TRENDS IN DENSITY, ABUNDANCE, AND RESPONSE TO STORM DAMAGE FOR WESTLAND PETRELS *PROCELLARIA WESTLANDICA*, 2007–2019

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ABSTRACT

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The density and distribution of Westland Petrel burrows was assessed over a 12-year period (2007–2019). During that time, burrow density increased while occupancy remained stable, commensurate with an annual population growth rate of 1.022 (95% confidence interval: 0.971–1.076), as estimated using mark recapture data. From our surveys, we estimated a 2019 baseline population of ~6 200 breeding pairs and a world population of 13 800–17 600 individuals, covering around 95% of the population. Transects were conducted to establish the location and density of 17 petrel sub-colonies in rugged, untracked terrain in Paparoa National Park, West Coast, New Zealand. Major storms in 2014–2018 caused widespread treefall and landslides, destroying breeding habitat throughout the species' breeding range. Demographic effects of the major and ongoing habitat loss may continue in the medium to long term, as birds re-establish burrows and partnerships following loss of their habitat. Our study illustrates the complex effects of climate-related disruption on the biology of a long-lived species. With a single nesting area in the West Coast region, climate change will likely have an ongoing influence on the species' global population, since an increase in the frequency of severe weather events, including ex-tropical cyclones, is expected. However, current indications suggest that the species has some flexibility to adapt and to occupy new areas following habitat disturbance.

Key words: Climate change, seabird population estimate, rare climate event, breeding habitat destruction, endangered endemic species, Westland Petrel

INTRODUCTION

The Westland Petrel *Procellaria westlandica* is an endangered, single-site endemic species (Birdlife International 2018) for which management requires a robust population estimate using repeatable methodologies (Dilley *et al.* 2019). These estimates are necessary to monitor population changes in response to management actions and to detect threats such as habitat destruction or depredation by invasive species (Dilley *et al.* 2017, Waugh & Wilson 2017). Key features of survey robustness include the error estimation, documentation of the exact areas surveyed, and a methodology that enables repeated measures through time (Thompson *et al.* 1998). The Westland Petrel nests in rugged, untracked terrain characterized by karst features and sheer bluffs. Therefore, despite its relative accessibility (within 40 km of an urban centre), it remains poorly characterized. The species has several issues requiring conservation management, including fishery bycatch and threats within its terrestrial habitat (Waugh & Wilson 2017).

For long-lived species such as petrels, adverse effects of climate change on population growth can be difficult to track. These effects can include catastrophic influences of adverse climate events on breeding seabirds (e.g., Barbraud & Weimerskirch 2001), or they can be more subtle, such as disruption to breeding cycles and displacement of optimal breeding and feeding habitat (e.g., Durant *et al.* 2005).

The aim of our study was to estimate changes in population density and burrow occupancy for the Westland Petrel. We assessed the trend in burrow density at 17 sub-colonies from 2007 to 2019, and we estimated a minimum breeding population from the 2019 surveys. The population trend was assessed using capture-mark-recapture (CMR) analyses at the largest sub-colony ("Study"), where demographic studies have been undertaken for over 50 years (Waugh *et al.* 2015a). These studies provided an independent assessment of the trends we observed for the population. Finally, a major storm event caused by ex-tropical cyclone Ita in 2014 and subsequent storms in 2018 destroyed breeding habitat in parts of many of the Westland Petrel sub-colonies (Waugh *et al.* 2015b). This provided a unique opportunity to study the change in the petrel's breeding areas and breeding parameters in response to these perturbations.

METHODS

The Westland Petrel nests in steep, forested terrain in Paparoa National Park, near Punakaiki, New Zealand (42.144°S, 171.343°E; Fig. 1). Sub-colonies were surveyed, mapping a series of strip transects 20–200 m long and 2 m wide. Lines were located based on knowledge from previous surveys (Wood & Otley 2013) and were composed of contiguous clusters of nests. We excluded four sub-colonies identified in 2013 (Wood & Otley 2013) from the assessment in 2019, as they were deemed too difficult and unsafe to access due to storm damage of surrounding areas. These omitted sub-colonies contributed < 5% of the estimated total population in 2013 (Wood & Otley 2013).

Typically, surveyed areas featured gardened soil with little undergrowth, produced as a result of the petrels' activity. Areas around the periphery of sub-colonies were searched for burrows; if a burrow was not found within 20–50 m, we defined the new edge of the sub-colony at the last burrow on the transect. Transects were randomly placed along the slopes of each sub-colony and were separated by at least 20 m. Teams of 1–4 people conducted the surveys and marked the start and end of each transect using hand-held Garmin GPS accurate to ±5 m. Area estimates were taken from QGIS estimates of area for each sub-colony perimeter polygon (QGIS Development Team 2019). Area of sub-colonies and damaged zones were not corrected for slope due to the difficulties of working in cliffy terrain and dense vegetation, meaning that slope and length were not measured by alternative means. We preferred to maximise the number of transects in order to reduce the variance in burrow densities rather than to spend long periods on each individual transect. The surveys were conducted primarily in the austral summer (non-breeding: January–April) of 2007–2011. From 2014, the surveys were undertaken while birds were incubating (May–July) or early during the chick-rearing period (August). As burrows persist between years, the estimates of burrow density taken during the summer were considered representative of the

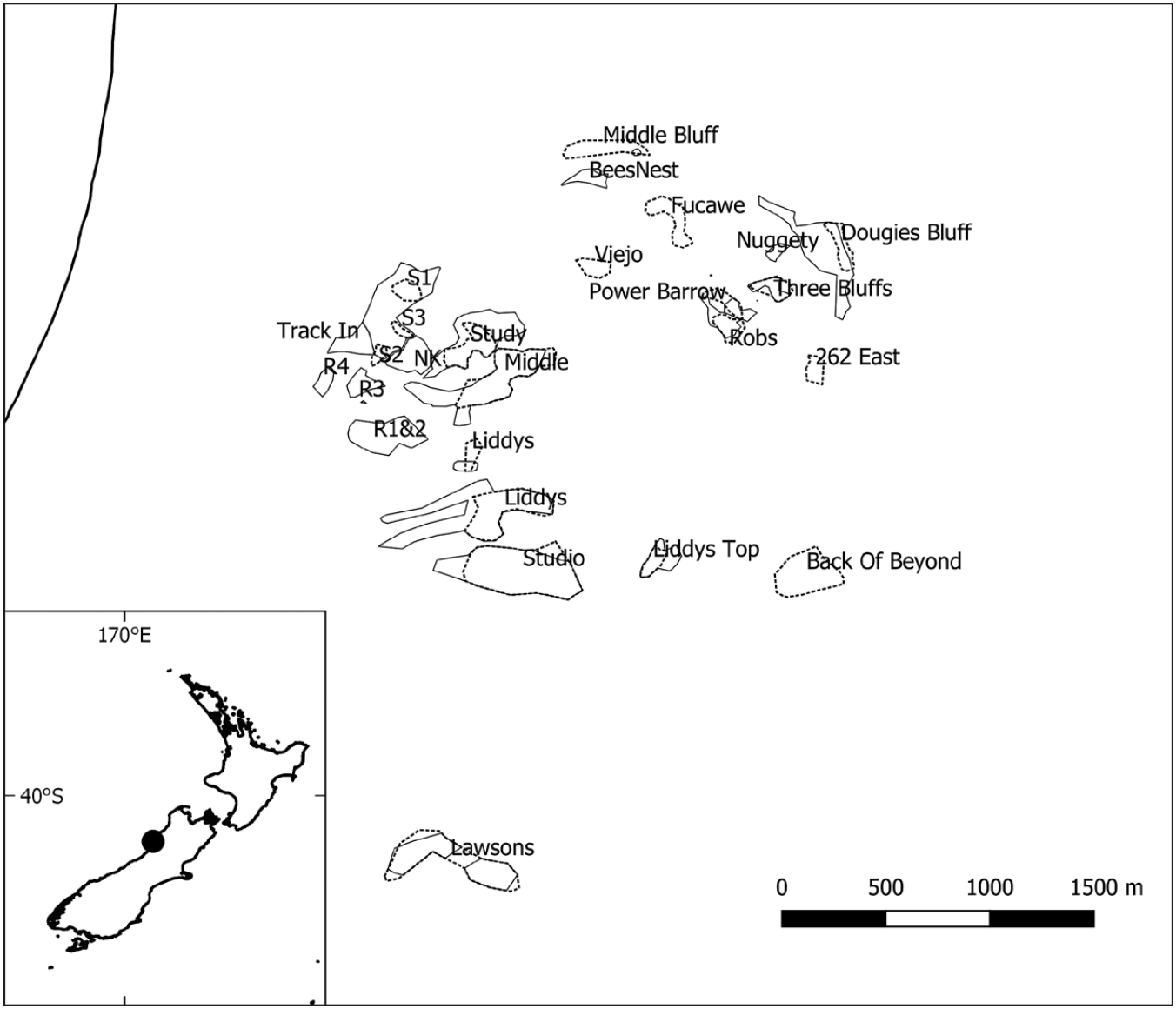

Fig. 1. Westland Petrel sub-colonies surveyed in 2007–2011 (dashed outlines) and 2019 (black outlines) on the mainland of the South Island of New Zealand at Punakaiki (black circle, inset). Sub-colony code names are S1–S3 for Solomon's 1–3, R1–4 for Rowe 1–4, NK for Noisy Knob. Areas with dashed outlines only were not surveyed in 2019.

breeding period density for the years immediately before and after the surveys. Burrowed areas are detectable mainly through visual cues and the lack of vegetation in the sub-colony areas. Other signs (odour, guano, sounds of birds) are not evident in the dense forest. The number of transects per year was as follows: 31 in 2007, 106 in 2008, 75 in 2011, 19 in 2014, 84 in 2016, 94 in 2017, and 367 in 2019. In 2019, a larger effort was deployed (around 50% of transects mapped) because funding and staff availability allowed a comprehensive coverage of most sub-colonies, including those in remote areas.

Following storm damage in 2014–2018, visual assessments and aerial photography (LINZ 2017) were used to identify sub-colonies that had been impacted by landslips or treefall. Most of these areas were visited in 2019 and, where possible, the perimeter of each landslip was assessed by taking GPS points at some of the margins. Not all these areas were fully mapped due to the danger and difficulty of working in unstable terrain. Slip and treefall area estimates are therefore considered to be qualitative.

Occupancy rate was assessed using burrow-scopes to see into randomly selected burrows. Occupancy rate was the proportion of burrows inspected that was occupied by one or more adult birds. A total of 31 burrow occupancy measures were taken at three of the 17 sub-colonies during 2008–2011 and at 12 of them in 2019. For each of these measures, 25 or more burrows were inspected, except at three sub-colonies where fewer were examined. The data were normally distributed (Shapiro-Wilk Test = 0.98, not significant). Between-year and sub-colony differences in occupancy rate were tested using ANOVA (in SYSTAT) with 12 sub-colonies and eight years of data. In 2019, burrows in three newly established areas were surveyed to assess occupancy rate differences between these areas and previously existing areas.

A 2019 estimate of breeding pairs was calculated for each sub-colony. The area of each sub-colony was assessed by marking a perimeter in GIS, mapping the entire area (i.e., including damaged areas); transects conducted within that perimeter enabled estimation of the average density of burrows. The area was then corrected for the estimated proportion of the surface damaged through slips and windfall. Burrow occupancy at each sub-colony was assessed during the 2019 incubation period to provide a corrected number of occupied burrows per sub-colony. The ratio of breeding to non-breeding birds was not assessed at each sub-colony. Instead, burrow occupancy was corrected for the proportion of breeders to non-breeders (0.480 ± 0.073) found in lidded study nests at Study

TABLE 1
Burrow density, occupancy, and estimated number of breeding pairs assessed in 2019[a,b]

Sub-colony ID	Breeding area name	A: total colony area estimated 2019 (m^2)	I: % colony impacted by storms since 2014	Number of transects 2007–2019	D: Mean (±SD) burrow density 2019	O: Occupancy rate 2019	Estimated number of occupied burrows 2019 (±SE)	Estimated number of breeding pairs 2019 (±SE)
1	Middle Bluff	708	0%	13	0.005 (0.015)	*	1 (1)	2 (0, LC)
2	BeesNest	7546	50%	34	0.029 (0.027)	0.50	55 (16)	26 (4)
4	Dougies Bluff	50566	38%	39	0.057 (0.630)	0.47	840 (1821)	403 (79)
5	Three Bluffs	7233	3%	7	0.015 (0.019)	*	40 (25)	19 (3, LC)
7	Solomon 1–3	62425	4%	34	0.064 (0.098)	0.40	1534 (470)	735 (113)
9	Power Barrow	6311	2%	14	0.050 (0.033)	*	118 (26)	56 (9)
10	Study	49356	6%	151	0.203 (0.133)	0.44	4144 (424)	1993 (305)
11	Track In	13581	0%	8	0.013 (0.019)	*	67 (35)	32 (5)
12	Robs	11160	3%	13	0.046 (0.035)	*	189 (72)	91 (14)
13	Noisy Knob	18755	9%	25	0.178 (0.090)	0.43	1306 (250)	624 (98)
14	Middle	59218	7%	119	0.035 (0.031)	0.42	810 (123)	388 (59)
18a	Rowe 1 & 2	33 540	11%	113	0.081 (0.091)	0.40	967 (222)	462(71)
18b	Rowe 3	9323	2%	7	0.025 (0.025)	*	87 (33)	42 (6)
18c	Rowe 4	5554	0%	14	0.011 (0.017)	0.43	26 (11)	12 (2)
19	Liddys	86933	3%	27	0.042 (0.044)	0.34	1204 (216)	577 (88)
20	Studio	86918	1%	49	0.026 (0.028)	0.43	962 (164)	463 (70, LC)
21	Liddys Top	13992	0%	21	0.075 (0.057)	0.38	399 (96)	192 (29)
24–26	Lawsons	24540	0%	45	0.016 (0.040)	*	149 (66)	72 (11)
27	Nuggety	3714	0%	13	0.047 (0.053)	*	66 (21)	32 (5)
Total		551373		776			12964 (1985)	6223 (380)

[a] For sub-colonies with no burrow-scoping data, the average occupancy value for 2019 (0.385) was used.
[b] LC = low confidence in estimated burrow numbers, SD = standard deviation, SE = standard error

Colony, estimated during 2015–2019 (n = 62–86 burrows/year). Using the data shown in Table 1, the estimated number of breeding pairs was calculated as A × (1–I) × D × O, where A is the area of occupancy, I is the percentage of area affected by storm damage, D is the mean burrow density, and O is the sub-colony-specific occupancy rate corrected by the proportion of birds breeding. Standard errors for the number of occupied burrows and number of breeding pairs were calculated using the delta method (Seber 1982).

Statistical methods

Burrow density analyses

Burrow density was modelled using generalized additive mixed models (GAMMs) in the mgcv library in R version 3.6.1 (R Core Team 2013, Wood 2017). This allowed for the possibility of nonlinear responses to covariates. GAMMs were specified with a Gaussian family, an identity link function, and restricted maximum-likelihood estimation. The response variable was the burrow density, and several models were fit to test different hypotheses. First, we modelled burrow density as constant across years. Second, we modelled burrow density as a function of year, with year specified as a categorical variable. The year 2015 was not included in this second model, since only two small sub-colonies were monitored and observed densities were clearly outliers compared to densities obtained in other years. Third, we tested for the effect of sub-colony on burrow density, where sub-colony was specified as a random factor. Fourth, we tested for spatial autocorrelation in burrow density by modelling spatial autocorrelation as an isotropic thin plate spline, set up as a two-dimensional smoother based on both x and y coordinates of the starting point of each transect. Finally, we tested for a temporal trend in burrow density by replacing the year effect with a continuous temporal covariate corresponding to the number of years monitored; this covariate was modelled using a smoother. Models were compared using the Akaike Information Criterion (AIC, Akaike 1973), and the model with the lowest AIC was selected. Model validation was conducted using residuals versus fitted values to verify homogeneity, QQ-plots and histograms of the residuals to verify normality, and residuals versus each explanatory variable to check independence (Zuur *et al.* 2009; see Figs. S1–S4 in Supplementary Materials).

Estimating population growth rate using CMR data

We used individual CMR data from 2010 to 2019 at Study Colony to estimate the population growth rate via marked individuals. Study Colony is a large, densely burrowed, and well-studied sub-colony, and it has been subject to demographic research projects conducted since the 1970s. During 2010–2019, we found Westland Petrels in 36–60 marked burrows having access lids. The birds were banded with stainless steel leg bands or recaptured if they were previously banded, and between 40 and 104 individuals were recaptured annually. Survival, recapture, and population growth rates were estimated from a sample size of 234 individuals. Over the study period, no band wear or loss was found, so we assumed that band loss was negligible. The birds' breeding status, band number,

TABLE 2
Modelling Westland Petrel burrow density[a]

Model name	Description	Model structure	AIC
Model 1	Density constant across years	density ~ 1	–786.1
Model 2	Density varying as a function of year	density ~ year	–877.7
Model 3	Density varying as a function of year and sub-colony	density ~ year + r(colony)	–1 139.4
Model 4	Density varying as a function of year, sub-colony, and spatial autocorrelation	density ~ year + r(colony) + s(x,y)	–1 156.9

[a] Density indicates burrow density, r(colony) indicates a random effect of sub-colony, and s(x,y) is a spatial smoother.

TABLE 3
Generalized additive mixed model (GAMM) results for Westland Petrel burrow density as a function of year, colony, and spatial autocorrelation (s(x,y))

Variable	Estimate (± standard error)	*t* value	*P* value	Estimated *df* [a]	*F*	*P* value
Intercept (2007)	0.070 (0.021)	3.346	<0.001			
2008	–0.013 (0.022)	–0.615	0.539			
2011	0.004 (0.022)	0.183	0.854			
2014	0.026 (0.031)	0.850	0.396			
2016	0.095 (0.022)	4.356	<0.001			
2017	0.061 (0.022)	2.823	0.005			
2019	0.014 (0.020)	0.732	0.464			
s(x,y)				13.94	1.912	0.015
Sub-colony				16.72	1.682	<0.001

[a] The year 2007 is used as a reference year.

weight, and burrow identifier were noted. This was a smaller number of burrows than was used for estimating nest changes (this study) and conducting earlier demographic analyses (Waugh *et al.* 2015a); these birds were in the part of the sub-colony that was unaffected by storm damage and that remained stable throughout the study period. Thus, recapture probability was used to estimate survivorship. To keep the study area constant and to avoid biases in population growth rate due to expansion or contraction of the study area following storm damage, we used CMR data that covered the whole 12-year period and discarded data from areas outside this core zone. In addition, since we used CMR data from 2010 to estimate population growth rate and since the CMR study started earlier (Waugh *et al.* 2015a), we were confident that growth rate was not biased upward due to individuals missed in the first years of the study.

We used Pradel's models (Pradel 1996) with the survival and lambda formulation in program MARK (White & Burnham 1999). We tested several models in which the adult survival probability (s) and the recapture probability were either constant or time-dependent but the population growth rate (l) was constant. Model selection was performed using AIC. Estimates were obtained from the Markov Chain Monte Carlo algorithm in MARK, with 20 000 tuning samples, 20 000 burn-in samples, and 50 000 stored samples.

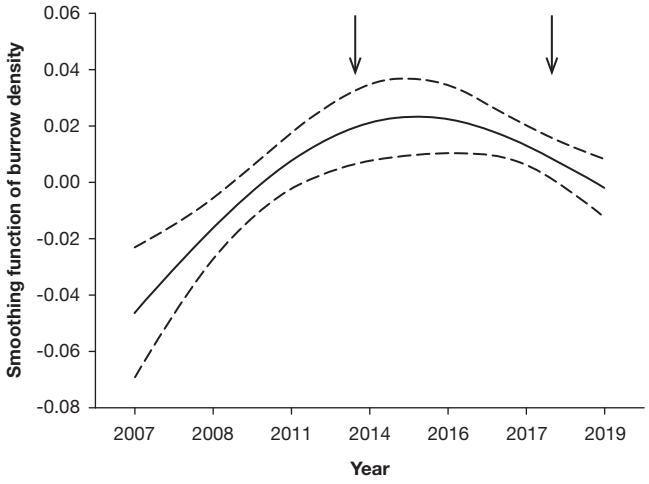

Fig. 2. Westland Petrel burrow density as a function of year. The plot shows the smoothing function of the predicted burrow density (solid line; estimated degrees of freedom of the smoothing function = –1.92) and 95% confidence intervals (dashed lines) from a generalized additive mixed model for the seven years during which data were collected. Arrows indicate approximate timing of storm events.

Effect of storms

To measure nest disruption due to storms, we used individual recapture histories to assess how many birds per year moved to new nests. Birds included in the sample were those that bred at least once before storm events and that were recorded using the study nests at Study Colony and Rowe Colony two or more times. We excluded the first capture if the bird was not recorded breeding in that year, to reduce the possible inclusion of pre-breeders. After the first observation, birds were classified as either having a new nest or the same nest compared to the previous observation (n = 392 bird-years; a bird-year is the sighting of a bird in a particular year). The proportion of birds observed in study nests breeding or not breeding in a given year was also analysed using these data. The number of study nests varied from 70 to 88 between 2010 and 2019, and we assumed that recapture effort was constant across years. Breeding success was assessed using the number of eggs observed in the early and middle portions of the incubation period (June to mid-July) that survived to fledge in November. Data were collected in 2010–2019 for these variables, but there was no breeding success data in 2010 or 2012. Differences between years were assessed using single-factor ANOVA in SYSTAT for each variable, grouping years into samples of 2010–2013 for pre-storm groups and 2014–2019 for post-storm groups.

RESULTS

Burrow densities and occupancy rates

Densities ranged 0.005–0.203 burrows/m^2 with most (75%) sub-colonies having densities of 0.015–0.075 burrows/m^2 (Table 1). The best-fitting model indicated that burrow density varied as a function of both year and sub-colony and was spatially autocorrelated (model 4; Tables 2, 3). This model explained 52% of the deviance in burrow density. Model validation indicated that there was no evidence for non-normality in residuals and that residuals were not related to fitted values (Supplementary Materials, Figs. S1–S4). Year-specific burrow densities indicated that densities were higher in 2016 and 2017 than in 2007 (Table 3). The model results for trends in burrow density indicated that there was a nearly quadratic temporal trend in burrow density with an increase in density from 2007 to 2016 and a slight decrease during 2017 to 2019 (Fig. 2, Table 4). From 2007 to 2019, burrow density increased by 20%, corresponding to a mean annual geometric increase of 1.5%. Sub-colony and spatial autocorrelation were also significant (Table 4).

There were no significant differences in burrow occupancy between years and sub-colonies or between new and established areas. Average burrow occupancy across all years and sub-colonies was 0.385 ± 0.116 (n = 31).

TABLE 4
Modelling temporal trends in Westland Petrel burrow density using generalized additive mixed modelling (GAMM)

Variable	Estimate (± standard error)	*t* value	*P* value	Estimated *df* [a]	*F*	*P* value
Intercept	0.095 (0.012)	7.814	<0.001			
s(trend)				1.925	7.937	<0.001
s(sub-colony)				8.023	1.288	<0.001
s(x,y)				17.505	2.692	<0.001

[a] The proportion of deviance explained is 49.2%.

Population growth rate

For Study Colony, the selected model indicated that adult survival and recapture probabilities were time dependent. The estimated population growth rate was 1.022 (95% higher posterior density confidence interval: 0.971–1.076). The probability that the population growth rate was higher than 1 was 0.80.

Number of breeding pairs and total population size

We estimated the number of breeding pairs based on burrow density estimates on a sub-colony by sub-colony basis (Table 1). The number of burrows in undamaged areas was estimated at 31 306 in 2019, of which an estimated 12 964 were occupied, giving an estimated 6 223 ± 380 (± standard error) breeding pairs in 2019 for the areas surveyed. Using the known age structure of the population to account for non-breeders (Waugh *et al.* 2015a) and assuming a 1:1 sex ratio, this gives a total population of 15 711 (95% confidence interval: 13 830–17 591) in 2019. At three sub-colonies (2 breeding pairs at Middle Bluff, 19 pairs at Three Bluffs, and 463 pairs at Studio), field teams had low confidence in the estimate produced by multiplying the area of the sub-colony by the densities (Table 1). They felt that the two smallest sub-colonies should have held more birds and that Studio was likely to hold fewer. The overall population estimate was not adjusted to account for these observations, but it was noted that for future surveys, greater effort would be needed to assess the density of burrows in areas within these sub-colonies to improve the quality of the estimates.

Storm damage and its impacts on breeding Westland Petrels

We qualitatively assessed the amount of habitat lost to landslips and treefall in 2014–2019 by identifying the perimeter of each sub-colony in 2019 (Table 5). These assessments included the areas damaged in the extensive 2014 storms and subsequent events, such as Cyclones Fehi and Gita in 2018. A qualitative assessment of the areas lost to landslips showed that most of the 17 sub-colonies surveyed in 2019 suffered some damage compared to the survey areas identified in 2007–2011. Three had 11%–50% of their area lost or damaged, nine sub-colonies had 1%–10%, and five had no signs of storm damage (Tables 1, 5).

For assessing changes in nesting habitat as a result of the storm damage, the dataset was composed of 409 banded individuals

TABLE 5
Storm damage at monitored colonies documented since 2014

Sub-colony ID	Breeding area name	Area estimated 2019 (m^2) including areas damaged	Assessment of landslip damage 2019 (m^2)	Estimate of windfall area 2019 (m^2)	% colony area impacted by storms since 2014	Summary of storm damage in 2019
1	Middle Bluff	708	0	0	0%	Burrows only in one small area, moderate vegetation damage but now landslips
2	BeesNest	7 546	443	3 344	50%	Significant damage throughout the colony
4	Dougies Bluff	50 566	480	18 715	38%	Severe windfall along ridge and eastern side
5	Three Bluffs	7 233	231	0	3%	Severe windfall on the upper section of the colony
7	Solomon's 1–3	62 425	931	1 666	4%	Smallish slips
9	Power Barrow	6311	0	141	2%	Minor tree damage, no slips observed
10	Study	49 356	1 178	1 686	6%	Slips and windfalls throughout
11	Track In	13 581	0	0	0%	Intact
12	Robs	11 160	0	284	3%	Minor tree damage, no slips observed
13	Noisy Knob	18 755	657	1 103	9%	Slip occurred in a small but densely burrowed area on the SE edge
14	Middle	59 218	400	3 809	7%	Windfall around outer edges, minor slips
18a	Rowe 1 & 2	33 540	1 197	2 607	11%	Large slips in the centre, and windfall throughout, continuing into 2019
18b	Rowe 3	9 323	0	215	2%	Tree damage, no slips observed
18c	Rowe 4	5 554	0	0	0%	No damage observed
19	Liddys	86 933	2 668	0	3%	One smallish slip on a steep slope
20	Studio	86 918	0	583	1%	Minor tree damage, no slips observed
21	Liddys Top	13 992	0	0	0%	Intact
24–26	Lawsons	24 540	0	0	0%	Intact
27	Nuggety	3 714	0	0	0%	Intact

sighted at Study Colony and 78 sighted at Rowe Colony during the study period. There were 278 nest transitions in the analysis, with 26 to new nests and 252 to the same nest. There was a minimum of one nest-year transition counted in these analyses for any bird (i.e., two years of data) and a maximum of eight. The proportion of birds moving to new nests was higher in 2014 (30%) than in other years, but there was no significant difference between the pre-storm period (average 2.6%, 2010–2013) and post-storm period (12%, 2014–2019; Fig. 3). The proportion of birds observed in study nests that made breeding attempts was stable, with an average of 41% (standard deviation (SD) = 5%), indicating no difference between the pre- and post-storm periods. Breeding success for study nests averaged 68.5% (SD = 0.11), and there was no significant difference between periods. We explored whether birds shifted long distances across the pre-and post-storm periods but found that only two adult birds were resighted away from their sub-colony of banding. Two birds banded at Rowe Colony in 2011 were recaptured on the surface, once each at Study Colony in the pre-breeding period in 2016. Neither was seen breeding at the second sub-colony.

DISCUSSION

The Westland Petrel population appears to have increased over the 12-year study period (2007–2019), as indicated by independent estimates of burrow density, burrow occupancy, area occupied, and population growth estimated from CMR analyses. Our transect surveys showed an overall increase in burrow density since 2007, with an average increase of 1.5% per year. Within the study period, the modelled densities increased between 2007 and 2016 and decreased slightly between 2017 and 2019. The population growth rate estimated from the CMR data between 2010 and 2019 (1.022) indicated an increase in population size and was similar to that obtained by Waugh *et al.* (2015a) from a 42-year dataset. These CMR data were collected at Study Colony, where density and burrow occupancy were measured multiple times over a 12-year period. Study Colony has an estimated 4 100 burrows, and our extensive transect sampling of other sub-colonies indicate that these changes can be generalized across the petrel sub-colonies.

The exceptions to this general increase were two sub-colonies (Dougies Bluff and Bees Nest, previously estimated to hold 13% of the population) that suffered extensive storm damage between 2014 and 2019 and decreased both in area occupied and estimated number of burrows. Three small sub-colonies (Three Bluffs, Power Barrow, and Robs; estimated to hold 3% of the total population) decreased in density but not area; these changes were unlikely to have affected the overall trends in numbers.

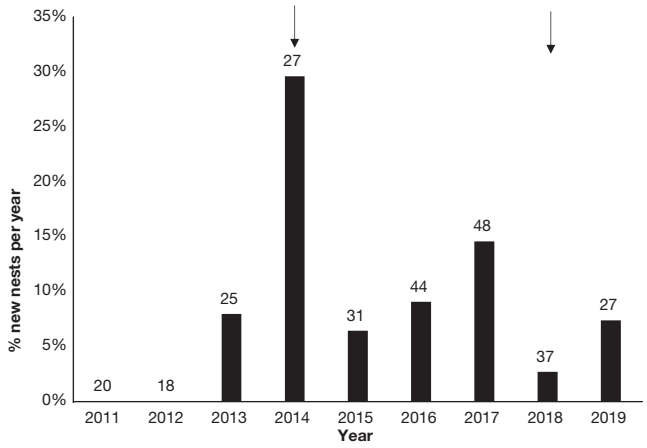

Fig. 3. Percentage of Westland Petrels changing nest per year (*n* per year shown above each bar), based on a sample of 278 bird-years for individuals that had previously bred. Arrows indicate approximate timing of storm events.

In addition to population growth inferred from the CMR dataset, the transect surveys identified areas of sub-colony growth, with the addition of some areas not found during the first four years of the study. Although surveys were equally thorough throughout the study period and the field teams included several of the same workers, it is possible that burrow density in newly identified areas may have been at the edge of detectability prior to 2012. In these areas, survey teams may not have detected very sparse burrows and thus assumed they were at the edge of the sub-colony. Many of these areas were between neighbouring sub-colonies (e.g., between Middle and Study, or between Noisy Knob and Solomon's) or were extensions into adjacent areas of the known sub-colonies (e.g. Dougies Bluff, Liddys, Rowe, and Studio). One area (Nuggety, identified for the first time as part of our surveys) is likely a newly established sub-colony, noted for the first time in 2019. These changes may be in part due to the natural population growth observed between 2007 and 2013 that saw individuals digging burrows in new areas, or it may be due to the relocation of displaced individuals in later years (2014–2018) , where birds moved away from sub-colonies damaged by landslips and treefall. Our individual capture and nest records showed an increase in birds changing burrows in 2014 immediately after the first major storm, though there was little evidence of birds moving between sub-colonies. Only two birds were seen outside of their original sub-colony, and they were non-breeding at the time of recapture in 2016. Our qualitative assessment of the zones occupied by burrowing petrels indicates that the spatial extent of sub-colonies has also been increasing.

The growth in burrow density despite stable occupancy rates at several medium and large sub-colonies indicates that the petrels are adapting to extreme weather events, and that they are establishing burrows within existing sub-colonies, extending these sub-colonies into new areas, or establishing new sub-colonies. Landslips have likely been a feature of their breeding habitat across time, with reports of important areas of slips seen historically in petrel breeding areas (J.A. Bartle pers. comm. in Waugh & Wilson 2017). Although the climate of the West Coast of New Zealand is known for its rainy and stormy weather, the frequency and intensity of storms and major cyclonic weather systems may be increasing (IPCC 2007, Rhein *et al.* 2013), leading to more disturbances at the petrel sub-colonies in the last 10 years. This is likely to remain a persistent threat to the petrel's habitat. Given that they nest within a restricted albeit protected area, the stability of their global population will likely remain threatened by changing climatic conditions over the coming years.

It is important to acknowledge the limitations to our methodologies. While our use of CMR studies to estimate changes in density and population growth in core areas of the sub-colonies are robust, our estimates of the area occupied by breeding petrels and of the total number of breeding pairs would benefit from further refinement. For example, the effort required to estimate burrow density over large areas of cliffy and untracked terrain meant that, in some areas, we were not able to sample intensively enough to estimate within-colony heterogeneity in density (e.g., for newly established

areas). Thus, for better statistical robustness, it would be advisable to refine the density measure for these areas. However, our study was aimed at assessing trends in the population rather than deriving an exact number of breeding pairs, although the dataset generated also enabled an assessment of total population and its error. Moreover, the effort required to increase the amount of sampling must be considered as a trade-off against other urgent work. Threat reduction work includes limiting predation by wild pigs *Sus scrofa*. For example, five weaner pigs were released into the Westland Petrel nesting area in May 2020, but fortunately they were observed and removed before they could reach breeding areas (KLJS pers. obs.). Mitigations to land-based threats include the reduction of habitat degradation and trampling of nests by feral goats *Capra hircus*, stabilization of the slip-damaged terrain within and adjacent to sub-colonies, minimization of fishery bycatch in poorly observed fleets/times of year, and reduction of birds grounded by lights near dwellings (Waugh & Wilson 2017).

Storm damage due to Cyclone Ita in 2014 caused significant perturbations at several Westland Petrel sub-colonies (Waugh *et al.* 2015b). In that event, 143 mm of rain fell in one week, with up to 28 mm on some days, as measured 2 km away by an on-site gauge. This was more than three times the weekly and daily averages for precipitation in this normally 'wet' area, which receives an average annual rainfall of 2 350 mm per year (J. Washer pers. comm.) The resulting damage was tracked in detail by annual visits to Rowe Colony and Study Colony. These areas continued to suffer treefall and slipping with subsequent major storm events such as cyclones Fehi and Gita in 2018. Of the 17 sub-colonies surveyed in 2019, which comprised over 95% of the breeding population of Westland Petrels, estimates of the area damaged by storms varied: 11%–50% was damaged at three sub-colonies, less than 10% was damaged at nine sub-colonies, and no damage at five sub-colonies. By 2019, 11% of the area at Rowe Colony and 6% at Study Colony was estimated lost; these areas contained 42% and 27% of monitored CMR study nests in 2014, respectively, and the areas lost were in higher-density parts of the sub-colonies (Waugh *et al.* 2015b). At two remote sub-colonies, Dougies Bluff and Bees Nest, an estimated 38%–50% of the area was lost to landslip and treefall by 2019, when the first on-the-ground survey was undertaken following the 2014 storms. This is particularly important for Dougies Bluff, as it represented the sub-colony with the largest surface area in 2019 and thus may have contained a sizable proportion of the Westland Petrel population. We expected that surviving birds would search for new breeding areas following this reduction in colony space. Landslips have been reported in the petrel sub-colonies through time (see Waugh & Wilson 2017), but these were noted at only four sites during 1969–2011. The data presented for the study period shows a major increase in the level of disturbance over and above background levels.

The fecundity measures available from our demographic dataset did not show a marked disturbance of the normal pattern of low breeding frequency and breeding output (Waugh *et al.* 2015a). The proportion of birds breeding in study nests and their breeding success were not significantly different before or after the storm events. For long-lived petrels, these are more likely to be driven by demographic constraint and marine environmental factors than by breeding habitat quality (Weimerskirch 2002). Despite the need of some petrels to establish new burrows, we did not detect differences in burrow occupancy between new and established areas. This may be because Westland Petrels usually have a low breeding frequency and low burrow occupancy (noted since the early 2000s; Waugh *et al.* 2003); their intermittent breeding characteristics may enable adaptation to change at a certain level. Westland Petrels show very high survivorship, yet their breeding output is typically low, like all Procellariiformes (Stearns 1992). Other more subtle changes may be undetected in our study, such as changes in breeding phenology relative to changing environmental conditions (Barbraud & Weimerskirch 2006). Logically, however, continued disruption to breeding habitat, such as that caused by the extreme weather events we observed (i.e., up to 50% of the breeding area of a sub-colony destroyed after a storm) should have negative consequences on the Westland Petrel population and its ability to survive in its only breeding area. Continued surveillance of the petrel colony and the drivers of population changes are therefore warranted, particularly in response to climate change.

CONCLUSIONS

This study presents the first long-term estimate of population trends for the endangered Westland Petrel and establishes a baseline breeding population of ~6 200 breeding pairs in 2019, which corresponds to a world population size of 13 800–17 600 individuals. Despite significant perturbations to the habitat of the Westland Petrel, independent measures of burrow density and CMR estimates indicate that the population continues to grow by ~2% per year, even after storm disturbances. From our surveys during 2007–2019, it is apparent that the space occupied by the petrel sub-colonies has extended, demonstrating the resilience of this long-lived species and giving a positive perspective for its future. It appears that Westland Petrels can cope with some disturbance of their breeding habitat by relocating to new sub-colony areas, as long as a wider area is protected from other factors, such as introduced predators. To this point, the petrels' ability to adapt to climatic events appears to be effective, although if the intensity and frequency of storms continues to increase, they will not be able to sustain positive population growth.

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