the neck in tree forks (e.g. illustration in Cemmick & Veitch 1985: 45), and it is possible that falcons were attracted to the flailing wings of trapped prions after day-break. We consider it unlikely that falcons were catching mottled petrels or broad-billed prions at sea before dark (e.g. as Clunie 1976 reported for a peregrine falcon hunting collared petrels *Pterodroma brevipes* and tropical shearwaters *Puffinus bailloni* in Fiji). We never saw these petrels from land before complete darkness, and the islets that they breed on are tiny specks near much larger landmasses with numerous potential perches or landing sites for falcons (i.e. it is unlikely that falcons returning from the sea carrying a petrel would land on a Fiordland petrel colony to feed on it).

Apart from Fiordland and the Marlborough Sounds, there are few other places where New Zealand falcons currently co-occur with dense colonies of breeding petrels. Petrels of six species formed a major portion of the diet of New Zealand falcons on Adams Island in the subantarctic Auckland Islands (Hyde & Worthy 2010; Elliott et al. 2020; Miskelly et al. 2020). Harrow (1976) and Cuthbert (2017) reported New Zealand falcons feeding on Hutton's shearwaters (Puffinus huttoni) in the Seaward Kaikoura ranges and suggested that they were catching departing birds in the half-light of dawn. When combined with our observations, these accounts from Kaikoura and the Auckland Islands reveal that New Zealand falcons readily exploit burrow-nesting seabirds as a food resource when present, and that they use a variety of hunting techniques to capture them, including hunting at night, and entering burrows. Studies using monitoring devices attached to falcons (including GPS, light sensors, and tri-axial accelerometers) and a network of trail cameras could be used to determine how often each method is used by individual birds and local populations, and the proportion of petrel burrows inspected or entered.

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Can small-scale predator control influence mallard duck (*Anas platyrhynchos*) nest survival? An experiment with artificial nests in Southland, New Zealand

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Abstract: Artificial mallard (*Anas platyrhynchos*) nests were used to identify potential nest predators and assess whether small, farm-scale predator control could reduce mallard nest predation in Southland, New Zealand. Artificial nests were deployed over the mallard nesting period (late winter – spring) in both 2019 and 2020 and monitored with motion detection cameras. Prior to 2020 artificial nest deployment, farm-scale trapping of mammalian predators was conducted on one farm whilst the other was left as a control. Feral cats (*Felis catus*), brushtail possums (*Trichosurus vulpecula*), and European hedgehogs (*Erinaceus europaeus*) frequently visited the artificial nests but seldom preyed on them (i.e. consumed the eggs). Swamp harrier (*Circus approximans*) were the most common predator and were responsible for the destruction or predation of at least one egg at 17% of the artificial nests. Mammalian predator trapping had no noticeable effect on artificial nest predation, but did reduce the probability an artificial nest was visited by a cat, possum, or hedgehog. Results suggest typical predator control efforts of gamebird hunters does not reduce mallard nest predation, but may reduce nest disturbance and consequently mallard hen predation and nest abandonment.

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Key words: mallard, mammalian, predator, predator control, trapping, artificial nest

INTRODUCTION

Globally, introduced mammalian predators are implicated in the decline of biodiversity (Blackburn *et al.* 2004; Doherty *et al.* 2016). In New Zealand, feral cats (*Felis catus*), stoats (*Mustela erminea*), weasels (*Mustela nivalis*), ferrets (*Mustela furo*), brushtail possums (*Trichosurus vulpecula*), and European hedgehogs (*Erinaceus europaeus*) are all

predators of native avifauna, negatively affecting their populations (Moors 1983; Sanders & Maloney 2002; Moorhouse *et al.* 2003; Jones & Norbury 2006). As a result, significant effort is invested into the control of these introduced predators using a variety of methods (Baber *et al.* 2009; O'Donnell & Hoare 2012; Fea *et al.* 2021). Numerous studies have documented the benefits of mammalian predator control for native forest bird species

Received 23 July 2021; accepted 20 November 2021 *Correspondence: cohen.stewart@southlandfishgame.co.nz (Baber *et al.* 2009; O'Donnell & Hoare 2012; Fea *et al.* 2021); however, no New Zealand studies have looked at the potential benefit of predator control for gamebirds, specifically the mallard duck (*Anas platyrhynchos*), New Zealand's most important gamebird.

Predation and disturbance of mallard duck nests has been well documented in New Zealand (Garrick 2016; Sheppard 2017; Sheppard *et al.* 2019). For example, Sheppard (2017) assessed mallard nest survival at two New Zealand study sites (Waikato and Southland) and found that almost 40% of nests were subjected to at least one predation event; predators completely removed or destroyed all eggs from 8% of nests. At the Southland study site, 9% of mallard hens were killed by predators whilst on the nest, resulting in the loss of the nest. If these nest failure rates are applicable across Southland, each year thousands of mallard nests are disturbed or fail due to predators.

Mustelids (stoats, ferrets, weasels) and cats (domestic and feral) are suspected predators of mallard nests and incubating hens in the Southland agricultural landscape (Sheppard 2017; Sheppard *et al.* 2019; Stewart *et al.* 2019; Southland Fish and Game *unpubl. data*); however, hedgehogs and possums may also prey on mallard nests as they are known to consume bird eggs (Brown *et al.* 1993; McDonald *et al.* 2000; Sanders & Maloney 2002). Swamp harriers (*Circus approximans*) and pukeko (*Porphyrio melanotus*) are native predators of avian nests (Boulton & Cassey 2006; Kross *et al.* 2013; Innes *et al.* 2015) and have been observed preying on mallard nests (Morgan *et al.* 2006; CS *pers. obs.*).

The predation and disturbance of mallard nests and the laying/incubating hen is of concern for gamebird hunters and managers. Due to the non-migratory nature of mallards in New Zealand (McDougall 2012), hunters are concerned that the loss of local nests or incubating hens may affect local hunting opportunities. Predators also have the potential to negatively affect the regional mallard population, which is of concern for gamebird managers because some areas have relatively low and/or declining mallard abundance (McDougall & Amundson 2017).

Amongst some hunters and landowners there is interest in undertaking mammalian predator control to improve local mallard nest and brood survival (CS *pers. obs.*). However, many trapping programslack adequate trap densities and sustained effort (CS *pers. obs.*). International studies have documented improved mallard nesting success with predator control (Duebbert & Lokemoen 1980; Garrettson & Rohwer 2001; Amundson *et al.* 2013), but these studies are not comparable to New Zealand because of vast differences in landscape and predator guilds. Predator control in these studies was also unrealistically intensive for the average landowner or hunter to conduct without support. Before gamebird managers advocate for and logistically support hunters to undertake predator control for improved mallard nest survival, there is a need to understand how control of New Zealand specific mallard predators, with realistic trap densities and effort, could affect localised mallard nest success.

This study used artificial mallard nests paired with motion detection cameras, and a Before-After-Control-Impact (BACI) study design, to (1) determine the most likely predators of mallard nests in the Southland agricultural landscape, and (2) test whether farm-scale predator trapping of mustelids, feral cats, hedgehogs, and possums affects the predation and predator visitation of artificial mallard nests during the spring breeding season.

METHODS

Study area

Two Southland dairy farms were selected and approximately 150 hectares of each farm were used as study sites. The treatment site (predator trapping) site) was located near Roslyn Bush (46°20'35.4"S, 168°27′44.8″E) and the control site was located c. 20 km away near Lochiel (46°11'37.2"S, 168°17'57.8"E). Both sites had flat topography, were *c*. 35 m above sea level and surrounding land use consisted of intensive agriculture, specifically dairy cattle and sheep farmed on predominantly rye grass (Lolium perenne) pastures. Small streams, agricultural drains and five small (<1 ha) man-made waterfowl hunting ponds were present at both sites. The remaining land cover was limited to road verges, ditches, rank grass, and shelterbelts of typically macrocarpa (*Cupressus macrocarpa*), pine (*Pinus*) radiata), gum tree (Eucalyptus spp.), or flax (Phormium tenax).

Artificial nest deployment

In 2019 and 2020, at each site, 17 artificial mallard nests (hereafter nests), spaced at least 145 m apart were deployed every 12 days, over three periods: late August – early September, early September – mid-September, mid-September – early October (a total of 51 nests per site, each year). These periods encompass the peak nest initiation (28th of August) and the peak nesting period (late-August – early October) for mallard ducks in Southland (Garrick 2016; Sheppard 2017). Nests were deployed for 12 days to mimic the average mallard laying period in Southland; the period whereby a mallard hen lays her eggs (one a day) before starting to incubate the whole clutch (typically 12 eggs) (Bellrose & Kortright 1976; Sheppard 2017).

The nests were constructed using methods adapted from Gunnarsson & Elmberg (2008) and Pasitschniak-Arts & Messier (1995). All nest bowls were constructed with dry grass to keep nest crypsis comparable for each nest. The dry grass was compressed into a bowl and fashioned into a nest with a c. 23 cm diameter and 8 cm depth. Three brown domestic hen eggs (length c. 55 mm) were added to the nest and covered with wild mallard hen down and breast feathers. Brown hen eggs are commonly used in artificial nest experiments (Padyšáková et al. 2010; Purger & Mužinić 2010) and artificial clutches baited with hen eggs have a survival rate comparable to those baited with mallard eggs (Kreisinger & Albrecht 2008). Four drops of Avery® mallard scent was also added to the nest.

Nests were placed on the ground, in hedgerows and shelterbelts, both of which are common mallard hen nesting habitat (Sheppard 2017). Each nest was paired with either a Browning® Spec Ops Advantage trail camera or a Moultrie® M-880i trail camera fastened to a stake *c*. 0.8 m from the nest. Cameras were set on a three trigger burst with a 30 second delay between bursts. The lowest trigger sensitivity was used for both camera types because wind can cause within-frame vegetation to move which can trigger the cameras (CS *pers. obs.*). Preliminary tests with the cameras indicated that both trail camera brands had comparable detection capabilities.

After 12 days of deployment, the nests were inspected, and nest fate recorded. Following nest assessment, each nest and camera were removed. A new nest was then redeployed with a camera and placed in a different location within the study site. In 2019, nest positions were marked with a handheld GPS and after the 12-day nest deployment period, a river stone painted bright pink was placed on the ground to help identify where the nest had been placed. The GPS waypoint and pink stone enabled nest locations to be replicated in 2020.

Reviewing trail camera photographs

Following collection of the cameras, the photographs were processed. Types of nest predators and predator visitation rates were recorded. A nest fate was recorded as preyed on if at least one egg was destroyed or displaced from the nest. If a nest was preyed on and then scavenged (remnants of a broken egg consumed), scavenging was not recorded as a predation event but was recorded as a nest visit.

When assessing nest disturbance, if a predator was photographed at a nest site multiple times within a ten-minute period, this was recorded as a single visit. If a predator was photographed at a nest site for more than ten minutes, without a break away from the nest of at least ten minutes, this was also recorded as single visit. However, if a predator was detected at a nest site, then was absent from the nest site for 10 minutes or more, then was again detected at the nest site, these were recorded as separate visits. Predator visits (disturbance) included predators touching the nest contents, smelling the nest, and walking in proximity (*c*. 1 m) to the nest. After recording the daily visitation rates for each predator, the total number of visits by each predator for the 12-day nest deployment period was determined.

The artificial mallard nests were not used to estimate survival rates of natural nests as mallard nest survival has already been assessed in Southland (Sheppard 2017; Sheppard *et al.* 2019). Furthermore, the survival rates of artificial nests often differ from natural nests due to the absence of an incubating female and differing predator abilities (Willebrand & Marcström 1988; Kreisinger & Albrecht 2008).

Predator control

Between 29 May and 28 August 2020, predator trapping was conducted at the Roslyn Bush site (treatment site). Small mustelids (stoats and weasels) and hedgehogs were targeted using four trap tunnels (length 800 mm, width 220 mm, height 180 mm) and two Mark IV Fenn traps baited with fresh chicken necks and placed alongside hedgerows or shelter belts. Chicken necks were selected as a bait because they are readily available and convenient. Larger mustelids (ferrets) and hedgehogs were targeted using two DOC 250 traps, also baited with a chicken neck. Trap tunnels were spaced 260–505 m apart and checked and re-baited weekly. Cats were targeted using six live capture treadle trigger cage traps. Prior to cat trapping, local landowners were contacted to determine whether they owned any pet or farm cats. Pictures or descriptions of these cats were collected so cats could be released if captured.

All traps were placed in hedgerows or shelter belts. To enable convenient trap checking and baiting, five of the six cage traps were paired (*c*. 10 m away) with a mustelid trapping tunnel and all traps were located near a paddock gateway. To acclimatise cats to the traps, they were pre-baited weekly with two chicken necks for at least three weeks. With each successive week of pre-baiting, the pre-bait was positioned further into the cage (closer to the treadle trigger). The bottom of the cage was covered in leaf litter, so cats did not feel the metal cage underfoot. Traps were only set when pre-baits were being constantly eaten and fine overnight weather was forecasted. The cages were set overnight on six occasions throughout the three-month period and captured feral cats were euthanised.

Possum trapping was conducted over two nights (7–8 August, 2020) by recreational possum hunters. Prior to trapping, potential trap sites were pre-baited with a lure comprised of flour, icing sugar, and cinnamon. Following pre-baiting, over two consecutive nights, recreational hunters set thirty Victor ® #1 coil spring leghold traps (each night), baited with flour-based lure. The traps were set in hedgerows and shelterbelts, checked each morning, and captured possums were euthanised.

Statistical analysis

A BACI (Before-After-Control Impact) (Morrison *et al.* 2008) study design was used to assess the effectiveness of the predator control for reducing nest predation and disturbance. The number of predation events and nest visits were compared between sites. A single predation event or predator visit to a nest was treated as a success (Binomial distribution). To analyse the data, a Bayesian approach, similar to that of Conner *et al.* (2016) was used to assess the effect of predator control on nest predation and disturbance.

The probability of at least one encounter (or predation event) (*m*) in year *t* at the control site (*C*), or treatment site (*T*), is *Encounter*_{*t*,*T*|*c*} \sim *binom*(*m*_{*t*,*T*|*c*}, *Cameras*_{*t*,*T*|*c*}). The treatment site in year *t* was not

trapped but was trapped in year *t*+1. The relative change in encounters after trapping to before trapping is:

$$\frac{m_{t,T}}{m_{t,C}} = K_{Before}$$
$$\frac{m_{t+1,T}}{m_{t+1,C}} = K_{After}$$
$$\frac{K_{After}}{K_{Before}} = K_{BACI}$$

Where K_{BACI} is the relative change in nest visits/predation after trapping cf. before trapping. We used an uninformative prior to derive the posterior binomial distributions and analysed the relative ratios of the posterior distributions using Program R (3.5.1; R Core Team 2018), package R2OpenBUGS (Sturtz et al. 2005). We ran 10,000 iterations, 3 chains, and discarded the first 1000 as burn-in (Gelman & Rubin 1992). Trace plots were checked for convergence. The accuracy of the posterior estimates was checked such that the MC error/sample sd < 0.05. We used the step function to calculate the probability that $K_{BACI} < 1$ (i.e., that trapping resulted in less predator encounters/ predation).

	201	19	202	20	
Predator –	Treatment (n = 48)	Control (n = 48)	Treatment (n = 45)	Control (n = 48)	Total (n = 189)
Cat	2	0	0	1	3 (2%)
Possum	1	0	0	1	2 (1%)
Hedgehog	2	0	3	0	5 (3%)
Weasel	0	0	0	0	0
Stoat	0	0	0	0	0
Ferret	0	1	0	0	1 (<1%)
Swamp harrier	1	15	1	16	33 (17%)
Rat	0	0	0	0	0
Australian magpie	0	0	0	0	0
Pukeko	0	1	0	0	1 (<1%)
Dog	0	0	0	0	0
Unknown	0	1	1	0	2 (1%)

Table 1. Number of artificial mallard nests predated/destroyed by different predators, by study site and yearin Southland, New Zealand (n = number of artificial nests).

	201	19	202	20	
Predator	Treatment (n = 48)	Control (n = 48)	Treatment (n = 45)	Control (n = 48)	Total (both sites and years) (n = 189)
Cat	30 (63%)	19 (40%)	21 (47%)	25 (52%)	95 (50%)
Possum	30 (63%)	10 (21%)	30 (67%)	16 (33%)	86 (46%)
Hedgehog	30 (63%)	17 (35%)	27 (60%)	27 (56%)	95 (53%)
Weasel	1 (2%)	6 (16%)	2 (4%)	5 (10%)	14 (7%)
Stoat	3 (8%)	1 (2%)	0	4 (8%)	8 (4%)
Ferret	0	9 (19%)	4 (9%)	1 (4%)	14 (7%)
Swamp harrier	1 (2%)	15 (31%)	3 (7%)	16 (33%)	35 (19%)
Rat	4 (8%)	4 (8%)	1 (2%)	5 (10%)	14 (7%)
Australian magpie	4 (8%)	1 (2%)	0	0	5 (3%)
Pukeko	0	1 (2%)	0	0	1 (<1%)
Dog	2 (4%)	0	0	1 (2%)	3 (1%)
Unknown	19 (40%)	6 (13%)	16 (36%)	9 (19%)	49 (26%)

Table 2. Number of artificial mallard nests visited on at least one occasion by different potential predators, by study site and year in Southland, New Zealand (n = number of artificial nests).

RESULTS

Nest predation and destruction

Overall, 204 nests were deployed at the two study sites over two years (n = 51 each site, each year). Data were obtained from cameras at 189 nests while data from 15 nests were lost due to camera malfunctions (n = 5), animals knocking over the cameras (n = 9) or vegetation obscuring the cameras (n = 1). Of the 189 nests for which data were collected, 47 (25%) were destroyed (at least one egg broken/displaced from nest) by predators (Table 1).

Swamp harriers were the most common nest predator and predated/destroyed 33 of the 189 (17%) nests (Table 1). Direct swamp harrier predation of at least one egg occurred at 31 nests. Despite observing swamp harriers at both sites throughout the study, most (94%) swamp harrier predation of the nests occurred at the control site (Table 1). During visits by swamp harrier, the eggs were typically removed from the nest and on some occasions were consumed 2–3 m away from the nest. The only other predators to actively prey on the eggs were pukeko (n = 1) and possum (n = 1)1). The pukeko moved eggs just outside the nest and consumed them over three visits (one egg consumed per visit). The possum kept the egg in the nest and removed a c. 3 cm by 3 cm piece of shell from the egg, but consumed little (if any) of the contents.

Cats, hedgehogs, and ferrets destroyed some nests by displacing the eggs from the nest bowl or damaging the eggs. However, these predators did not consume any eggs. Hedgehogs and a ferret displaced eggs outside the nest bowl (15–20 cm) by rummaging through the nest, while cats displaced eggs from the nest bowl or broke eggs by trampling on them.

Artificial nest disturbance

Predators visited 181 of the 189 nests (96%). Hedgehogs, cats, possums, and swamp harriers were the most common nest visitors (Table 2). Further, the frequency in which the potential predators disturbed the nests varied (Table 3). Possums were the most frequent nest visitors and would often disturb the nests by smelling the nest or walking in proximity of the nests. On average, across both study sites and years, possums visited a nest an average of 2.7 times (Table 3). Cats and hedgehogs were frequently observed smelling the nests but would seldom physically disturb the nest. Rats (Rattus spp.) walked over the nests but did not appear to affect the eggs or nest structure. Stoats, weasels, and ferrets investigated the nest by climbing over the nest bowl and eggs, but they did not consume the eggs.

Predator control

Six trapping tunnels were deployed for 87 days capturing 18 hedgehogs and two stoats. Six cage traps were set overnight on six occasions and captured seven feral cats and one farm cat that was captured and released on four occasions. During the two nights of possum trapping, 31 possums were captured.

	201	9	202	0		
Predator	Treatment (n = 48)	Control (n = 48)	Treatment (n = 45)	Control (n = 48)	Total (both sites and years) (n = 189)	Number of visits $(\bar{x} \pm 1 \text{ se, range})$
Cat	55	68	38	113	274	1.45 ± 0.25 (0, 40)
Possum	170	49	218	75	512	$2.71 \pm 0.36 \; (0, 28)$
Hedgehog	121	46	82	93	342	$1.82 \pm 0.27 \; (0, 37)$
Weasel	3	8	2	6	19	$0.10 \pm 0.03 \; (0, 3)$
Stoat	3	1	0	12	16	$0.08 \pm 0.05 \; (0, 9)$
Ferret	0	13	8	3	24	$0.13 \pm 0.04 \; (0, 4)$
Swamp harrier	5	34	6	24	69	$0.37 \pm 0.07 \; (0, 5)$
Rat	6	11	1	23	41	$0.22 \pm 0.07 \; (0, 9)$
Australian magpie	12	1	0	0	13	$0.07 \pm 0.04 \; (0, 5)$
Pukeko	0	3	0	0	3	$0.02 \pm 0.02 \; (0, 3)$
Dog	2	0	0	1	3	$0.02 \pm 0.01 \; (0, 1)$
Unknown	41	11	29	19	100	$0.53 \pm 0.10 \; (0, 13)$
Total	418	245	384	369	1,416	6.87 ± 0.55 (0, 48)

Table 3. The number of times predators visited artificial mallard nests (frequency of disturbance) by study site and year in Southland, New Zealand (n = number of artificial nests).

Effect of predator trapping on artificial nest predation

Very few nests were preyed on or destroyed by cats, possums, hedgehogs, and mustelids at both sites and during both study periods (Table 1). An insufficient number of nests were preyed on by each mammalian predator to meaningfully test whether predator trapping had any effect on artificial nest survival, so it was inferred that small, farm-scale trapping of mammalian predators did not affect the nest predation rate.

Effect of predator trapping on disturbance at artificial nests

Predator trapping led to a decrease in the number of nests visited by feral cats, possums and hedgehogs. Nest visits of feral cats decreased by 40% ($K_{BACI} = 0.60$ (95% Bayesian Credible Interval (BCI) 0.316–1.016, median = 0.577) P($K_{BACI} < 1$) = 0.97. Nest visits by possums decreased by approximately 27%, $K_{BACI} = 0.73$ (BCI 0.32–1.39, median = 0.68), $P(K_{BACI} < 1) = 0.85$. For hedgehogs, nest visits decreased by approximately 36%, $K_{BACI} = 0.64$ (BCI 0.34–1.05, median = 0.61), $P(K_{BACI} < 1) = 0.96$.

DISCUSSION

In New Zealand, mallard nest predation, partial predation and nest failure is often attributed to cats and mustelids (Sheppard 2017; Stewart *et al.* 2019; CS *pers. obs.*). However, this study suggests that effects of mammalian predation on mallard

nests is relatively minor compared to predation by swamp harriers. It is therefore unlikely that current mammalian predator control efforts are achieving reduced mallard nest predation rates in Southland. Swamp harriers are known predators of bird nests throughout New Zealand (Boulton & Cassey 2006; Morgan *et al.* 2006; Kross *et al.* 2013; Innes *et al.* 2015), but this is the first study to illustrate that swamp harriers are probably the most important mallard nest predator in southern New Zealand.

Swamp harriers are abundant throughout New Zealand (Eakle 2008) and were frequently observed at both sites in this study. Under current legislation, swamp harriers are partially protected (Wildlife [Australasian Harrier] Notice 2012) and provision for control exists when they cause problems for domestic livestock. Predation of wild gamebirds on private land is not justification for swamp harrier control. The only way to reduce swamp harrier predation of mallard nests would be to establish initiatives to reduce their foraging success. Sheppard (2017) found that mallard nest survival was higher when hens selected more densely vegetated nesting sites. This may be because dense vegetation offers better nest crypsis, particularly for highly visual predators like swamp harriers. To enhance mallard nest survival, managers should encourage landowners to protect and create densely vegetated habitat (hedges and woodlots).

At both study sites, very few nests were preyed on or destroyed by cats, possums, hedgehogs, and mustelids both before and after trapping. Therefore, farm-scale control of mammalian predators will likely have little effect on mallard nest predation rates. Limited predation of the nests by cats, stoats, and ferrets was unexpected because these predators are known to consume bird eggs in both real (Sanders & Malonev 2002; Stewart et al. 2019) and artificial nests (Smith et al. 2008; Kross et al. 2013). The reason for limited nest predation may be related to the availability of alternative prey. At both study sites, mice (Mus musculus), Eurasian blackbird (Turdus merula), song thrush (Turdus philomelos), and common starling (Sturnus vulgaris) appeared locally abundant and were frequently photographed by the trail cameras. Reduced predation pressure on mallard nests due to the availability of alternative prey has been observed in North America. Ackerman (2002) found that mallard nest success was positively correlated with rodent abundance and concluded that rodents provided predators with an alternative food supply. Furthermore, in Southland, passerines and their eggs have been identified as the most common prey item in the diet of stoats during the mallard breeding season (Stewart *et al.* 2019) which suggests they are highly available and/or selected for.

Very limited predation of the eggs by possums and no predation by hedgehogs may be explained by their typical foraging habits in agricultural environments. Although hedgehogs and possums have been documented consuming bird eggs in some habitats (Brown *et al.* 1993; Sanders & Maloney 2002), in agricultural habitat, hedgehog diets typically consist of vegetation and invertebrates (Campbell 1973) whilst possum diets are comprised of vegetation (Harvie 1973).

Despite limited mammalian predation, hedgehogs, possums, and cats were photographed visiting the nests with some nests receiving multiple visits within the 12-day nest deployment period. Predator visitation of real nests may have negative consequences for the laying/incubating hen and the nest. A nest visit from a cat for example, may result in the predation of the hen, and loss of breeding females is a key driver of mallard productivity in New Zealand (Sheppard 2017). Additionally, nest disturbance may cause the mallard hen to abandon her nest (Sheppard *et* al. 2019; CS pers. obs.). This could have profound impacts on the population because the probability of renesting decreases with successive nests and clutch sizes become smaller (Arnold et al. 2010). In this study, predator trapping reduced the number of nests visited by 27-40%, depending on predator type. This finding suggests that small scale trapping programmes can decrease nest disturbance, which may enhance breeding productivity. This finding should be communicated to landowners and gamebird hunters to help encourage the uptake of predator trapping programs on private land.

Results from this study indicate that swamp harriers are the most likely mallard nest predator and that small scale removal of cats, possums, and hedgehogs could reduce the number of mallard nests disturbed by these predators. However, it is acknowledged that this study has some limitations. Firstly, an obvious criticism of artificial nests is that they lack realism. There are unavoidable foreign scents associated with the construction of artificial nests and the absence of a female bird which may influence predation rates (Willebrand & Marcström 1988). Secondly, the presence of a trail camera at nests may influence predation rates (Richardson et al. 2009). Finally, this study has limited spatial and temporal replication (the study was conducted over two years at two sites) so the magnitude of the effect of the predator control on nest disturbance should be interpreted prudently. Despite these limitations, this study has still provided some insight into mallard nest predation, how predators may interact with nests and the potential effect small-scale predator control could have on mallard nest survival and disturbance. Future studies should use trail cameras to validate the identity of mallard nest predators and those causing nest abandonment and, assess the effect of predator control on duckling survival, as it is the most important variable governing mallard population growth in New Zealand (Sheppard 2017).

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SHORT NOTE

Red-crowned parakeet (kākāriki, *Cyanoramphus novaezelandiae*) mortality inside and outside a fenced sanctuary in Wellington City, New Zealand

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Red-crowned parakeet (kākāriki, Cyanoramphus novaezelandiae) were translocated to Zealandia Te Māra a Tāne, a 225 ha fenced sanctuary, from Kāpiti Island in 2010–2011 (55 in 2010, 52 in 2011). At that time, kākāriki had not been successfully translocated to the mainland, with failed translocations in Mt Bruce Scenic Reserve (1968) and the Waitakere Ranges (1977-1985) (Miskelly & Powlesland 2013). Translocation to Zealandia presented several challenges, as the sanctuary is bordered by contiguous forest and suburban areas. Individuals leaving the sanctuary must contend with both introduced predators and novel conditions presented by urbanisation, such as the presence of buildings/windows, cars, exotic avian competitors, and fragmented habitat (Marzluff & Ewing 2001; van Heezik et al. 2010; Ausprey & Rodewald 2013; Machtans et al. 2013). Kākāriki are known to be vulnerable to introduced mammalian predators due to their habits of feeding on the ground and nesting in single entry cavities, resulting in them being primarily confined to

Received 25 May 2021; accepted 27 August 2021 *Correspondence: ellen.irwin@visitzealandia.com offshore islands (Pratt *et al.* 1987; O'Donnell 1996; Greene 1998, 2003; Higgins 1999; Ortiz-Catedral & Brunton 2009). Furthermore, predation by introduced predators, specifically cats (*Felis catus*), was cited as a potential cause of at least one of the failed translocations (MacMillan 1990).

The population established well in the sanctuary, and the translocation is now considered a success (Miskelly & Powlesland 2013); nevertheless, kākāriki establishment outside of the sanctuary is less certain. Studies of mortality can be used to evaluate risks to wild populations and indicate areas of conservation concern (Silva-Rodríguez *et al.* 2010; Scheelings 2015; Gonzalez-Astudillo *et al.* 2017). To better understand the threats the birds are facing in Wellington, we examined mortality records of kākāriki compiled by Zealandia staff.

After translocation, Żealandia staff kept records of any birds found dead inside or outside the sanctuary, noting the band combination if present, the sex and age class (adult/juvenile) of the bird, and the cause of death if known. If the body was found in good condition and the cause of death was not known, birds were sent off for necropsy. For the purposes of this study, we focused only on juvenile and adult birds, removing records of nestlings that failed to fledge as we had no comparative data from birds hatched outside the sanctuary, and nestlings were almost never sent for necropsy. We also compared the number of mortality records to the number of fledglings produced from Zealandia artificial nest boxes each season (as birds at Zealandia typically begin breeding in August or September, we denoted August as the start of the season). Because the number of nest boxes varied slightly between seasons, we divided the total number of fledglings by the number of nest boxes monitored to control for monitoring effort.

From 2010-2016, Zealandia staff recorded 39 deceased kākāriki; 85% of the birds died outside the sanctuary (n = 33) while 15% (n = 6) were within Zealandia. The majority (n = 27, or 73%of those whose age was known) were juveniles, mostly juvenile males (n = 16, or 57% of all birds whose age and sex were known). Only six females were found in total, two of which were juvenile, and there were records for six adult males. Half (n = 5) of the adult records were of birds transferred from Kāpiti that were killed within a few weeks or months after translocation. 54% of the total records (n = 21) and 59% (n = 16) of records for juveniles occurred between January and April. Of birds outside the sanctuary whose cause of death was known, 65% (n = 15) were killed by predators, mostly by cats (n = 9), and one record each for a mustelid (Mustelidae), dog (Canis familiaris), and avian predator, as well as three unknown predator kills. The next most common cause of death was collision into a window (26%; n = 6) followed by being hit by a car (9%; n = 2) (Table 1).

Overall, predation was the most common cause of death for kākāriki. Some predation by native avian predators, i.e. ruru (Ninox novaeseelandiae), kārearea (Falco novaeseelandiae), and kāhu (Circus approximans), would be expected even in a protected population. However, mammalian predators, specifically cats, were most frequently reported, likely because of the high number of roaming domestic cats in the suburban areas and reserves that surround Zealandia (Woolley & Hartley 2019); New Zealand has the highest recorded rate of cat ownership in the developed world (Mackay 2011). Some of the birds retrieved in this study were feeding on the ground in small, confined garden lawns surrounded by good cover when they were pounced upon (M. Booth pers. comm.); the tendency of kākāriki to feed on the ground may put them at extra risk from cats. However, people may also have been more likely to find birds killed by cats, as cats either bring their kills to their owners or because cat kills are often close to houses, and so more likely to be discovered (though it should be noted that despite this, cat kills are often underestimated;

Loyd *et al.* 2013). Mustelids, on the other hand, often cache their prey, making bodies difficult to find (Cuthbert 2003). Other mammalian predators may therefore still represent a threat to kākāriki population establishment outside Zealandia, particularly to females when they are incubating or brooding young nestlings, as they cannot escape from their nest cavity.

Most of the mortality records were of juvenile males. Kākāriki exhibit male-biased dispersal, where juvenile males tend to disperse greater distances than females post-fledging (Irwin et al. 2021). The skew in the records may therefore be from juvenile males dispersing from the sanctuary in greater numbers. Accordingly, most of the records took place between January and April, at a time when many juveniles are dispersing. Previous research on other bird species has noted greater juvenile mortality (specifically due to window-strikes) potentially related to longer postfledging dispersal movements (Hager & Craig 2014). In addition, summer and autumn are when many plants are flowering or fruiting (Irwin 2017). Kākāriki can be very selective for particular food sources, e.g. the fruits of certain trees like totara (Podocarpus totara) (Bellingham 1987; Irwin et al. 2021), and may therefore be more likely to leave the sanctuary and move around more when those ephemeral sources are available outside the fence.

As the number of kākāriki fledglings produced in Zealandia increased, particularly over 2014-2016, so did the number of mortality records, presumably because of the higher numbers of dispersing juveniles (Fig. 1A, B). The greater number of mortality records in the first few years after translocation was likely a result of postrelease dispersal, as most of the records were of founder (Kāpiti) birds. In addition, while the number of fledglings increased substantially in 2013/14, there was not a corresponding increase in mortality records. Given that most of the mortality records across all years were of juveniles outside Zealandia, this pattern could be due to fewer juveniles dispersing out of the sanctuary during this period. Juvenile retention into the population within Zealandia was still relatively high in 2013/14 (26% in 2013/14 versus 3% in 2014/15; Gray 2016).

As most of the recorded deaths were outside the sanctuary and related to anthropogenic threats, it is unlikely that the Zealandia population itself will crash. However, dispersal outside the sanctuary has the potential to result in source/sink dynamics between Zealandia and surrounding areas, as birds dispersing outside of the sanctuary likely have a much higher risk of mortality. Previous research radio-tracking juvenile kākāriki at Zealandia found that approximately one-third of juveniles that dispersed outside the sanctuary were killed by **Table 1.** Recorded deaths of red-crowned parakeet (kākāriki, *Cyanoramphus novaezelandiae*) in Wellington. Five of the birds (highlighted in grey) had transmitters attached as part of a radio-tracking study on juvenile dispersal, which led to their discovery. Birds whose origin is a question mark were unbanded. Data were compiled by Zealandia staff from 2010–2016.

Sex	Juvenile/ Adult	Origin	Date of death	Likely cause of death (if known)	Location of death (inside/outside sanctuary)
М	Adult	Kāpiti	July 2010	Cat kill	Outside
F	Adult	Kāpiti	September 2010	-	Outside
М	Adult	Kāpiti	October 2010	Car-run over	Outside
М	Adult	Kāpiti	October 2010	Window strike	Outside
F	Adult	Kāpiti	September 2011	Mustelid kill	Outside
М	Adult	Kāpiti	February 2012	Cat kill	Outside
?	?	?	March 2012	Cat kill	Outside
?	Juvenile	?	April 2012	Window strike	Outside
М	Juvenile	Zealandia	June 2012	Crop impaction-overeating	Inside
М	Adult	Zealandia	October 2012	Window strike	Outside
F	Adult	Zealandia	February 2013	-	Inside
М	Juvenile	Zealandia	December 2013	Window strike	Outside
?	Juvenile	?	January 2014	Window strike	Outside
М	Juvenile	Zealandia	February 2014	Cat kill	Outside
?	Juvenile	Zealandia	March 2014	Unknown predator kill	Outside
М	Juvenile	Zealandia	September 2014	-	Outside
F	Juvenile	Zealandia	November 2014	Flew into fence?	Inside
?	Juvenile	Zealandia	November 2014	-	Outside
М	Juvenile	Zealandia	January 2015	-	Outside
?	Juvenile	?	January 2015	Cat kill	Outside
М	Adult	Zealandia	February 2015	-	Outside
М	Juvenile	Zealandia	February 2015	-	Outside
?	Juvenile	?	February 2015	Cat kill	Outside
М	Juvenile	Zealandia	February 2015	Starvation	Inside
М	Juvenile	Zealandia	April 2015	Unknown predator kill	Outside
М	Juvenile	Zealandia	April 2015	Cat kill	Outside
F	Adult	Zealandia	August 2015	-	Outside
М	Juvenile	Zealandia	January 2016	Cat kill	Outside
?	Juvenile	Zealandia	March 2016	-	Inside
F	Juvenile	Zealandia	April 2016	Window strike	Outside
М	Juvenile	Zealandia	April 2016	-	Outside
?	?	?	April 2016	-	Outside
?	Juvenile	Zealandia	April 2016	Car-run over	Outside
М	Juvenile	Zealandia	May 2016	Cat kill	Outside
?	Juvenile	Zealandia	May 2016	Avian predator kill	Outside
М	Juvenile	Zealandia	June 2016	Unknown predator kill	Outside
М	Juvenile	?	June 2016	-	Outside
М	Juvenile	Zealandia	June 2016	Dog kill	Outside
М	Juvenile	Zealandia	August 2016	-	Inside



Figure 1. A. Number of red-crowned parakeet (kākāriki, *Cyanoramphus novaezelandiae*) mortality records and, B. the average number of chicks fledged from artificial nest boxes monitored at Zealandia from 2010–2016. To account for monitoring effort, the number of fledglings was divided by the number of nest boxes monitored each season.

predators within a few months (Irwin *et al.* 2021). These threats may therefore pose a risk to kākāriki population establishment outside the sanctuary, and more research should be done to assess the survival of birds outside Zealandia.

In conclusion, predation and other factors related to urbanisation (window strikes, cars) present a threat to kākāriki dispersing outside Zealandia. However, it should be noted that most dead birds both inside and outside the sanctuary are assumed to be never found, and there may have been biases in those that were recorded; for example, juveniles or males may be easier to locate than adult females, which could be more likely to die on the nest. Birds may also have been more likely to be found in areas (neighbourhoods, Zealandia tracks) frequented by people; this might have biased the data towards birds that were killed by dangers in those areas (cats, windows). Therefore, further investigation is required to examine the survival and threats to life stages not as well captured by this dataset, particularly birds breeding or hatched outside the sanctuary.

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- **Keywords:** kākāriki, red-crowned parakeet, mortality, translocation, dispersal, predation, urbanisation

SHORT NOTE

Extreme female-biased sexual size dimorphism in *Euryapteryx* moa (Aves: Dinornithiformes: Emeidae)

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The major conclusion of the most recent morphometric analyses of the moa genus *Euryapteryx* was that, apart from a north-south cline of increasing size in the North Island, there were no significant size differences between regional populations (Worthy 1987, 1992). As the regions and sites chosen did not include any of the populations west of the South Island's Main Divide (Worthy 1992), I measured leg bone lengths of individuals from the West Coast, Oparara, Takaka Hill, and Takaka Valley to provide a more complete geographic coverage but in the same manner as the original analyses. In particular, I wanted to see if there were any differences in size between birds in the glacial age "Western" and those in the Holocene "Eastern" faunas proposed by Worthy & Holdaway (1993, 2002). For further comparisons outside the regions dealt with in Worthy (1992), I measured bones from the glacial age deposit in Merino Cave (on the Annandale plateau in southern Marlborough), from Holocene sites in South

Canterbury, and of an individual from Wakapatu on the Southland coast. The study was not intended to be a comprehensive multidimensional morphometric analysis but rather to extend the coverage of the original papers, and to look for patterns in those data that may have been missed at the time. All specimens and elements measured are listed in Appendix 1. Locations of regions and sites are shown in Figure 1.

To ensure valid comparisons with the values cited in Worthy (1992), I measured the lengths of femora, tibiotarsi, and tarsometatarsi with a steel tape between the same morphological landmarks and rounded measurements to the nearest millimetre. Two contralateral elements of the same or very near the same length from the same site were treated as being from a single individual; only one, usually the left unless the right was less worn, was included in the analyses. In all, the lengths of 30 femora, 5 tibiotarsi, and 24 tarsometatarsi were obtained, representing the seven regions and sites, plus one individual with no locational data. The sample size of complete, adult tibiotarsi was too small for further analysis.

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Figure 1. Map of areas and sites (bold) for which new mensural data on *Euryapteryx* were obtained, and of regions and sites for which data are listed in Worthy (1992).

Available radiocarbon ages for the West Coast (Worthy & Holdaway 1993) and Takaka area (Worthy & Holdaway 1994) populations support the view that *Euryapteryx* was present west of the Main Divide only during the late Weichselian-Otiran glacial and the glacial-interglacial transition (17,000 to 11,000 years BP). A new radiocarbon age (UBA43573, 13,455 \pm 86 ¹⁴C years; 16,156 \pm 138 cal BP) for the sole Honeycomb Hill Cave *Euryapteryx* (Worthy 1993) confirmed its glacial-interglacial age. For Merino Cave (Annandale) although only two individuals were listed by Worthy & Holdaway (1995), the S33404 series in the Museum of New Zealand includes three right femora (S33404.4, _4.6, and _4.10) and one left femur (S33404.7) whose length (300 mm) may or may not match that of _4.10 (290+ mm). None of the Merino Cave *Euryapteryx* has been dated but ages on six of the co-occurring *Pachyornis* range from 14,010 ± 110 (NZA4447) to 38,200 ± 980 (NZA3816) ¹⁴C years (Worthy & Holdaway 1995). These are equivalent to a calibrated calendar date range of 16,974 \pm 181 to $42,442 \pm 630$ years BP (SHCal20 calibration curve

(Hogg et al. 2020) in OxCal4.4 software (Bronk Ramsey 1995, 2009).

I calculated summary statistics and performed statistical tests using PAST® Version 3.26b statistical software (Hammer *et al.* 2001). Only basic comparisons were possible with the information in table 1 in Worthy (1992) because that includes only summary statistics (sample size, mean, range, and coefficient of variation): for the *t*-tests I calculated the standard deviations from the means and coefficients of variation.



Figure 2. Measurements of leg bones of moa identified (mostly by morphology) as *Euryapteryx* in the collections of Te Papa Tongarewa Museum of New Zealand and Canterbury Museum from sites west of the axial mountain ranges of the South Island, New Zealand, and from the Annandale plateau (southern Marlborough), South Canterbury, and a site (Wakapatu) in Southland. A, black circles, femur lengths by site or region; grey bars, 5 mm bin histogram of femur lengths; black square, overall mean, with 1 σ error bars; pink symbol, mean for femora > 260 mm, with 2σ error bars; blue symbol, mean for femora < 260 mm, with 2σ error bars. **B**, black symbols, lengths of tarsometatarsi by site and region; *, holotype tarsometatarsus of Euryapteryx pygmaeus Hutton, 1891; other symbols and conventions as in A. In both, vertical dotted lines are centred on the gap between the 2σ error bars for the distributions of larger and smaller elements.

Table 1. Comparisons by Student's *t*-test between mean pooled femur lengths (mm) for *Euryapteryx* populations west of the New Zealand South Island Main Divide (WoMD) with those from east of the Divide (EoMD) and Annandale (Merino Cave) (this study) and measurements in Worthy (1987) and Worthy (1992). Individuals from west of the South Island Main Divide, Annandale, and Tangatupura of Weichselian-Otiran and glacial-interglacial age; remainder of Holocene age. Significant differences in **bold**. See Fig. 1 for locations of sites and regions.

	Site or region	Mean	SD	п	t	df	Р
Comparison	WoMD all	281.81	28.05	21	-	-	-
	WoMD "large"	293.35	14.37	17	-	-	-
	WoMD "small"	232.75	13.4	4	-	-	-
WoMD all versus	EoMD	279.3	28.37	8	0.2190	27	0.8283
WoMD all versus	Annandale	295.5	13.7	4	0.9427	23	0.3557
WoMD all versus	Pyramid Valley	288.4	10.38	8	0.6418	27	0.5264
WoMD all versus	Herbert	289.7	22.13	20	0.9966	39	0.3251
WoMD all versus	Hamilton's	291.5	20.46	16	1.8811	35	0.0683
WoMD all versus	O'Malley's, Paerau	300	19.95	21	2.4217	40	0.0201
WoMD all versus	Papatowai	274.3	14.26	41	1.4031	60	0.1657
WoMD all versus	Southern North Island	255.7	19.77	10	2.6374	29	0.0133
WoMD all versus	Tangatupura	194.4	17.2	88	18.2811	107	< 0.0001
WoMD large versus	Tangatupura "large"	204.2	9.2	62	31.0534	77	< 0.0001
WoMD small versus	Tangatupura "small"	171.2	5.4	26	17.0317	28	< 0.0001
WoMD all versus	Northland	224.7	9.44	7	5.2309	26	< 0.0001

It was clear that the pooled distributions for both femur and tarsometatarsus length were bimodal (Fig. 2), with ranges of 216-245 mm for the smaller and 270-320 mm for the larger. There were no differences in femur length between sites for the large birds from western sites (Single factor ANOVA, $F_{3,13} = 0.5366$, P = 0.6654), so the site samples were pooled for further analyses. With the pooled samples, the larger birds from west of the South Island Main Divide were the same size as those from east of the Divide (Table 1). This was so both for the (glacial age) contemporary eastern population on the Annandale plateau, and for most of the eastern Holocene sites and regions (Worthy & Holdaway 1995, 1996; Worthy 1997, 1998a, 1998b, 1998c) (Table 1). Only birds in the population preserved at Paerau in eastern Otago were significantly larger than the western birds Table 1).

The birds from the western South Island were, however, much larger than those from the North Island ("Southern North Island", Tangatupura, and "Northland", Table 1). The late glacial aged birds from the Tangatupura site in southern Hawke's Bay were even smaller than those in the sample from Northland measured by Worthy (1992). The Tangatupura birds were much smaller than those from the Holocene of the southern North Island (Table 1), 15,000 years later. If these two populations were of the same taxon, that would be unusual as a temporal application of Bergmann's Rule suggests that birds living in a glacial climate will be larger than those living in warmer climates.

lengths for both Mean femora and tarsometatarsi in individuals in the larger and smaller size classes, taken from either side of the major discontinuity in their distributions were highly significantly different. For femora, the difference between female mean femur length (293.2 mm, 95% confidence interval [CI] 287.41-299.02; *n* = 23) and that of males (234 mm, 95% CI = 221.22–246.78; n = 7) was highly significant (Equal variances, t = 10.151, $P = 6.9082 \times 10^{-11}$, $P_{\text{Monte Carlo}} =$ 0.0001. F test for equal variances, 1.059, P [same var.] = 0.832; Critical F value [P = 0.05] = 3.0546; $P_{\text{Monte Carlo}}$ [same var.] = 0.9274). Analysis using single factor ANOVA yielded the same (extremely high) level of significance: $F_{1,28} = 103$, $P = 6.908 \times 10^{-11}$, with homogeneous variances (Levene's test from means P = 0.8335). For the tarsometatarsi, the difference between the size classes (sexes) was also highly significant (Equal variances, t = 9.4805, $P = 3.16 \times 10^{-9}$) with means and 95% CIs of females being 220.33 mm and 213.46-227.21 mm, and for males, being 164.17 mm and 157.1-171.24 mm. Variances for the sexes were the same by *F* test (F = 4.2114, P = 0.1191). The differences were highly significant by single factor ANOVA ($F_{1,22} = 89.88$, $P = 3.16 \times 10^{-9}$), but the data (just) failed Levene's test for homogeneity of variances (P = 0.0455), probably because of the small samples (Welch's F test for unequal variances gave $F_{18,29} = 173.6$, $P = 8.907 \times 10^{-11}$).

The size difference between the sexes in the western South Island birds was as marked as that between the "large" and "small" femora in the



Figure 3. Comparison of body mass estimates between (B) a female *D. robustus* by volumetric analysis (Brassey *et al.* 2013) and two bone length algorithms (black solid line, Prange *et al.* [1979]; dashed, Field *et al.* [2013]). Algorithm estimates from Worthy (1994) (W) using the Prange *et al.* (1979) algorithm for "large" and "mid-sized" and "small" birds now understood to represent (large) females from drier environments, (mid-sized) females from wet forest, and (small) males.

Tangatupura sample (t = 17.0636, df = 86, 2-tailed P < 0.0001). These results show that *Euryapteryx* populations were highly sexually size dimorphic, regardless of whether they were from, overall, larger or smaller populations. The degree of size dimorphism (2 to 1 in favour of females) matched that of the South Island giant moa, which is usually considered as having the most extreme difference between the sexes (Allentoft *et al.* 2010).

Predicted body masses

Allometric formulae relating bone dimensions to body mass, e.g. those of Prange et al. (1979) and Field et al. (2013), derived from measurements on non-ratite birds have nevertheless been much used to estimate body masses for extinct ratites, including moa, e.g. Worthy & Holdaway (2002). These algorithms are now being supplemented, but not yet supplanted, by new techniques involving the generation of digital "envelopes" of body volumes (Brassey et al. 2013), which can provide independent estimates of body mass. As body mass is a key factor in the biology and physiology of organisms (Brassey 2016), once femur lengths for the populations and those separately for the males and females were obtained, the next step was to, as it were, put flesh on the bones and estimate the body masses of different populations and for the sexes within those populations.



Figure 4. Estimated mean body masses (kg) of moa identified as *Euryapteryx* in the collections of Te Papa Tongarewa Museum of New Zealand and Canterbury Museum. Masses derived from allometric relationships between femur length and mass developed by Prange et al. (1979) and Field et al. (2013). Individual moa from sites west of the axial mountain ranges of the South Island, New Zealand, and from the Annandale plateau (southern Marlborough), South Canterbury, and a site (Wakapatu) in Southland. A, black circles, body mass by site or region according to algorithm in Prange et al. (1979); grey bars, 5 kg bin histogram of body mass; black square, overall mean, with 1 σ error bars; pink symbol, mean for birds > 50 kg, with 2σ error bars; blue symbol, mean for femora < 50 kg, with 2 σ error bars. **B**, black symbols, body mass according to algorithm in Field et al. (2013) by site and region; symbols and conventions as in A. In both, vertical dotted lines centred on gap between the 2 σ error bars for the distributions of larger and smaller birds.

The mean (196 kg) for the body mass of a female South Island giant moa (*Dinornis robustus*) estimated by the body volume method (Brassey *et al.* 2013) was much higher than the estimated means (160.48 kg, 166.56 kg; Prange *et al.* 1979, Field *et al.* 2013, respectively) for the large females reported by Worthy (1994) (Fig. 3). The lower limit of the volume-based predicted range (155 kg) was also well above those (109–112 kg) from the algorithms. However, the upper limit of 245 kg agreed well

with 254–265 kg – although better with the lower Prange *et al.* (1979) value of 254 kg – from the femur length calculations. It appears that the volumetric method in this instance provided a mass range for large females, but not for the full range of female sizes, and not at all for the males. On this basis, I used the estimates from femur lengths, as being the best available at present, for the comparisons of *Euryapteryx* populations.

The estimated body masses for the South Island *Euryapteryx* populations are summarised in Fig. 4, and the western South Island populations compared with the North Island birds in Table 2. Using the more conservative Prange et al. (1979) algorithm, the mean body mass estimated for western South Island Euryapteryx females was 11.18% higher than for the pooled sample (Table 2): in contrast, the mean male body mass was only 58.7% of the pooled mean. For the contemporary Tangatupura population in the North Island, the proportions were 14.7% for females and 70.2%, respectively. Hence, the pooled data consistently underestimate the mean body mass of females and overestimate that of males, obscuring the dramatic sexual difference.

Sex ratios

A female-biased sex ratio in giant moa (*Dinornis* spp.) was confirmed by early ancient genetics studies (Bunce *et al.* 2003; Huynen *et al.* 2003). The expectation from a later genetic analysis of four species of moa in North Canterbury (Allentoft *et al.* 2010) was that, if the South Island populations were uniform, a pooled sample from *Euryapteryx* populations would have adult sex ratios close to 2.5:1 in favour of females.

The size distributions of the western South Island birds were numerically skewed, with larger femora outnumbering smaller by 23 to 7, and larger tarsometatarsi outnumbering smaller by 18 to 6. Taking the larger individuals as being females (as they are in taxa where genetic evidence is available (Allentoft *et al.* 2010, 2014), this suggests a sex ratio in the pooled samples of 3.29:1 based on the femora and 3:1 based on tarsometatarsi.

Both the femoral (3.29:1) and tarsometatarsal (3.33:1) sex ratios in the samples from the western South Island were higher than expected from the 2.5:1 of the North Canterbury genetic sample, which was shared by another emeid moa *Pachyornis elephantopus*. In the new data the sex ratio based on the number of femora was statistically significantly different from unity ($\chi^2 = 8.533$, P = 0.0035), as it was for the numbers of tarsometatarsi ($\chi^2 = 6.000$, P = 0.0143) as well.

The sex ratio in the North Canterbury sample was lower, though, than that for the third emeid there, *Emeus crassus*. Its North Canterbury population was represented in Pyramid Valley and Bell Hill Vineyard by 5.5 females for each male (Allentoft *et al.* 2010). The great difference (19.0:1 *vs* 1:1.5) between the sex ratios of South Island giant moa (*D. robustus*) from adjacent sites was attributed to habitat differences between the sexes (Allentoft *et al.* 2010).

The histograms in Worthy (1987: his figures 5 & 6) suggest that the sex ratios in samples from the late glacial Tangatupura population were, for the femora, nearly a 2:1 ratio in favour of large birds (61 v. 27; 2.26:1), and an even lower dominance at 1.65:1 of females with the tarsometatarsi (38:25, with two indeterminate). The distinction between "large" and "small" was much less clear for the tibiotarsi,

Table 2. Body masses (BM, kg) from femur length (FL, mm) for the western South Island, the contemporary Tangatupura (lower North Island), and Holocene Northland populations of *Euryapteryx*, according to the Prange *et al.* (1979) algorithm (transposed as $\log BM = (\log FL - \log 61.64)/0.359$ and that of Field *et al.* (2013) ($\ln BM = (2.82 \times \ln FL) - 4.74$).

				Body mass esti	imates (kg)		
		Pra	nge et al. (1	979)	Fie	eld et al. (20)13)
		Mean	SD	Range	Mean	SD	Range
Western South Island	All	68.98	17.74	32.88-98.28	70.85	18.43	33.47–101.38
	Males	40.49	6.4	32.88-46.71	41.31	6.61	33.47-47.74
	Females	77.14	10.55	61.22–98.28	79.34	10.99	62.79–101.38
Tangatupura	All	24.52	-	13.52-35.94	24.86	-	13.61–36.62
	Males	17.21	-	13.61–18.88	17.37	-	13.61–19.09
	Females	28.12	-	19.79-35.94	28.56	-	20.01-36.62
"Northland"	All	36.71	-	32.46-46.71	37.41	-	33.03-47.74

but taking the two in the third smallest bin as being "small", the ratio was 2.33:1 (28:12). Worthy (1987) does not comment on the contrast between the Tangatupura ratios and those from Tokerau Beach in the Far North, which did not depart from 1:1. For Tokerau Beach femora, counts from the histogram for the femoral sample are 52 large to 42 small (1:0.81), for the tibiotarsi, 38 large to 36 small (1:0.95), and for the tarsometatarsi, 37 large to 32 small (1:0.86).

Conclusions

Sexual size dimorphism in moa was detected first in leg bone dimensions (Cracraft 1976a, 1976b, 1976c) and explored in several taxa over the next 15 years (Worthy 1987, 1988a, 1988b, 1992), with varying conclusions as to its presence or absence. Female-biased extreme sexual dimorphism is now well established for giant moa (Dinornis spp.), based on genetically sexed individuals (Bunce et al. 2003; Huynen et al. 2003), after being suggested first on the basis of multivariate statistical analyses of leg bone dimensions (Cracraft 1976c). The invocation (Cracraft 1976c) and confirmation (Bunce et al. 2003; Huynen *et al.* 2003) of sexual dimorphism allowed the resolution of problems within a previously primarily size-based, species-rich complex, taxonomy which had endured into the 21st century (Worthy & Holdaway 2002). Whether recognition of size dimorphism in *Euryapteryx* foreshadows taxonomic changes is beyond the scope of this study.

This study has showed that birds of different geological ages from east and west of the South Island's Main Divide were generally of equal size. It is the first to show extreme sexual size dimorphism in all populations of *Euryapteryx* moa, with differences of the same magnitude (females near twice the size of males) as in giant moa. In terms of body mass, females ranged from 60-100 kg, with the males at 30–40 kg. These numbers may have some interest for studies of exploitation of *Euryapteryx* moa by early Polynesians, in so far as whether males or females were preferentially included in their diet. That in turn would have to consider the different sex ratios among *Euryapteryx* populations, ranging from two or more to one in most populations to equality in a far northern population. In the pre-human landscape, the body mass per unit area of adult females in most populations of Euryapteryx moas was 3-5 times that of males. Females would have consumed a similarly disparate proportion of the available diet.

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- **Keywords:** *Euryapteryx*, moa, Dinornithiformes, sexual size dimorphism, sex ratio

Appendix 1. *Euryapteryx* leg bones measured in Te Papa Tongarewa Museum of New Zealand and Canterbury Museum for this study.

Te Papa Tongarewa Museum of New Zealand - Wren Wrecker Passage, Honeycomb Hill Cave System, Oparara: S25656, Lfem, Ltbt, Ltmt, Tarakohe Lime Works, Takaka: DM 427, fem, tmt. Irvine's Tomo, Payne's Ford, Takaka: S27850, tmt; S27851, tmt; S27854, tmt; S27855, tmt; S27870, Lfem; S27871, Lfem; S27872, Lfem; S27874, Rfem; S27877, Lfem. Payne's Ford, Takaka: S30210, Rfem; S30211, Rfem. Kairuru Cave, Takaka Hill: S27798, tmt; S27895, Rtmt. S39016. Takaka Fossil Cave, Takaka Hill: S39016, fem, RLtbt, tmt (noted by T. Worthy as "very small"; tbt sampled for radiocarbon dating; N. Rawlence sampled fem for DNA); S39017, fem, tbt, tmt; S38942. "Takaka Hill": S24327, Rtmt. "Takaka" (probably Takaka Hill): S24322, LRtmt (Holotype of Euryapteryx pygmaeus Hutton, 1891. "Nelson District" (probably Takaka Hill): S24328, Rtmt. "No data": S24343, LRfem (Rfem sampled for DNA by A.

Cooper). Locality 13, upper level, Madonna Cave, West Coast: S28083, fem. Madonna-Equinox Cave system, Site 16: S28121, Rfem (intensively sampled), Rtmt. Madonna-Equinox Cave system, S28222, Rfem. Netherton Cave, South Canterbury: S33743, Rfem. Holocene Hole, southern Marlborough: S33370, fem. Merino Cave, Annandale, southern Marlborough: S33404.1, Ltmt; S33404.2, Ltmt; S33404.4, Rfem; S33404.6, Rfem; S33404.7, Lfem; S33404.10, Rfem. Home Creek, Waipara, North Canterbury: S33728, Rtmt. Wakapatu, Southland coast: DM455, Rfem, LRtbt, LRtmt.

Canterbury Museum - Bone Cave, Takaka Hill: Av21330, Lfem. "Takaka Hill, 4 Jan 1945": Av8551, Rfem; Av8555, Rfem; Av21329, Lfem, Ltmt. Av22361, Ltmt. "Charleston District", West Coast: Av29440, LRfem, Ltmt; Av29439, Rfem; Av29450, Rfem. Nettletrench Cave, West Coast: Av31223, Rfem. "Cowan, near Inangahua", West Coast: Av34552, Rtmt. Albury Park, South Canterbury: Av19283, Rtmt; Av19288, Ltmt; Av31328, LRfem, Rtmt.

SHORT NOTE

New Zealand falcon (*Falco novaeseelandiae*) attempts to adopt Muscovy duck (*Cairina moschata*) ducklings

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For a period of four weeks, starting in early September 2020, Hamurana (Rotorua) resident Bernie Kerr witnessed some extraordinary behaviour by an adult male New Zealand falcon (Falco novaeseelandiae). One morning when about to feed his chickens (Gallus gallus), and Muscovy duck (Cairina moschata) and her very young ducklings, he noticed them all behaving defensively, hiding under bushes within their 15 x 3 m open-topped pen. After hearing a loud 'kekking', he became aware of a New Zealand falcon perched in a tree nearby. The falcon identified, as an adult male, was subsequently observed flying to the metre-high enclosure fence with a small prey item and plucking it while perched on a post. The falcon then dropped into the pen, ran up to the ducklings, and attempted to offer them the prey item.

Over the following three weeks, the falcon was regularly observed near the pen, and became quite territorial, actively defending the area by frequently swooping at Bernie Kerr and fellow observer Lee Ormsby. The falcon also swooped at a feral cock common pheasant (*Phasianus colchicus*) and struck it on the head, when it ventured too close to the pen. The following summary is based on the author's own observations over four days in late September, supplemented by those made by Bernie and Lee.

The falcon visited the pen at least three times a day, usually in the early morning, around midday, and mid- to late afternoon. Once with a rock pigeon (*Columba livia*) but usually with a small passerine,

a house sparrow (Passer domesticus), yellowhammer (Emberiza citrinella), Eurasian blackbird (Turdus merula), or song thrush (Turdus philomelos). The chickens, and the Muscovy duck and ducklings, soon accepted his presence and thereafter largely ignored him. The prey was often already plucked. After landing in the pen, the falcon would run up to the ducklings and try to offer them pieces of the prey that he had bitten off. The ducklings were never observed taking the food and just ignored it so he would leave the prey with them, or take it away to cache. "Often there was a various collection of bird bits left behind daily. Usually up to 3 or 4 small passerines, mainly whole plucked sparrows, but some odd bits and pieces as well" (Bernie Kerr pers. comm., 8 October 2020).

If the falcon arrived without a prey item, he would frequently search for and retrieve a previously cached corpse from clumps of grass in the adjoining paddock, before entering the pen. On other occasions, the falcon perched in a large tree that overlooked the pen, and spent several minutes preening and looking around, before flying away. The falcon was never aggressive to the chickens, duck, or ducklings.

Unfortunately, no photos were taken of the falcon interacting with the ducklings; however, two short videos of the falcon attempting to bring prey to the ducklings were taken by Bernie Kerr. Although this footage does not provide conclusive evidence supporting the description of "adoption" above, it does demonstrate the activity of the falcon in the presence of the ducks, and their lack of alarm in its presence.

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The falcon was trapped and colour-banded by the author on 30 September 2020. By this date his visits had become irregular. The last food delivery to the ducklings was observed by Bernie Kerr on 2 October, and the falcon was last recorded in the area on 4 October 2020.

Adoption of other species (predominantly prev species) has been previously recorded by at least five species of raptors, including: black-breasted buzzards (Hamirostra melanosternon) adopting Nankeen kestrels (Falco cenchroides) (Cupper 1977); bald eagles (Haliaeetus leucocephalus) adopting redtailed hawks (Buteo jamaicensis) (Stefanek et al. 1992; Watson et al. 1993; Watson & Cunningham 1996), and a glaucous-winged gull (Larus glaucescens) (Anthony & Faris 2003) and white-tailed eagles (Haliaeetus albicilla) adopting common buzzards (Buteo buteo) (Literak & Mraz 2011), great spotted eagle (Aquila glanga) adopting marsh harrier (Circus aeruginosus) (Karyakin 2014), and steppe eagle (Aquila nipalensis) rearing long legged buzzards (Buteo rufinus) (Pulikova & Tugarev 2021). All these cases were presumed to be non-lethal predation, where live prey had been taken back to the nest. Most live prey delivered to raptor nestlings are killed and eaten. However, if the prey is a young bird which begs for food, it may on rare occasions be adopted and fed, and even reared to fledging (Spoffard & Amadon 1993).

Further to these cases of interspecific adoption involving a buzzard and four eagle species, the author is aware of only two previous examples of falcons adopting other species. A pair of peregrine falcons (*Falco peregrinus*) adopted three young herring gulls (*Larus argentatus*) (http:// southwestperegrine.org.uk>2014/06/13), and a pair of American kestrels (Falco sparverius) adopted a brood of common starlings (Sturnus vulgaris) (Tlusty & Hamerstrom 1992). Following a breeding failure at the brood stage, the kestrels transferred their attention to a nestbox 1.1 km away, which contained a brood of young common starlings, and so the adopted chicks came with the nest site, rather than being delivered as intended food items (Tlusty & Hamerstrom 1992).

While the circumstances under which adoption of potential prey species by raptors may differ, it is likely that this behaviour is due to an innate drive to care for begging young. "The instincts around breeding are very strong and the male New Zealand falcon especially, has to match his behaviour with whatever is going on, rather than being more closely governed by the cycle of hormones as the female is. It appears that being in breeding condition, and for one reason or another his own breeding effort has failed or maybe not materialised, he could be triggered by a stimulus such as the ducklings which are small, fluffy, and have a plaintive cheeping call, and his paternal instincts have taken over" (Nick Fox *pers. comm.*, 7 October 2020).

The attempted adoption of Muscovy ducklings described here is particularly notable as it occurred away from any known falcon nest site, and the male falcon persisted for several weeks, despite the ducklings not being observed showing any interest in the food items offered.

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SHORT NOTE

Breeding and movement of a banded fairy tern (*Sternula nereis exsul*) in New Caledonia

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There are currently three subspecies of fairy tern (*Sternula nereis*) recognised; *S.n. nereis* in Australia, *S. n. exsul* in New Caledonia, and *S. n. davisae* in New Zealand (Harrison *et al.* 2021). In New Caledonia, fairy terns nest on islets close to the west coast of Grande-Terre, off both the northern and southern regions of the island (Barré *et al.* 2012).

In the northern lagoon, on Magone Islet (Fig. 1), in 2018, the first clutches were laid in mid-May and the last clutches still incubating in late August but the colony was deserted in early September (PV *pers. obs.*). In the southern lagoon, on the islet Amédée (Fig. 1), in 2019–2021, breeding took place from April to the end of September, and the first clutches were found in early May and the last ones in late August to mid-September, with clutches in 3–4 periods (PB *pers. obs.*). On both islets, the last clutches were all abandoned, even one that still had a growing embryo in the shell.

Over 68 days during 29 June to 5 September 2018, we monitored the breeding behaviour of a small fairy tern colony (40 nests) on Magone Islet (Villard et al. 2020). On 1 July 2018, a previously banded female fairy tern was observed incubating two eggs. After four days of observation, one of the eggs hatched (Fig. 2a). Nine days later, the chick was preyed on by a whistling kite (Haliastur sphenurus), which removed it; the unhatched egg, which had been incubated up until this time (Fig. 2b), was found to have disappeared. On the same day and the next, the nesting pair returned to the nest site several times with fish, presumably to feed the now absent chick. The pair then disappeared, returning to the colony nine days later. The banded female mated with its partner (Fig. 2c) and the pair attempted to re-nest, i.e. a territory was established and three nest scrapes made (Fig. 2d), but a replacement clutch was never laid. Forty-three days later, the banded female left the deserted colony site. She had begun to moult into post-nuptial plumage, indicated by increased blackening at the

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Figure 1. Grande-Terre, New Caledonia, with the islets of Pouh (24 September 2013), Magone (29 June to 5 September 2018) and Amédée (May 2019 to September 2021), where observations of fairy terns were made.

tip and base of the yellow bill, and mottling of the black head cap (Fig. 2e, see Dunlop 2018; Greenwell *et al.* 2021).

After departing Magone Islet at the end of the present study period, the female was observed again *c*. 16 months later on 11 January 2020 in eclipse plumage (Fig. 2f). She was sighted 317 km southeast of Magone Islet on Amédée Islet. She was originally banded five years earlier (24 September 2013, SCO) on Pouh Islet, 10.5 km from Magone Islet (Fig. 1).

On Amédée Islet, outside of the breeding season, colonies of *S. n. exsul* are known to exceed 100 individuals (about 95% adult and 5% immature). Counts of 111 and 124 fairy terns were recorded on 30 January 2010 and 23 January 2011, respectively (*unpubl. data*). Outside the breeding season, the southern lagoon hosts a relatively large proportion of the New Caledonian fairy tern population, with a total of 255 and 233 individuals recorded in January 2010 and 2011, respectively (*unpubl. data*).

These counts suggest that the southern lagoon may be an important post-breeding area for the species, including for those birds breeding on the northwestern islets like Magone Islet (*unpubl. data*). On the Australian west coast, mark-recapture records of *S. n. nereis* show that one population is semi-migratory, with one individual moving as far as 1,100 km between breeding and wintering grounds (Dunlop & Greenwell 2020). At the end of the breeding season large numbers have been observed aggregating on Rottnest Island on the Peel Harvey estuary, lower west coast. Also, in



Figure 2. Observations of the banded female (yellowaluminium on the left leg and green-yellow on the right leg, with the yellow band sometimes slipping over the aluminium band) on Magone Islet (Fig. 2a-e) and Amédée Islet (Fig. 2f). (a) The male incubating the chick and the female with a fish to feed the chick (hatched 6 July 2018). (b) The female incubating the second egg when the chick is 7 days old (11 July 2018). (c) The male with a food offering for the female just before mating, 12 days after the chick was preved upon (26 July 2018). (d) The pair in a nest scrape 13 days after the predation of the chick (27 July 2018). (e) The female before leaving the nesting colony. She is beginning to lose her breeding plumage as the base of the upper mandible is starting to turn from yellow to black (4 September 2018). (f) The female in eclipse plumage on Amédée Islet (11 January 2020). Images: (a-e) ©PV, (f) ©PB.

New Zealand North Island there is seasonal movement form the east coast nesting grounds to the west coast (Parrish & Pulham 1995).

Our observation of a banded adult female provides the first record of such movements by *S. n. exsul* between islets in the north and south of the lagoon, around Grande-Terre. Further observations of banded individuals are needed to determine the extent in which New Caledonian fairy terns travel between these islets outside the breeding season.

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SHORT NOTE

At-sea surveys reveal new insights of fine-scale distribution and foraging behaviour of Chatham albatrosses (*Thalassarche eremita*) in central southern Peru

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The Chatham albatross (*Thalassarche eremita*) is a highly migratory species, breeding exclusively on The Pyramid, a small rocky islet, in the southern outskirts of the Chatham Islands (44°26'S, 176°14'W), located ~900 km eastward of the New Zealand South Island (ACAP 2010; Deppe 2012). Between 5,304 and 5,500 pairs breed annually (Robertson

Received 23 August 2021; accepted 17 November 2021 *Correspondence: javierantonioquinones@gmail.com *et al.* 2003; Bell *et al.* 2017) Eggs are laid from September to October and hatch during November and December, with chicks fledging from March to April (ACAP 2010; Deppe 2014). Until the 1990s it was thought that Chatham albatrosses did not venture beyond the Central Pacific (Reid & James 1997), with some rare records south of Tasmania in Australia and on the South African coast (Reid & James 1997; Ryan 2002). However, vessel sightings and the first satellite tracking studies in the 1990s



Figure 1. Chatham albatrosses (*Thalassarche eremita*) in southern Peru, one individual was photographed eating offal discards in the longline SSF off Ilo. Photo credits: Top Left, Cristian Moreno; others, Javier Quiñones

identified the coastal waters of Chile and Peru as regularly visited areas during their winter (Robertson *et al.* 2000; Spear *et al.* 2003; BirdLife International 2004; Latham *et al.* 2004; Nicholls & Robertson 2007).

Incidental records of Chatham albatrosses along the Peruvian coast exist since July 1988, when one individual was registered about 165 nautical miles (nm) off Chiclayo (07°54'S, 82°21'W) (Haase 1994), and in 1999, a satellite-tagged adult was caught off the coast of Chimbote (~09°S), north Peru (Jahncke et al. 2001). Spear et al. (2003), over 15 years (1980–1995), identified approximately six Chatham albatrosses in Peruvian waters, all of them south of 13°27'S. In June 2008, one adult was sighted at 57 nm off Tacna (17°40'S, 73°15'W) (Pizarro-Neyra 2010). The first studies using Global Location Sensing (GLS) confirmed the species' wide distribution off the Peruvian coast. A total of 15 Chatham albatrosses that were fitted with archival light-recording tags at The Pyramid in 2007 showed trans-Pacific migration, with the highest densities recorded in Peruvian waters between 10°S and 20°S mainly in late autumn, evidencing that these birds spent a high amount of time in these waters (Deppe 2012). In addition, an incidental bycatch (~17°S) was recorded in the Ilo longline Small Scale Fishery (SSF) targeting sharks (Mangel 2012). There is more evidence (n = 4) of the presence of adult individuals in waters off southern Peru (15°-18°S) and one individual off Callao (12°S) for the period 2005–2017 (eBird 2021). With the exception of satellite tracking studies conducted in New Zealand (Deppe 2012), reports of the presence of Chatham albatrosses in Peru have been opportunistic, and consequently, there are some limitations to explaining the recurrent presence of Chatham albatrosses in Peru. This novel information provides onboard systematic studies that evidence their fine-scale

spatial distribution year-round and their foraging ecology in detail.

While there is good evidence of the general presence and distribution of the species in Peruvian waters during their wintering period (Deppe 2012), we do not have sufficient information on their fine-scale distribution. Spear *et al.* (2003) focused on their broad-scale distribution, abundance, behaviour, and seasonal patterns in the southeast Pacific. While this study is of extraordinary value, not least due to its long-term approach of 15 years, the vessel's course did not follow a regular pattern, survey tracks were more than 180 nautical miles [nm] apart, and the number of surveys comparatively small with fewer than two surveys per year (12 in autumn and 9 in spring).

In this study, we undertook systematic vesselbased survey observations of Chatham albatross occurrence along the Peruvian coast. Seven at-sea pelagic surveys were conducted during 2018-2020 (three in the austral summer, three in spring, and one in autumn) onboard the BIC Humboldt and Jose Olaya, both research vessels of the Peruvian Marine Research Institute (IMARPE). The surveys were part of the biannual Pelagic Anchovy Surveys and covered a latitudinal range for almost the entire Peruvian coast from 04°00'S (Punta Sal, Tumbes) to 18°20'S (border with Chile) except in autumn 2019 from 06°57'S (Isla Lobos de Tierra, Lambayeque) to 18°20'S. Distances covered during the surveys ranged from 3.5 km to 180 km (100 nm) offshore (Fig. 2), encompassing 45 parallel transects, each separated by 15 nm. Birds were sighted with the aid of 10 x 50 binoculars within a 300 m striptransect by two observers on both sides of the bridge. Observations were continuous from civil dawn to dusk (approximate 0530 h – 1830 h local time, GMT – 0500 h) at a cruise speed of 10 knots. Transects were partitioned every 6 minutes or 1 nm for density calculation purposes.

Three additional sources of information were added to the IMARPE vessel-based surveys. First, we obtained information from a reliable observer network led by the NGO ProDelphinus, which was working onboard the longline SSF fleet of Ilo (17°38'S, 71°20'W) and Salaverry (08°13'S, 78°58'W). This fishing fleet operates throughout the year from the continental slope to the border of the Exclusive Economic Zone (EEZ) at 200 nm (370 km) offshore. In summer and early autumn they target dolphinfish (Coryphaena hippurus), and during late autumn, winter, and spring they target blue sharks (Prionace glauca) and mako sharks (Isurus oxyrhynchus). It should be noted that part of the Ilo fleet during the summer moves to Pucusana (12°28'S, 76°47'W), located more than 1,000 km to the north. The information obtained consisted of sightings of Chatham albatrosses that were



Figure 2. Spatial distribution and abundances of Chatham albatrosses (*Thalassarche eremita*) during 2004–2021 (solid yellow circles). The continuous blue line represents the 200 m isobaths (continental shelf break) and the continuous brown line represents the Exclusive Economic Zone boundaries.

identified during fishing operations from 2004 to 2010. Second, observations were also made by IMARPE personnel in the SSF commercial fleet targeting jumbo squid (Dosidicus gigas), between Lomas, Arequipa (15°34'S) and Mollendo (17°S) up to 210 km offshore, during 16 fishing trips from spring 2015 until autumn 2017, covering all seasons. Third, sightings were carried out by the Universidad Científica del Sur (UCSUR) in conjunction with IMARPE in two trips (29 May -6 June 2021 and 1–9 July 2021) in the longline SSF targeting sharks in The Hague Triangle (18°36'S, 72°49′W) between the 180 km and 250 km offshore. In combination, the IMARPE, ProDelphinus, and IMARPE-UCSUR data provided sufficient information to analyse the spatial distribution, seasonal variability, and habitat preference of the Chatham albatross in the Peruvian sea.

Species identification was determined using Shirihai (2008), Howell & Schmitt (2018), and Howell & Zufelt (2019). The intense sampling design allowed us to determine the use of different habitats by Chatham albatrosses over short periods, i.e. a snapshot of their distribution in different seasons. We characterized habitat use by this species according to ocean depth: continental shelf (0 to 200 m isobath); continental slope (201–4,500 m); Peru-Chile Trench (>4,500 m), and the Abyssal plain (offshore, beyond the Peru-Chile Trench). Habitat classification was an adaptation of Wakefield *et al.* (2011) for the specific bathymetric zones off the Peruvian coast.

A total of 7,215 observation hours were completed for all surveys. A total of 82 Chatham albatrosses were sighted from Callao (12°S) to the oceanic border with Chile (19°S) and 12-290 km offshore (Fig. 2). Most of the sightings (71%, n = 58)occurred in autumn, followed by winter (21%, n =17) and spring (5%, n = 4). Very few birds (4%, n =3) were observed during summer, despite the large survey effort during this season (three scientific cruises and five Jumbo squid trips by IMARPE and 30% of the longline effort by ProDelphinus). In autumn, birds occurred between 12°50'S and 19°15'S, 44-290 km offshore. In winter, birds were sighted between 12°S and 18°26'S, 32-145 nm. In spring, birds were recorded between 12°S to 15°36'S, 15–105 km, and finally in summer very few individuals at 13°40'S, 15°17'S and 16°50'S, 65–150 km (Fig. 2). No Chatham albatrosses were sighted north of 12°S.

The majority of sightings were over the continental slope (55%, n = 49), followed by the Abyssal plain (28%, n = 25) and the Peru–Chile Trench (15%, n = 13). Finally, only two individuals were sighted over the continental shelf (2%) (Table 1). The highest concentrations were in oceanic waters offshore the area between Mollendo (17°S) and the southern part of the Hague Triangle (18°50'S), at 50–220 km offshore. In this area, 52 Chatham albatrosses were observed, representing 63% of all sightings (Fig. 2). The mean distance of Chatham albatross sightings was 110.9 km offshore (range: 12.4–293.2 km, n = 68, Fig. 2). On three occasions, groups ≥3 Chatham albatrosses were observed. In autumn and winter 2016, during an "El Niño" year, these birds were observed gathered among highly active multispecies bird flocks (≥ 10 birds and ≥ 3 species), such as large groups (>30) individuals) of waved albatrosses (Phoebastria irrorata), Salvin's albatrosses (Thalassarche salvini), white-chinned petrels (Procellaria aequinoctialis), sooty shearwaters (Ardenna grisea), Hornby's storm petrels (Oceanodroma hornbyi), and Cape petrels (Daption capense). During autumn 2021, a group of four Chatham albatrosses was registered in The Hague Triangle. On this occasion these birds gathered with black-browed albatrosses (n = 10), white-chinned petrels (n = 25), Buller's albatrosses (*Thalassarche bulleri*) (n = 4), Chilean skuas (Catharacta chilensis) (n = 2), De Filippi's petrel (*Pterodroma delfilippiana*) (n = 2), Hornby's

Table 1. Habitat use of Chatham Albatross (*Thalassarche eremita*) off Peru. Habitat was characterized according to depth: Continental Shelf (0–200 m isobath), Continental Slope (201–4,500 m), Peru-Chile Trench (>4,500 m), and Abyssal plain (offshore the Peru Trench).

Habitat	Mean depth (range) (m)	Mean coast distance (km)	No. of birds (%)	No. of flocks	Mean no. of birds per flock
Continental Shelf	53 (52–54)	37.1	2 (2)	0	0
Continental Slope	2,267 (634–6,721)	84.8	49 (55)	6	2.3
Peru-Chile Trench	5,663 (4,589–6,773)	136.6	13 (15)	1	3
Abyssal plain	4,327 (3,132-5,527)	155.4	25 (28)	2	3

storm petrels (n = 10), and Elliot's storm petrels (*Oceanitis gracilis*) (n = 8). Single birds composed the majority (>72%) of sightings on this trip. A total of nine groups were recorded, each with a mean of 2.6 individuals (range: 2-4 birds) (Table 1).

All the surveys carried out by IMARPE (Research cruises and the jumbo squid observer program), all the UCSUR-IMARPE surveys, and the eBird sightings, included additional observations (including photographic captures), allowing us to determine the age-class composition and behavioural patterns of the Chatham albatross. Most individuals were adults (76.5%, n = 39), and the remainder were sub-adults (23%). During the non-breeding period in autumn, 15% were subadults (n = 5), while during the time when adult birds were at their colonies (winter – summer) sub-adults increased to 39%. Fifty-three percent (n = 27) of the birds were observed flying, 27% (n = 14) were on the water, 8% (n = 4) exhibited pelagic feeding and 12% (n = 6) were feeding on shark offal discards.

The capture of live prey by one first-year Chatham albatross was observed in autumn 2019 when the bird glided slowly at about 1m above the water at 98 km off Punta Caballas (15°30'S, 76°15'W) and landed in the middle of a multispecies bird flock. The flock was composed of more than 20 white-chinned petrels, more than 15 sooty shearwaters, 12 Hornby's storm petrels, and five Inca terns (*Larosterna inca*). We photographed this Chatham albatross feeding on a medium-size cephalopod, probably a giant squid (Dosidicus gigas). In addition, a couple of adult Chatham albatrosses were also observed feeding on offal discards in autumn 2016 at 71 km off Ilo (17°50'S, 71°57'W) in the middle of another multispecies bird flock composed of 40 sooty shearwaters, 13 whitebellied storm petrels (Fregetta grallaria), 12 whitechinned petrels, eight Hornby's storm petrels, seven wedge-rumped storm petrels (Oceanodroma tethys), four Salvin's albatrosses, and two blackbrowed albatrosses (Thalassarche melanophris).

The occurrence of Chatham albatrosses in central and southern Peru is the result of a vast

trans-Pacific migration of ~11,000 km from The Pyramid in the Chatham Islands. It is known that they disperse towards central Chile at the end of the breeding season around March-April each year (ACAP 2010; Deppe 2012). According to 45 individuals tracked in 2008-2010 using GLS loggers, all birds traverse the South Pacific Ocean at a mean latitude of 40°S, with a latitudinal extension from 30°S to 50°S (Deppe 2012). Juveniles and sub-adults tend to disperse great distances from their breeding colonies, often with an eastward movement driven by the strong prevailing westerly winds that dominate the Southern Ocean between 30°S and 60°S (Weimerskirch et al. 2000). The influence of winds on albatrosses and petrel migrations is well documented (Weimerskirch et al. 2000; Suryan et al. 2008). The majority of our sightings (65%) were in autumn, coinciding with post-breeding timing. During this season the Subtropical let Stream (STJ) in the south Pacific Ocean is not fully developed (Nakamura & Shimpo 2004). Still, Chatham albatrosses traverse the Southern Pacific Ocean on both post- and pre-breeding migrations probably using low-pressure systems to progress rapidly downwind and slowing when caught up in a high-pressure ridge as was registered in southern Buller's albatrosses (Stahl & Sagar 2000). After traversing the Southern Pacific Ocean they are probably arriving in Chile at offshore waters in latitudes between Talca (35°S) and Puerto Aysen (45°S) and then shifting northward toward Peru, where in May they are mainly congregated off central and southern Peru in offshore pelagic waters (Quiñones et al. 2021). The Chatham albatross concentration in front of Mollendo appeared to indicate an important core area, as in this zone there were similar aggregations during 1997-1999, even in years influenced by strong "El *Niño*" events (Pashkow 2020), which means that the species continues to use those areas regardless of strong environmental changes.

Despite our observation effort, we did not see any Chatham albatross north of Callao (12°S), probably due to a mix of the prevailing environmental conditions, lack of food availability, and intraspecific competition with other albatross species. The highest aggregations of these birds (57% of our sightings) were in autumn in an area characterized by a complex interaction between the northward, cold and fresher Humboldt Current System (HCS) and the poleward subtropical Peru-Chile Undercurrent (PCUC), whose interaction forms eddy-like structures offshore the Peruvian shelf and shelf-slope, 15°S to 17°S (Chaigneau et al. 2013). In the south east Pacific eddies can extend the propagation of high primary productivity to offshore waters far from the coastal upwelling (Chaigneau et al. 2008). This productivity influx towards more oceanic waters in central and southern Perú coincides with the offshore spatial distribution of our observations of Chatham albatrosses, occurring in higher densities at an average distance of 107 km from the coast which is in the range where individuals have been recorded in their northward movements through the continental slope between isobaths 500-5,000m (BirdLife International 2004). In far oceanic waters, there is evidence of small-sized giant squid (Alegre *et al.* 2014) being more suitable prey for this albatross species. Finally, the presence of other albatross species during autumn, such as the more frequently observed Salvin's albatrosses and waved albatrosses (Phoebastria irrorata), both of which are particularly numerous in oceanic waters of the northern and central coast (Spear *et al.* 2003; Awkerman et al. 2006; Quiñones et al. 2021) and, consequently, probably outcompeting Chatham albatrosses.

In southern Perú, we observed several SSF fishing vessels targeting giant squid using squid jigs mainly over the continental slope, and targeting blue sharks (Prionace glauca) and shortfin mako sharks (*Isurus oxyrinchus*) using longlines, mainly over the Peru-Chile Trench and the Abyssal Plain (Adams et al. 2016). Both SSF are very common in oceanic waters in southern Perú (Adams et al. 2016; Csirke et al. 2018). In autumn, there is a spatial overlap of Chatham albatrosses with the SSF targeting giant squid in southern Peru (15°45'S – 18°S) (Sueiro & de la Puente 2013). One Chatham albatross was hooked by a squid jig in autumn 2016 and was safely released in Peruvian waters. In southern Peru, medium- and large-sized giant squids are distributed in oceanic waters (Paredes & de la Puente 2014). This was evidenced by a photo of a juvenile Chatham albatross feeding on a medium-size squid at ~100 km offshore at 15°30'S, 76°15'W in autumn 2019.

The longline SSF targeting sharks in Peru is active between March and November (Doherty *et al.* 2014). In southern Peru, the higher CPUE hot spots of both shark species occur in offshore waters over the Peru-Chile Trench and the Abyssal plain in the 16°–19°S and over the continental slope in the 17°30'S – 18°30'S (Adams *et al.* 2016). This spatially overlaps with 61% of our sightings of Chatham albatrosses. Due to the strong overlap of SSF and this albatross species in southern Perú, they are likely feeding in offal discards. For instance, when we used information with onboard observers on SSF, such as on the giant squid fishery (16 fishing trips), and the pelagic longline targeting sharks (two fishing trips), we register that in 37% of the cases, the Chatham albatrosses fed on offal discards, preferably eating the liver, after the sharks and giant squids were butchered. Apart from being a possible anthropogenic influence on species distribution in the region, this behaviour could also produce interactions or even bycatch. It is, therefore, a priority to identify the spatial overlap of the areas used by the birds and by the fishery to identify potential species conservation and management measures. Given the vast size of the small-scale fleets operating in Peru (Alfaro-Shigueto et al. 2010) and the overlap of fishing grounds with species distribution, the potential negative impacts on albatross and petrels are very high. The provided information both demonstrates and confirms the importance of offshore waters in central and southern Peru for adult and juvenile Chatham albatrosses during autumn. The finescale resolution of the observational data presented as well as the behavioural studies are giving new insights for the proper management of this vulnerable species.

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- **Keywords:** Southern Peru, Chatham albatross, Small Scale Fisheries, Foraging ecology.

Erratum

With reference to the paper: Walker, S.; Monks, A. 2018. Estimates of local occupancy for native land birds from the New Zealand bird atlases. *Notornis* 65(4): 223–236.

Table 2 runs over three pages (pp. 230–232), and on the third page (p. 232) of the table a typesetting error has required correction. An amended version of the pdf has been created and this is available for download on the website of the Birds New Zealand website https://www.birdsnz.org.nz/publications/. No changes are made to page length and the citation provided above remains applicable.



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