

BREEDING POPULATION SIZE OF THE PINK-FOOTED SHEARWATER *ARDENNA CREATOPUS* ON ISLA MOCHA, CHILE

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ABSTRACT

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Species population estimates are a fundamental component of conservation planning, but there are deficiencies in reliable data for many seabirds. The Pink-footed Shearwater *Ardenna creatopus* is a seabird that breeds on three islands worldwide, with the largest population on Isla Mocha, Chile. We aimed to update the breeding population estimate of Pink-footed Shearwaters on Isla Mocha, comparing results from design- and model-based estimation methods. We counted shearwater burrows in 220 randomly generated five-meter-radius plots across pre-defined strata on Isla Mocha. We estimated total number of burrows using area-based extrapolation (design-based method), and separately using a model predicting burrow density based on habitat (model-based method). We multiplied burrow abundance estimates by burrow occupancy for final population estimates. The stratum-area-weighted burrow density estimate for the 15.8 km² study area was 0.0106 burrows·m⁻² (standard error [SE] = 0.0030). The average island-wide proportion of occupied burrows was 0.758 (standard deviation [SD] = 0.121). The design-based method estimated 168 209 burrows (95% confidence interval [CI] = 74 715–261 704, coefficient of variation [CV] = 0.28), and 127 503 breeding pairs (95% CI = 87 610–167 395). The model-based method estimated 233 436 burrows (95% CI = 151 237–332 179, CV = 0.19) and 181 859 breeding pairs (95% CI = 95 773–267 945, CV = 0.24). These population estimates are greater than previous estimates for Isla Mocha, whose means ranged from 19 440–42 095 breeding pairs. Because our study design differed from those used to generate previous estimates, our estimate should be considered a stand-alone result rather than an increase in the breeding population. Because of the low fit of the model-based result, the design-based result may be a more reliable estimate to use for species management efforts. Based on our estimate, approximately 90% of the Pink-footed Shearwater world population breeds on Isla Mocha, and with its restriction to only three breeding localities world-wide, the species remains vulnerable. The full manuscript in Spanish can be found in Appendix 1, available on the website.

Key words: population model, burrowing seabird, Juan Fernández Islands, stratified-random sampling, fisheries bycatch

RESUMEN

Las estimaciones de población de especies son un componente fundamental de la planificación de la conservación, pero existen deficiencias en los datos de población de muchas aves marinas. La Fardela Blanca *Ardenna creatopus* es un ave marina que se reproduce en tres islas del mundo. Isla Mocha, Chile, alberga la población reproductora más grande del mundo. Actualizamos la estimación de la población reproductora de la Fardela Blanca en la Isla Mocha y comparamos los resultados de los métodos de estimación basados en diseños y modelos. Contamos las madrigueras de fardela en 220 parcelas de cinco metros de radio generadas al azar en estratos predefinidos en Isla Mocha. Estimamos el número total de madrigueras utilizando una extrapolación basada en el área (método basado en el diseño) y, por separado, utilizando un modelo para predecir la densidad de las madrigueras en función de relaciones con el hábitat (método basado en el modelo). Multiplicamos las estimaciones de abundancia de madrigueras por la ocupación de madrigueras para estimaciones de población finales. La estimación de la densidad de madrigueras ponderada por área de estrato para el área de estudio de 15,8 km² fue de 0,0106 madrigueras·m⁻² (error estándar [ES]= 0,0030). La proporción promedio de madrigueras ocupadas en toda la isla fue de 0,758 (desviación estándar [DE] = 0,121). El método basado en el diseño estimó 168 209 madrigueras (Intervalo de confianza del 95% [IC del 95 % = 74 715–261 704, coeficiente de variación [CV]= 0,28) y 127 503 parejas reproductoras (IC del 95% = 87 610–167 395). El método basado en modelos estimó 233 436 madrigueras (IC del 95% 215 237–332 179, CV = 0,19) y 181 859 parejas reproductoras (IC del 95% = 95 773–267 945, CV = 0,24). Ambos resultados son mayores que las estimaciones de población anteriores para Isla Mocha, cuyas medias oscilaron entre 19 440 y 42 095 parejas reproductoras. Nuestra estimación debe considerarse un nuevo resultado independiente, y no necesariamente indica un crecimiento en la población reproductora, debido a las diferencias en el diseño con respecto a estimaciones anteriores. Debido al bajo ajuste del resultado basado en el modelo, el resultado basado en el diseño puede servir como una estimación más conservadora y confiable para la gestión. Según nuestra estimación, aproximadamente el 90% de la población mundial de Fardela Blanca se reproduce en Isla Mocha, y con su restricción a solo tres localidades de reproducción en todo el mundo, la especie sigue siendo vulnerable. El manuscrito completo en español se encuentra en el Apéndice 1.

INTRODUCTION

Population estimates for species are a fundamental component of conservation planning and prioritization (Brooks *et al.* 2004). Systems of conservation prioritization, such as the IUCN Red List, have developed standardized quantitative metrics to evaluate species' extinction risks (Hoffmann *et al.* 2008), but data deficiency is often a limiting factor for conservation planning. This is especially true for taxa that are poorly studied, located in remote areas, and/or located in the global South (Brito 2010, Morias *et al.* 2013, Bland *et al.* 2016). Even for relatively well-studied taxa such as seabirds, most species have major data gaps for metrics such as population estimates and trends, at-sea distribution, and threats (Croxall *et al.* 2012, Rodriguez *et al.* 2019, Dias *et al.* 2019). For instance, population estimates for many major breeding colonies are unquantified or outdated, or they are based on limited field data collection (Croxall *et al.* 2012, Phillips *et al.* 2016). This is of particular relevance because seabirds are the most threatened taxa of birds globally, with over half of all seabird species declining worldwide (Croxall *et al.* 2012, Dias *et al.* 2019).

Many seabird species nest in burrows, and quantifying the populations of these species is particularly challenging because of difficulties associated with finding burrows in rugged terrain on remote islands and accurately determining burrow occupancy, both of which can result in a high level of uncertainty in population estimates (Bird *et al.* 2021). Two approaches are commonly used to estimate burrowing seabird populations: “design-based” approaches, which involve sampling seabird burrows and burrow occupancy, then extrapolating density across suitable habitat (Reyes-Arriagada *et al.* 2006, Scott *et al.* 2009, Pearson *et al.* 2013, Felis *et al.* 2020), and “model-based” approaches, in which the relationships between habitat parameters and burrow densities are used to model predicted densities (Rayner *et al.* 2007, Clark *et al.* 2019, Bird *et al.* 2022). “Design-based” approaches of population estimation often involve many assumptions, such as that burrow density is consistent across large areas, whereas “model-based” methods are reliant on habitat data inputs that be may non-existent or have only coarse resolutions (Bird *et al.* 2022). Likewise, seabird nesting density may be strongly influenced by coloniality, or it may not be limited by available suitable nesting habitat; therefore, seabird nesting density may not be tightly coupled with easily-modeled habitat variables (Olivier & Wotherspoon 2006).

The Pink-footed Shearwater *Ardenna creatopus* is a burrow-nesting, highly migratory procellariid seabird that breeds on three islands worldwide, all located in Chile (Murphy 1936; Fig. 1). Breeding colonies are Isla Mocha, located 34.2 km offshore of the mainland of south-central Chile, and Islas Robinson Crusoe and Santa Clara in the Juan Fernández Islands, located 660 km off the South American mainland (Fig. 1). Pink-footed Shearwaters migrate to non-breeding areas in waters off Peru and the Pacific coast of North America (Felis *et al.* 2019). The species is listed as Vulnerable by the IUCN (BirdLife International 2023), Endangered in Chile and Canada (Ministerio del Medio Ambiente 2019, COSEWIC 2016), and under Annex I of the Agreement on the Conservation of Albatrosses and Petrels (ACAP; Azócar *et al.* 2013). The primary justification for these listings are the species' small breeding range, which is restricted to only three islands (BirdLife International 2023). Other reasons for conservation concern are threats within breeding colonies, including impacts of invasive mammals (García-Díaz *et al.* 2020, Carle *et al.* 2021) and chick-harvesting on Isla Mocha (Guicking *et al.* 1999, López 2019),

and mortality from bycatch in multiple fisheries (Vega *et al.* 2019, Carle *et al.* 2019, Felis *et al.* 2019).

An important data gap for informing the conservation of Pink-footed Shearwaters is accurate information on population size and trends (Carle *et al.* 2022). All previous population estimates for the species have concluded that $\geq 70\%$ of the world's known nesting population is located on Isla Mocha (Guicking *et al.* 1999, Brooke 2004, COSEWIC 2016). However, estimating the total population of breeding Pink-footed Shearwater on Isla Mocha is difficult because of the island's large size (47.82 km²), rugged topography, and difficulty of access to remote areas. Because counting all the burrows directly is impractical, most previous published population estimates from Isla Mocha have been coarse extrapolations based on limited data collection (Ibarra-Vidal & Klesse 1994, Guicking *et al.* 1999). Ibarra-Vidal & Klesse (1994) used extrapolations of burrow densities and area, along with the number of chicks harvested annually by the local community, to estimate 42095 breeding pairs. Guicking *et al.* (1999) estimated 25000 breeding pairs on Isla Mocha using minimal habitat sampling and qualitative local knowledge to extrapolate the area of suitable habitat. More current conservation assessments for ACAP (Azócar *et al.* 2013) and Canada (COSEWIC 2016) estimated 19190 breeding pairs on Isla Mocha based on an estimate of burrow density in suitable habitat measured in plots sampled along transects (Muñoz 2011) paired with unpublished data on burrow occupancy (Azócar *et al.* 2013, COSEWIC 2016). An important issue with all previous estimates was that no associated variance or uncertainty were reported.

A more robust population estimate for Pink-footed Shearwaters is needed for monitoring the conservation status of the species. A baseline understanding of Isla Mocha's breeding population



Fig. 1. Locations of Pink-footed Shearwater *Ardenna creatopus* breeding colonies in Chile.

size will help with prioritization of conservation actions for the species, as well as evaluation of the success of conservation measures proposed in species recovery plans (e.g., endangered species plans for Chile and Canada). Better quantifying the Pink-footed Shearwater population will also help determine the species' vulnerability relative to other seabird species. For example, inputs of population data are important for efforts that prioritize seabird conservation across the Pacific using meta-population viability models (Madrigal Ruiz 2021, Tinker *et al.* 2022). Given the importance of the Isla Mocha nesting population for understanding the global conservation status for Pink-footed Shearwaters, our goal was to produce an updated and refined Pink-footed Shearwater nesting population estimate for the island. We conducted field data collection on burrow density and habitat in 2016 and used data from a long-term burrow occupancy study, and newly collected Lidar-based habitat data, to produce and compare both design- and model-based population estimates for Pink-footed Shearwaters on Isla Mocha.

METHODS

Study area

Isla Mocha (38.383°S, 73.900°W) is located 34.2 km offshore of the mainland of south-central Chile. A densely forested central mountain range on Isla Mocha rises to 390 m and is protected as a Chilean National Reserve (Fig. 2). Approximately 650 people live in decentralized homesteads on a coastal plain skirting the mountains. Fieldwork was permitted and approved by the Chilean Corporación Nacional Forestal (CONAF; the Chilean National Park Agency) and Reserva Nacional Isla Mocha.

Sampling design

We used a stratified-random sampling approach to determine where to sample habitat across the island to optimize our field effort toward collecting data and to minimize variance in areas where Pink-footed Shearwater burrows are most abundant (Fig. 3). This approach used prior knowledge of the distribution of nesting habitat to define sampling strata (Pearson *et al.* 2013, Bird *et al.* 2022). Based on previous reproductive monitoring, a 2011 population survey (Muñoz 2011), and local knowledge from park rangers and ecologists, we created two sampling strata. We sampled areas expected to have high nesting densities at a higher rate, areas with low expected densities at a lower rate, and excluded areas expected to have no nests. Muñoz's (2011) model found that Pink-footed Shearwater burrows on Isla Mocha occurred only at ≥ 210 m above sea level and on slopes $\geq 37^\circ$, with ocean-facing aspects and exposed tree roots. We based our sampling strata on slope and elevation only, because when we began the study, these variables were the only habitat metrics with data available at an island-wide level. We defined an "A" stratum that was expected to have the greatest burrow densities, based on the elevation and slope cutoffs defined by Muñoz's (2011) suitable habitat model. We used a 25% buffer below Muñoz's (2011) minimum suitable habitat values as the bounds of our strata (see Table 1 for definitions of each stratum). Our "B" stratum was expected to have burrows at low densities, in areas with lesser slopes and/or lesser elevations (Table 1). B stratum values were chosen based on field experience indicating that burrows sometimes occur at lesser slopes at higher elevations, and on steeper slopes in lower elevations, than what was described by Muñoz (2011). All land outside these strata was excluded from the study under the assumption that Pink-footed Shearwaters would not be breeding there.



Fig. 2. Central mountain range of Isla Mocha, Chile, with coastal plain in the foreground. Pink-footed Shearwaters *Ardenna creatopus* nest primarily at higher elevations in the mountains, often near ridgetops.

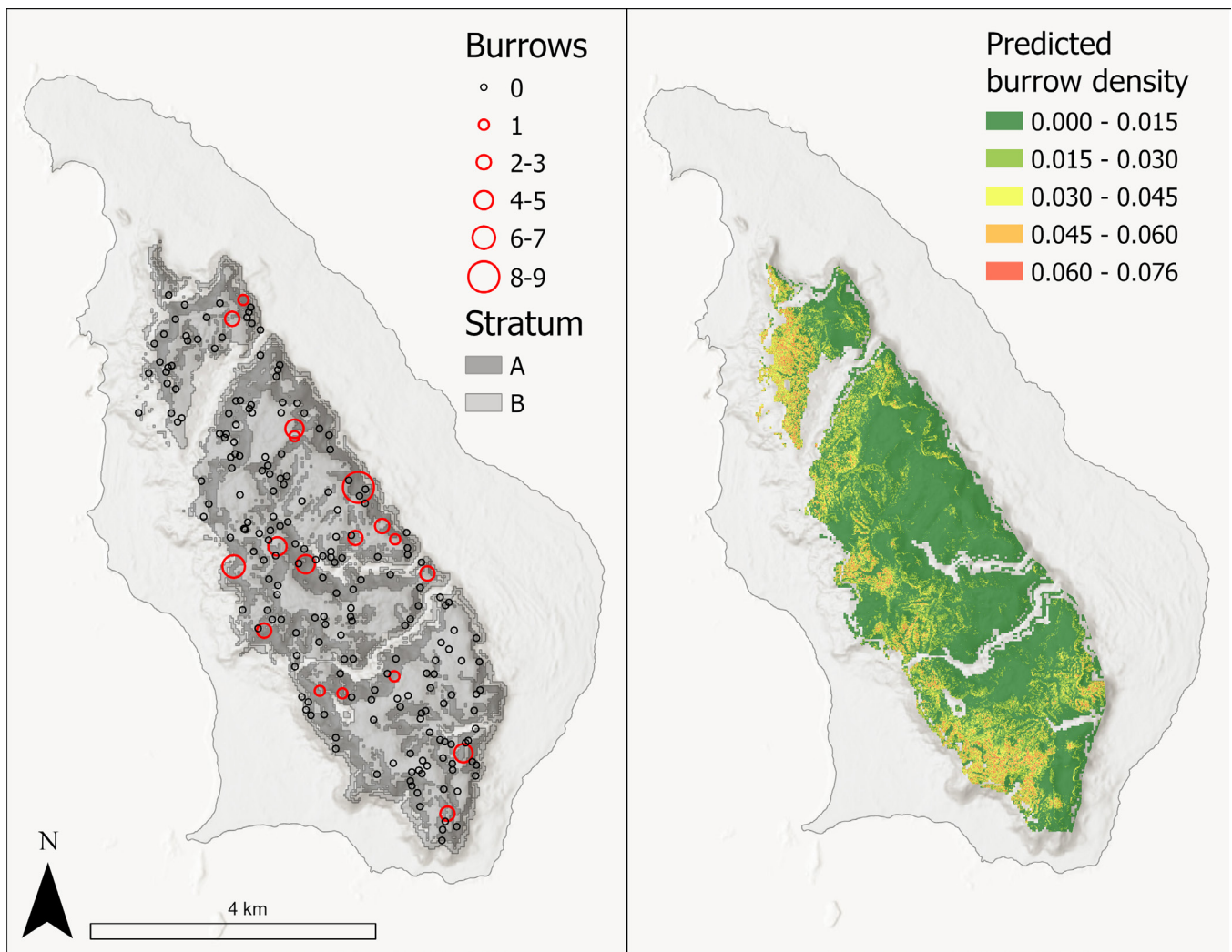


Fig. 3. Left: Sampling strata, plots, and burrow counts for estimating Pink-footed Shearwater *Ardenna creatopus* burrow density and abundance on Isla Mocha, Chile. Right: Predicted burrow density of Pink-footed Shearwaters on Isla Mocha, Chile. All white areas fell outside the elevation and slope bounds use to define the study area.

We generated digital representations of the A and B strata using elevation and slope values from a 30-m digital elevation model

(NASA JPL 2013). We generated 220 random sampling plots using ArcGIS (ESRI 2016; Fig. 3), with 70% of our sampling effort

TABLE 1
Stratum definitions, sampling effort, and results for Pink-footed Shearwater *Ardenna creatopus* burrows on Isla Mocha, Chile

Stratum	Expected burrow density	Definition	Stratum area (km ²)	# plots sampled (% total)	% stratum area sampled	Total burrows found	Mean burrows·m ⁻² (standard error)
A	High	≥ 158 m elevation and ≥ 18.5° slope	6.67	145 (70%)	0.043%	40	0.0140 (0.0048)
B	Low	100–157 m elevation and ≥ 18.5° slope, OR ≥ 158 m elevation and ≤ 18.5° slope	9.15	75 (30%)	0.016%	12	0.0081 (0.0039)
Total			15.82	220		52	0.0106 (0.0030) ^a

^a Mean burrow density for total study area is stratum-area-weighted and total standard error is weighted by sampling effort (see design-based methods).

in the A stratum (0.043% sampling rate by area) and 30% in the B stratum (0.015% sampling rate by area; Table 1). We weighted models used to estimate final population size by sampling effort in each stratum to avoid a sampling bias. The choice of 220 plots was based on the practical realities of the extensive effort required to sample many random plots on the rugged and mostly trail-less terrain of Isla Mocha.

From February–September 2016, we collected data on the number of Pink-footed Shearwater burrows on Isla Mocha in five-meter-diameter (19.63 m² area) circular plots. Fieldwork spanned the breeding and non-breeding seasons of the Pink-footed Shearwater. On Isla Mocha, burrows persist for many years (T. Varela, pers. obs.), so we believed that sampling during the non-breeding season would not result in lower burrow numbers during those months. We navigated to plots using a hand-held GPS unit, marked the center of the plot, and counted burrows within the plot. We considered burrows to be viable Pink-footed Shearwater nesting burrows if they were at least 1 m long, based on reported minimum burrow lengths (Brooke 2004, Carle *et al.* 2022), and we did not count any hole or subterranean tunnel shorter than 1 m. We included burrows in counts if any part of the burrow entrance was within or intersecting the sample circle. We excluded plots that were inaccessible because of steep terrain and replaced those plots with other randomly generated plots. Exclusion of dangerously steep areas could have introduced a bias toward recording fewer burrows, particularly in our design-based population estimate. Our model-based population estimate methods somewhat address this potential bias by predicting the relationship between burrows and slope based on sampled plots.

Burrow occupancy

To quantify occupancy rates of burrows to use as a multiplier for population estimation, we monitored Pink-footed Shearwater burrow occupancy from 2012–2021 in five 1–2 ha (0.01–0.02 km²) “sub-colonies,” each of which had an aggregation of > 100 burrows. All sub-colonies were spatially separated by > 2 km, with the exception of two that were 0.9 km apart. All sub-colonies were in forested areas at 200–350 m elevation, on or near steep slopes near the tops of ridges. We monitored 20–42 burrows (mean $n = 33.6$, standard deviation [SD] = 4.6) per year in each sub-colony using an infra-red burrow camera. To determine annual burrow occupancy, we checked burrows twice during the period in which the species typically lays eggs (15 December–15 January). Regardless of activity status during the egg-laying period, we also checked all burrows again during 15–28 February (chick-hatching period) and 10 April–10 May (just before chick fledging; Carle *et al.* 2022). We considered burrows “occupied” if an egg was observed once, or if a shearwater was seen on two different occasions during incubation check (García-Díaz *et al.* 2020). If no activity was observed during incubation but an egg or chick was observed on a later check, the burrow was considered occupied. We defined burrow occupancy as the proportion of occupied burrows out of the number of viable burrows in the sample. We calculated annual island-wide burrow occupancy estimates by pooling all monitored burrows across the five sub-colonies and calculating a single occupancy result (n range = 152–210 burrows annually; Appendix 2, available on the website). We calculated the average and variance of the island-wide burrow occupancy across nine years (2012–2021, excluding 2013) to determine a single occupancy estimate to apply to the modeled burrow count.

Population size estimation

Design-based estimate

We generated a design-based burrow abundance estimate, N_b , for the entire study area by multiplying the stratum-area-weighted average burrow density by the total study area. Stratum-specific variances were weighted and combined for a total variance, s_b^2 , based on stratum-specific sampling effort (Cochran 1977):

$$s_b^2 = \sum_{h=1}^L \left(\frac{w_h^2 s_h^2}{n_h} (1 - f_h) \right)$$

where w_h is the stratum weight (stratum area divided by total area), s_h^2 is the variance of stratum h , n_h is the sample size (number of plots) in stratum h , and f_h is the sampling fraction (total plot area surveyed divided by stratum area) in stratum h . We calculated the standard error (SE) and coefficient of variation (CV) for our estimate, and generated a 95% confidence interval (CI) as:

$$95\% \text{ CI} = \pm t\sqrt{s^2}$$

where t is the critical value (1.96).

We generated an occupied burrow abundance estimate by multiplying the average annual occupancy rate, O , by the total burrow abundance estimate, and we calculated the occupied burrow variance, s_{bO}^2 , as that of products (Goodman 1960):

$$s_{bO}^2 = O^2 s_b^2 + N_b^2 s_O^2 - s_b^2 s_O^2$$

where s_O^2 is the variance of occupancy. The 95% CI was calculated as described above.

Model-based estimate

We used a model-based approach to predict the density of burrows across Isla Mocha based on the relationships of burrow presence/absence and burrow counts with habitat parameters. Unless otherwise stated, we carried out analyses using R (R Core Team 2021).

We mapped the uplands of Isla Mocha with Lidar during 2020, providing centimeter-scale physical environmental data. We used Lidar data to derive ground elevation, ground slope, tree canopy height, and topographic position index (TPI) habitat variables for each plot. We calculated an additional variable, distance to the coast, using a coastline shapefile provided by CONAF. We calculated tree canopy height by subtracting the elevation of the canopy from the elevation of the ground, based on Lidar layers. We calculated slope and TPI using the “terrain” function in the “raster” package in R (Hijmans 2021). TPI is a measure of the relative topographic position of a point and is based on measuring the difference between a focal point’s elevation and the mean elevation of the surrounding points (Gallant 2000). TPI has been widely applied to spatial analyses in the physical and biological sciences (Francés *et al.* 2011, De Reu 2013). We included these parameters in the model because (1) we were able to calculate them with the available data for Isla Mocha, and (2) other studies have shown them to have important influences on burrowing seabird distribution (Rayner *et al.* 2007, Dilley *et al.* 2019, Raine *et al.*

2022). We generated each habitat variable at a range of resolutions (1, 5, 10, 20, 30, and 50 m) to evaluate which resolution resulted in the best-fit model (based on R^2 values) and extracted those values to the center point of each sampling plot.

Ninety-two percent of points sampled had no burrows present, so we used a Poisson hurdle model (Zuur *et al.* 2009), which compensates for zero-inflation data by modeling presence/absence and positive count data as separate components of the same model. Building the Poisson hurdle model involved (1) modelling the probability of presence/absence of burrows at plots using a binomial distribution (hereafter called burrow “binomial model”), and (2) modelling the counts of burrows in plots that had at least one burrow present using a truncated Poisson distribution (hereafter called burrow “count model”). This leads to the following probability distribution:

$$f_{\text{hurdle}}(y; \beta, \gamma) = \begin{cases} f_{\text{binomial}}(y = 0; \gamma) & y = 0 \\ (1 - f_{\text{binomial}}(y = 0; \gamma)) \frac{f_{\text{poisson}}(y; \beta)}{1 - f_{\text{poisson}}(y = 0; \beta)} & y > 0 \end{cases}$$

where γ are the counts of burrows, and β and γ are the unknown regression parameters in the model.

We adjusted for different levels of sampling effort in each stratum by creating model weights equivalent to the inverse of the sample size of the strata, where the A stratum was weighted as 1.51 (i.e., $1/[145/220]$) and the B stratum was weighted as 2.93 (i.e., $1/[75/220]$). Conspecific attraction between Pink-footed Shearwaters could manifest as spatial autocorrelation, so for each plot we created a “neighborhood” auto-covariate calculated by averaging burrow density in the four nearest plots (Augustin *et al.* 1996, Olivier & Witherspoon 2006, Clark *et al.* 2019). We ran the Poisson hurdle model using the R package “pscl” (Jackman 2020). We conducted backwards stepwise model selection on the habitat variables until ΔAIC was minimized (Burnham & Anderson, 2003; Table 2). For the final model fit, we calculated a pseudo- R^2 value (Nakagawa & Schielzeth 2013).

We estimated the final breeding population estimate of Pink-footed Shearwaters, together with its associated uncertainty, using a parametric bootstrapping technique following Clark *et al.* (2019). For each cell on the study area grid, we bootstrapped mean burrow

density and 95% confidence intervals using our hurdle model and parameter values drawn randomly from the multivariate normal distribution. We then multiplied the predicted burrow density by randomly drawn occupancy values from a normal distribution associated with our occupancy data. We repeated this procedure 1000 times and calculated the mean and its associated 95% confidence intervals for the breeding population.

RESULTS

Burrow occupancy and plot sampling

The average island-wide proportion of occupied burrows was 0.758 (SD = 0.121; range = 0.547–0.961; $n = 9$ years, 2012–2021, excluding 2013; Appendix 2). Burrow occupancy in 2016, the year that population survey data were collected, was 0.816 (Appendix 2). Burrows were present in 13 of 145 plots in Stratum A (9% of plots) and five of 75 plots in Stratum B (7% of plots). Across both strata, burrows were present in 8% of plots. In plots with burrows present, number of burrows ranged from one to nine in Stratum A (mean = 3.1 [SD = 2.5]) and one to four in Stratum B (mean = 2.8 [SD = 2.1]).

Design-based abundance estimates

Mean burrow density was 0.0140 burrows- m^{-2} (SE = 0.0048) in Stratum A and 0.0081 burrows- m^{-2} (SE = 0.0039) in Stratum B (Table 1). The stratum-area-weighted burrow density estimate for the entire study area was 0.0106 burrows- m^{-2} (SE = 0.0030; Table 1). The design-based methods resulted in an overall estimate of 168 209 burrows (95% CI = 74 715–261 704, CV = 0.28), and after incorporating burrow occupancy, an estimate of 127 503 breeding pairs (95% CI = 87 610–167 395).

Model-based abundance estimates

We chose a 20 × 20 m model resolution because it had the best whole-model fit and was the best predictor for most habitat parameters. The best-fit model of the Pink-footed Shearwater habitat used all the habitat variables that were originally included. Coefficient values for the binomial model are provided in Table 3, and values for the count model are provided in Table 4. The final whole model had a pseudo- R^2 of 0.289.

TABLE 2
Summary of Pink-footed Shearwater
Ardenna creatopus burrow density model selection

Model ^a	Degrees of freedom	AIC	ΔAIC
Full model	12	334.45	0
- elevation	10	336.60	2.15
- canopy height	10	349.10	14.65
- distance to coast	10	349.70	15.25
- topographic position index	10	352.89	18.44
Intercept only	2	375.17	40.72
- slope	10	379.70	45.25

^a Models are ranked by ΔAIC .

TABLE 3
Standardized parameter estimates for the
binomial model of Pink-footed Shearwater
Ardenna creatopus burrows as a function of habitat

Parameter	Estimate	Standard error	P value ^a
Intercept	-2.786	0.236	< 0.001*
Elevation	0.452	0.201	0.029*
Canopy height	0.208	0.191	0.277
Slope	1.052	0.225	< 0.001*
Topographic Position Index	-0.127	0.184	0.488
Distance to coast	-0.133	0.195	0.495

^a Significance at $P \leq 0.05$ indicated by bold type and asterisk.

Elevation and slope were significantly positively correlated with the presence of burrows (Table 3). No other parameters had a significant positive or negative correlation with burrow presence (Table 3). The number of burrows per plot was significantly positively correlated with canopy height and significantly negatively correlated with slope, TPI, and distance to coast (Table 4). This indicated that within the zone in which burrows occurred, there were more burrows per plot in areas closer to the coast, with lesser slopes, in areas with lower or similar elevations to their surroundings, and with higher forest canopies. Elevation was not significantly correlated with burrow counts (Table 4).

Our model predicted an average burrow density of 0.009 burrows·m⁻² (SE = 0.005) across the sampled area on Isla Mocha. Areas predicted to have the greatest densities of shearwater burrows were the steep western edge of the mountain range, as well as in the extreme north and south parts of the range (Fig. 3). Fewer burrows were predicted to occur in the relatively flat plateau in the middle of the mountains (Fig. 3).

Summing the density per grid cell across the study area resulted in a predicted 233436 burrows (95% CI = 151237–332179; CV = 0.19). After incorporating burrow occupancy, the model results indicated 181859 (95% CI = 95773–267945; CV = 0.24) Pink-footed Shearwater breeding pairs on Isla Mocha.

TABLE 4
Standardized parameter estimates for the count model of Pink-footed shearwater *Ardenna creatopus* burrows as a function of habitat

Parameter	Estimate	Standard error	<i>P</i> value ^a
Intercept	1.073	0.154	< 0.001 *
Elevation	-0.054	0.157	0.727
Canopy height	0.888	0.222	< 0.001 *
Slope	-0.952	0.208	< 0.001 *
Topographic Position Index	-1.260	0.292	< 0.001 *
Distance to coast	-0.860	0.212	< 0.001 *

^a Significance at *P* ≤ 0.05 indicated by bold type and asterisk.

DISCUSSION

Both our model- and design-based breeding population estimates for Pink-footed Shearwaters on Isla Mocha were substantially larger than previous estimates (Ibarra-Vidal & Klesse 1994, Guicking *et al.* 1999, COSEWIC 2016). Given that approximately 10000–15000 Pink-footed Shearwater breeding pairs nest on their only other breeding islands in the Juan Fernández Archipelago (Carle *et al.* 2022), our results indicate that approximately 90% of the world breeding population of the species nests on Isla Mocha. These results should be interpreted as a new, stand alone estimate rather than a true increase in the Pink-footed Shearwater population size because they rely on different methods than were used in previous studies. Combining the estimates of the three islands, the world breeding population of the species would be approximately 140000 breeding pairs (based on the mean only of our Mocha design-based estimate [127503 pairs] and the mean of the estimate range from the Juan Fernández Archipelago [12500 pairs]). Our estimates of the size of the Isla Mocha population improve on previous estimates by providing more detailed reporting of variability and a standardized methodology. However, our estimates contain a great deal of variability and could be improved by greater sampling effort and ground-truthing of burrow densities predicted by our model result.

Our design-based population estimate (127503 breeding pairs, 95% CI = 87610–167395) was substantially lower than our model-based estimate (233436 burrows, 95% CI = 151237–332179). A recent study found that design-based estimates were more accurate for populations of patchily distributed petrels on large islands in Australia compared with model-based study designs which tend to result in over-estimates (Bird *et al.* 2022). On the other hand, model-based designs accurately reflected population sizes for more abundant and evenly distributed species in the same setting (Bird *et al.* 2022). Given that only 8% of our plots (18 of 220) had Pink-footed Shearwater burrows present, Pink-footed Shearwaters on Isla Mocha may have been more similar to the patchily distributed species described in Bird *et al.* (2022). Based on these considerations and the relatively low fit of our model, our design-based result could be considered the more conservative and reliable estimate for use in management and conservation assessments. A probable driver of the variability in both results is that we sampled only a small proportion of the total study area, and the majority

Table 5
Breeding population estimates of Pink-footed Shearwaters *Ardenna creatopus* on Isla Mocha, Chile, from this and previous studies

Study	Population estimate (breeding pairs)	Method	Reported burrow densities (burrows·m ⁻²)	Occupancy multiplier	Area of habitat included km ²
Ibarra-Vidal & Klesse (1994)	42095	Design-based	Unknown	Unknown	Unknown
Guicking <i>et al.</i> (1999)	25000	Rough extrapolation	Up to 0.4 in some areas	“< 50% in some areas”	Unknown
COSEWIC 2016, Azócar <i>et al.</i> 2013 (based on Muñoz [2011] and Oikonos unpubl. data)	19440	Design-based	0.03648 (0.0936 SD)	0.715	0.74
This study (design-based)	127503 (87610–167395 95% CI)	Design-based	0.0106 (0.003 SE), whole study area	0.758 (0.04 SE)	15.8
This study (model-based)	181859 (95773–267945 95% CI)	Model-based	0.009 (0.005 SE), whole study area	0.758 (0.04 SE)	15.8

of our plots contained zero burrows. An increased plot size and/or greater sampling effort of more plots would likely improve the precision of either method. We chose our five-meter-diameter plot size based on plots used in previous studies (Muñoz 2011, Pearson *et al.* 2013). However, it was clear that with Isla Mocha's large size and relatively low burrow densities, ≥ 10 -m-diameter plots would be more appropriate for detecting burrows. In addition, our choice of sampling 220 total plots was largely determined by feasibility of field effort. Reaching random points on Isla Mocha was time-consuming due to the rugged topography and lack of trails, so only eight to 15 plots could be sampled per field day. Thus, increasing the plot size could be a more feasible and efficient option than increasing the number of plots sampled.

Previous breeding population estimates of Pink-footed Shearwaters on Isla Mocha were substantially lower than ours (Table 5). The maximum previous estimate was 42095 pairs based both on extrapolations of burrow density and number of chicks harvested by the local community (Ibarra-Vidal & Klesse 1994). The hunting of Pink-footed Shearwaters became illegal in Chile in 1998 (Servicio Agrícola y Ganadero 1998), and the number of chicks currently harvested is difficult to quantify, so we did not include information on chick harvests in our model. Guicking *et al.* (1999) compared their estimate of 25000 breeding pairs to that of Ibarra-Vidal & Klesse (1994) and suggested that there had been a population decline, though the two studies used different methods. Guicking *et al.*'s (1999) estimate incorporated an unreported burrow occupancy multiplier, but they stated that in some areas $< 50\%$ of burrows were occupied. Annual burrow occupancy from our study ranged from 0.547–0.961 (mean = 0.758 [SD = 0.121] over nine years), suggesting that in the years covered by the study of Guicking *et al.* (1999), burrow occupancy was at a low point. Alternatively, comparisons of older and newer burrow camera models have found that new technologies result in more detections of active burrows (Lavers *et al.* 2019), which could be a factor in the different occupancy rates found by Guicking *et al.* (1999) and our study. It is also possible that reduced chick-harvest and reduced associated damage to burrows could have increased burrow occupancy rates since the 1990s. In comparing our results to those of Ibarra-Vidal & Klesse (1994) and Guicking *et al.* (1999), it is notable that neither previous study reported uncertainty in their population estimates, making it difficult to compare or assess the potential sources of error.

The population estimate for Isla Mocha used in the species' ACAP listing and Canadian national conservation assessment was 19440 pairs (Azócar *et al.* 2013, COSEWIC 2016). This was based on a total burrow estimate of 27156 burrows (Muñoz 2011) and a burrow occupancy of 0.715 (derived from the same long-term burrow occupancy study data we used, with fewer years). Importantly, those conservation assessments did not report uncertainties of either burrow density or occupancy (Azócar *et al.* 2013, COSEWIC 2016). The burrow estimate from Muñoz (2011) was based on a reported burrow density of 0.03648 burrows·m⁻² (SD = 0.0936) within suitable habitat. It is notable that the SD exceeded the mean in that result, indicating a large amount of uncertainty. A likely driver of the differences between our results and the estimate used by the conservation assessments (Azócar *et al.* 2013, COSEWIC 2016) was the amount of potential habitat included in the burrow estimate. Both our design- and model-based results included 15.68 km² of potential habitat, whereas Muñoz's (2011) burrow count model included only 0.74 km² of potential habitat. The Muñoz (2011) burrow estimate excluded habitat at < 210 m elevation on

slopes $< 37^\circ$, as well as all interior-facing slopes. In contrast, we found burrows in study plots at elevations as low as 160 m on slopes as low as 10° , and on interior-facing slopes (although we did not try to quantify interior vs. exterior facing slopes because we deemed this too subjective to accurately measure on Isla Mocha). Several plots with relatively high burrow densities were located below 210 m elevation. In the course of fieldwork, we also opportunistically documented several large aggregations of burrows at lower elevations, including approximately 50 burrows at 120 m and approximately 100 burrows at 150 m (these were not in plots and were not included in our results; T. Varela, pers. obs.). Thus, the suitable habitat cutoffs identified by Muñoz (2011) likely resulted in exclusion of a substantial amount of appropriate nesting habitat and a lower extrapolated total burrow abundance estimate.

The comparison of our results with previous studies indicates that large differences in breeding population estimates can be caused by the use of different burrow occupancy multipliers, suitable habitat definitions, and sampling methodologies (Sutherland & Dann 2012, Bird *et al.* 2021). Burrow occupancy is difficult to measure for an entire island because occupancy rates may vary over space and time, non-breeding birds may be present in burrows, and there is observer error associated with viewing the contents of long, complex burrows (Sutherland & Dann 2012, Lavers *et al.* 2019). Our burrow occupancy metric incorporated nine years of inter-annual variability, and it included spatial variability by monitoring five sub-colonies in different parts of Isla Mocha. However, we sampled the same areas of relatively high burrow densities each year and did not sample lower-density burrow areas that could have different occupancy rates. The effect of habitat and burrow density on occupancy is variable across species and islands. For example, burrow occupancy rates varied significantly by habitat or stratum for Blue Petrels *Halobaena caerulea* (Dilley *et al.* 2017), Sooty Shearwaters *Ardenna grisea* (Clark *et al.* 2019), Wedge-tailed Shearwaters *Puffinus pacificus* (Felis *et al.* 2020), and Buller's Shearwaters *Puffinus bulleri* (Friesen *et al.* 2021), but not for Cook's Petrels *Pterodroma cookii* (Rayner *et al.* 2007). Despite these issues with estimating burrow occupancy, the amount of suitable habitat included in each study was a far greater driver of the differences between various population estimates of Pink-footed Shearwaters on Isla Mocha.

Model results indicated that the presence of Pink-footed Shearwaters on Isla Mocha was positively correlated with habitat having steeper slopes and higher elevations, as has been identified by other authors (Bullock 1935, Guicking *et al.* 1999, Muñoz 2011). The preference for nesting at higher elevations and/or steep slopes is similar to many other Procellariid species (Rayner *et al.* 2007, Whitehead *et al.* 2014, Clark *et al.* 2019, Friesen *et al.* 2021). Isla Mocha is densely forested, and Pink-footed Shearwaters frequently climb trees in order to access an unimpeded path to take off from breeding colonies (Carle *et al.* 2022). Thus, steep, high elevation areas might provide Pink-footed Shearwaters suitable locations for unimpeded take-offs, such as trees overhanging cliffs or steep slopes. Given that some Pink-footed Shearwaters nest on relatively flat areas near sea level on the Juan Fernández Islands (Carle *et al.* 2022), the preference for high, steep, remote areas on Isla Mocha could also be related to the > 3000 -year habitation of the island and associated lower-elevation habitat modification (Campbell 2015, Campbell & Pfeiffer 2017). Archaeological evidence at a site at 125 m elevation on Isla Mocha indicated that human-related forest-type conversion from large trees to shrubs and forbs occurred there around 1760 years before present (LeQuesne *et al.* 1999). Introduced

mammalian predators could also limit shearwater nesting at lower locations. Cats *Felis catus*, dogs *Canis lupus familiaris*, and rats *Rattus* spp. regularly occur in high-elevation shearwater breeding colonies on Isla Mocha (Hahn *et al.* 2016, Carle *et al.* 2021), but they may be more prevalent at lower elevations closer to human habitations.

The number of burrows per plot showed different relationships to habitat than the presence/absence of shearwater burrows (Tables 3, 4). Elevation was not a significant predictor of higher burrow counts, but more burrows were located in plots closer to the coast that had lower TPI scores (indicating lower or similar elevations to the mean elevation of the surrounding area), greater canopy heights, and lower slopes. The relationships with distance to coast might be explained by birds preferring to nest closer to the ocean for ease of commuting to foraging areas, or because the edges of the island are steeper and easier to take off from than the relatively flat, densely forested interior. Lower TPI values may be explained by the prevalence of Pink-footed Shearwaters nesting in the middle of sloping surfaces or near the base of steeper slopes, where exposed tree roots facilitate burrow excavation.

Our population estimate for Isla Mocha increases the world breeding population estimate for Pink-footed Shearwaters from approximately 30 000 breeding pairs to approximately 140 000 breeding pairs. At-sea abundance estimates also indicate a Pink-footed Shearwater population in the range of hundreds of thousands; during 1975–1983, an estimated ~530 000 individuals were present off-shore of southern and central California (based on aerial surveys and density extrapolations; Briggs *et al.* 1987), which is only a portion of the overall non-breeding range (Felis *et al.* 2019). More recently, Leirness *et al.* (2021) modeled at-sea seabird densities based on > 20 years of at-sea survey data for California Current waters off California, Oregon, and Washington, which summed to an estimate of ~347 000 Pink-footed Shearwaters in the boreal summertime (Leirness *et al.* 2021). Although these at-sea estimates also include immature non-breeding birds and are, therefore, greater than the breeding population, they likely do not represent the entire world population due to exclusion of waters off Mexico and Peru, which are also heavily used by Pink-footed Shearwaters in the non-breeding season (Felis *et al.* 2019). It is unlikely that a global breeding population as small as previously estimated (~30 000 pairs) could support such large overall at-sea populations based on estimated ratios of breeding adults to immature birds for similar seabird species (1.2:1–1.6:1; Furness 2015).

Our new estimate indicates a larger breeding population of Pink-footed Shearwaters on Isla Mocha than previously thought, but with its restriction to only three breeding localities world-wide, the species remains vulnerable. Our estimation that > 90% of the world population of Pink-footed Shearwaters nests on Isla Mocha highlights the island's importance for the conservation of the species as a whole. Mortality from fisheries bycatch is a particularly serious threat to the species because the foraging range of breeding birds on Isla Mocha overlaps extensively with central Chilean Anchoveta *Engraulis ringens* and Common Sardine *Strangomera bentincki* purse-seine fisheries (Suazo *et al.* 2014, Carle *et al.* 2019, Adams *et al.* 2019). High bycatch rates of Pink-footed Shearwaters in those fisheries alone (i.e., > 1500 birds directly observed caught as bycatch during 2015–2017 with 16%–23% and 1%–2% observer coverage of industrial and artisanal fisheries, respectively; Vega *et al.* 2018) may threaten the stability of the Isla Mocha population, and thereby the world

population. Birds breeding on Isla Mocha also face a variety of land-based threats, such as predation from introduced cats, dogs, and rats, which regularly occur in shearwater breeding colonies there (Carle *et al.* 2021). Chick harvesting by humans became illegal in 1998, but poaching remains a conservation concern on Isla Mocha (COSEWIC 2016), as does further habitat modification and introduction of additional non-native species due to a lack of biosecurity (Carle *et al.* 2021, López *et al.* 2021). Fallout of shearwaters from light pollution is also an increasing issue on Isla Mocha and Isla Robinson Crusoe (Silva *et al.* 2020, López *et al.* 2021, Colodro *et al.* 2023). Our updated understanding of the Isla Mocha Pink-footed Shearwater breeding population will help prioritize conservation action for the species in the face of these continuing serious threats.

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REFERENCES

- ADAMS, J., FELIS, J.J., CZAPANSKIY, M., CARLE R.D. & HODUM, P.J. 2019. Diving behavior of Pink-footed Shearwaters *Ardenna creatopus* rearing chicks on Isla Mocha, Chile. *Marine Ornithology* 47: 17–24.
- AUGUSTIN, N. H., MUGGLESTONE, M.A. & BUCKLAND, S.T. 1996. An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology* 33: 339–347. doi:10.2307/2404755
- AZÓCAR, J., GARCÍA, M., COLODRO, V., ARATA, J., HODUM, P. & K. MORGAN. 2013. *Listing of New Species - Pink-footed Shearwater, Puffinus creatopus. Chile*. Agreement on the Conservation of Albatrosses and Petrels Seventh Meeting of the Advisory Committee, 06–10 May, La Rochelle, France. [Available online at <https://www.acap.aq/en/advisory-committee/ac7/ac7-meeting-documents/1981-ac7-doc-24-rev-1-listing-of-new-species-pink-footed-shearwater-puffinus-creatopus/file>].
- BIRD, J.P., TERAUDS, A., FULLER, R.A., PASCOE, P.P. ET AL. 2022. Generating unbiased estimates of burrowing seabird populations. *Ecography* 2022: e06204 doi:10.1111/ecog.06204
- BIRD, J.P., WOODWORTH, B.K., FULLER, R.A. & SHAW, J.D. 2021. Uncertainty in population estimates: A meta-analysis for petrels. *Ecological Solutions and Evidence* 2: e12077. doi:10.1002/2688-8319.12077
- BIRDLIFE INTERNATIONAL. 2023. *Species factsheet: Ardenna creatopus*. Cambridge, UK: Birdlife International. [Accessed at <http://datazone.birdlife.org/species/factsheet/pink-footed-shearwater-ardenna-creatopus> on 08 November 2023.]

- BLAND, L.M., BIELBY, J., KEARNEY, S., ORME, C.D. L., WATSON, J.E. & COLLEN, B. 2017. Toward reassessing data-deficient species. *Conservation Biology* 31: 531–539. doi:10.1111/cobi.12850
- BRIGGS, K.T., TYLER, W.B., LEWIS, D.B. & CARLSON, D.R. 1987. Bird communities at sea off California: 1975 to 1983. *Studies in Avian Biology* 11: 1–74
- BRITO, D. 2010. Overcoming the Linnean shortfall: data deficiency and biological survey priorities. *Basic and Applied Ecology* 11: 709–713. doi:10.1016/j.baae.2010.09.007
- BROOKE, M. 2004. *Albatrosses and Petrels Across the World*. Oxford, UK: Oxford University Press.
- BROOKS, T. M., DA FONSECA, G. A. & RODRIGUES, A.S. 2004. Protected areas and species. *Conservation Biology* 18: 616–618. doi:10.1111/j.1523-1739.2004.01836.x
- BURNHAM, K. P. & ANDERSON, D. 2003. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York, USA: Springer Science & Business Media.
- CAMPBELL, R. 2015. So near, so distant: Human occupation and colonization trajectories on the Araucanian islands (37° 30' S. 7000–800 cal BP [5000cal BC–1150 cal AD]). *Quaternary International* 373: 117–135. doi:10.1016/j.quaint.2014.11.060
- CAMPBELL R. & PFEIFFER M. 2017. Early public architecture in southern Chile: archaeological and pedological results from the mocha island mounds-and-platform complex. *Latin American Antiquity* 28: 495514.
- CARLE, R.D., FELIS, J.J., VEGA, R. ET AL. 2019. Overlap of Pink-footed Shearwaters and central Chilean purse-seine fisheries: Implications for bycatch risk. *Condor: Ornithological Applications* 121: duz026. doi:10.1093/condor/duz026
- CARLE, R.D., COLODRO, V., FELIS, J., ADAMS, J. & HODUM P.J. 2022. Pink-footed Shearwater (*Ardenna creatopus*), version 2.0. In: RODEWALD, P.G. & KEENEY, B.K. (Eds.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. doi:10.2173/BOW.PIFSHE.02
- CARLE, R.D., FLEISHMAN, A.B., VARELA, T. ET AL. 2021. Introduced and native vertebrates in pink-footed shearwater (*Ardenna creatopus*) breeding colonies in Chile. *PLoS One* 16: e0254416. doi:10.1371/journal.pone.0254416
- CLARK, T.J., MATTHIOPOULOS, J., BONNET-LEBRUN, A. ET AL. 2019. Integrating habitat and partial survey data to estimate the regional population of a globally declining seabird species, the Sooty Shearwater. *Global Ecology and Conservation* 17: 1–15. doi:10.1016/j.gecco.2019.e00554
- COCHRAN, W.G. 1977. *Sampling Techniques*. 3rd Edition. Hoboken, USA: John Wiley & Sons.
- COLODRO, V., GUTIÉRREZ GUZMÁN, H, LARA, M. ET AL. 2023. *Collaborative solutions for light pollution affecting seabirds*. Seventh Meeting of the Population and Conservation Status ACAP Working Group, 18–19 May, Hobart, Australia. [Available online at <https://www.acap.aq/documents/working-groups/population-and-conservation-status-working-group/pacswg7/pacswg7-information-papers/4285-pacswg7-inf-13/file>].
- COSEWIC. 2016. *COSEWIC assessment and status report on the Pink-footed Shearwater *Ardenna creatopus* in Canada*. Ottawa, Canada: Committee on the Status of Endangered Wildlife in Canada. [Accessed online at <http://www.registrelep-sararegistry.gc.ca/default.asp?lang=en&n=24F7211B-1> on 24 February 2024.]
- CROXALL, J.P., BUTCHART, S.H.M., LASCELLES, B. ET AL. 2012. Seabird conservation status, threats and priority actions: A global assessment. *Bird Conservation International* 22: 1–34. doi:10.1017/S0959270912000020
- DE REU, J., BOURGEOIS, J., BATS, M. ET AL. 2013. Application of the topographic position index to heterogeneous landscapes. *Geomorphology* 186: 39–49. doi:10.1016/j.geomorph.2012.12.015
- DIAS M.P., MARTIN R., PEARMAIN E.J. ET AL. 2019. Threats to seabirds: a global assessment. *Biological Conservation* 237: 525–537. doi:10.1016/j.biocon.2019.06.033
- DILLEY, B. J., DAVIES, D., SCHRAMM, M., CONNAN, M. & RYAN, P.G. 2017. The distribution and abundance of Blue Petrels (*Halobaena caerulea*) breeding at subantarctic Marion Island. *Emu-Austral Ornithology* 117: 222–232 doi:10.1080/01584197.2017.1298403
- ESRI. 2016. *ArcGIS Desktop: Release 10.0*. Redlands, USA: Environmental Systems Research Institute.
- FELIS, J.J., ADAMS, J., HODUM, P.J., CARLE, R.D. & COLODRO, V. 2019. Eastern Pacific migration strategies of Pink-footed Shearwaters *Ardenna creatopus*: Implications for fisheries interactions and international conservation. *Endangered Species Research* 39: 269–282. doi:10.3354/esr00969
- FELIS, J.J., KELSEY, E.C., ADAMS, J., STENSKE, J.G. & WHITE, L.M. 2020. Population estimates for selected breeding seabirds at Kilauea Point National Wildlife Refuge, Kaa'i, in 2019. U.S. Geological Survey Data Series 1130. Santa Cruz, USA: USGS. doi:10.3133/ds1130
- FRANCÉS, A.P. & LUBCZYNSKI, M.W. 2011. Topsoil thickness prediction at the catchment scale by integration of invasive sampling, surface geophysics, remote sensing and statistical modeling. *Journal of Hydrology* 405: 31–47. doi:10.1016/j.jhydrol.2011.05.006
- FRIESEN, M.R., SIMPKINS, C E., ROSS, J. ET AL. 2021. New population estimate for an abundant marine indicator species, Rako or Buller's Shearwater (*Ardenna bulleri*). *Emu-Austral Ornithology* 121: 231–238. doi:10.1080/01584197.2021.1924066
- FURNESS, R.W. 2015. *Non-breeding Season Populations of Seabirds in UK waters: Population Sizes for Biologically Defined Minimum Population Scales (BDMPS)*. Natural England Commissioned Reports 164. Glasgow, UK: Natural England. [Accessed online at <https://publications.naturalengland.org.uk/publication/6427568802627584> on 24 February 2024.]
- GALLANT, J.C. 2000. Primary topographic attributes. In: WILSON, J.P. & GALLANT, J.C. (Eds.) *Terrain Analysis: Principles and Application*. Hoboken, USA: John Wiley & Sons.
- GARCÍA-DÍAZ, P., HODUM, P., COLODRO, V., HESTER, M. & CARLE, R.D. 2020. Alien mammal assemblage effects on burrow occupancy and hatching success of the vulnerable pink-footed shearwater in Chile. *Environmental Conservation* 47: 149–157. doi:10.1017/S0376892920000132
- GOODMAN, L.A. 1960. On the exact variance of products. *Journal of the American Statistical Association* 55: 708–713. doi:10.1080/01621459.1960.10483369
- GUICKING, D., MICKSTEIN, S. & SCHLATTER, R.P. 1999. Estado de la población de fardela blanca (*Puffinus creatopus*) en Isla Mocha, Chile. *Boletín Chileno de Ornitología* 6: 35–38.
- HAHN, I., RÖMER, U., SOTO, G. E., BAUMEISTER, J. & VERGARA, P. M. 2016. Diversity, biogeography, abundance, and conservation of the birds of Mocha Island National Reserve, Chile. *Vertebrate Zoology* 66: 397–410.

- HIJMANS, R.J. 2021. *raster: Geographic Data Analysis and Modeling*. R package Version 3.4-13. [Manual accessed at <https://CRAN.R-project.org/package=raster> on 24 February 2024.]
- HOFFMANN, M., BROOKS, T.M., DA FONSECA, G.A. ET AL. 2008. Conservation planning and the IUCN Red List. *Endangered Species Research* 6: 113–125. doi:10.3354/esr00087
- IBARRA-VIDAL, H. & KLESSE, M.C. 1994. Nota sobre la Fardela de Vientre blanco (*Puffinus creatopus*, Coues, 1864) (Aves, Procellariidae) de la isla Mocha, VIII región, Chile. *Comunicaciones Museo Historia Natural Concepción* 8: 49–54.
- JACKMAN, S. 2020. *pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory*. R package version 1.5.5. Sydney, Australia: United States Studies Centre, University of Sydney. [Accessed online at <https://github.com/atahk/pscl/> on 24 February 2024.]
- LAVERS, J.L., HUTTON, I. & BOND, A.L. 2019. Changes in technology and imperfect detection of nest contents impedes reliable estimates of population trends in burrowing seabirds. *Global Ecology and Conservation* 17: e00579. doi:10.1016/j.gecco.2019.e00579
- LEIRNESS, J.B., ADAMS, J., BALANCE, L.T. ET AL. 2021. *Modeling At-Sea Density of Marine Birds to Support Renewable Energy Planning on the Pacific Outer Continental Shelf of the Contiguous United States*. OCS Study BOEM 2021-014. Camarillo, USA: US Department of the Interior, Bureau of Ocean Energy Management. [Accessed online at https://ospis.boem.gov/final%20reports/BOEM_2021-014.pdf on 24 February 2024.]
- LEQUESNE, C., VILLAGRÁN, C. & VILLA, R. 1999. Historia de los bosques relictos de “olivillo” (*Aextoxicon punctatum*) y Mirtáceas de la Isla Mocha, Chile, durante el Holoceno tardío. *Revista Chilena de Historia Natural* 72: 31–47.
- LÓPEZ, V. 2019. *Desafíos y Lecciones Aprendidas Para Abordar la Cosecha de Polluelos de Fardela Blanca en Isla Mocha, Chile*. Fifth Meeting of the Population and Conservation Status ACAP Working Group, 09-10 May, Hobart, Australia. [Available online at <https://www.acap.aq/documents/working-groups/population-and-conservation-status-working-group/population-and-conservation-status-wg-meeting-5/pacswg5-information-papers/3419-pacswg5-inf-17-desafios-y-lecciones-aprendidas-para-abordar-la-cosecha-de-polluelos-de-fardela-blanca-en-isla-mocha>].
- LÓPEZ, V., COLODRO, V., GUTIÉRREZ, H., LARA, M. & VARELA, T. 2021. *Nuevas Amenazas Para Fardela Blanca en Sus Zonas de Nidificación*. Sixth Meeting of the Population and Conservation Status ACAP Working Group, 25–26 August, online. Available online at <https://www.acap.aq/documents/working-groups/population-and-conservation-status-working-group/pacswg6/pacswg6-information-papers/3853-pacswg6-inf-13-nuevas-amenazas-para-fardela-blanca-en-sus-zonas-de-nidificacion>].
- MADRIGAL RUIZ, D., TINKER, M.T., TERSHY, B.R., ZILLIACUS, K.M. & CROLL, D.A. 2021. Using meta-population models to guide conservation action. *Global Ecology and Conservation* 28: e01644. doi:10.1016/j.gecco.2021.e01644
- MORAIS, A.R., SIQUEIRA, M.N., LEMES, P., MACIEL, N.M., DE MARCO JR., P. & BRITO, D. 2013. Unraveling the conservation status of Data Deficient species. *Biological Conservation* 166: 98–102. doi:10.1016/j.biocon.2013.06.010
- MINISTERIO DE MEDIO AMBIENTE. 2019. *Plan de Recuperación, Conservación y Gestión de la Fardela Blanca (Ardenna creatopus)*. Santiago, Chile: Ministerio de Medio Ambiente. [Accessed at <https://simbio.mma.gob.cl/PlanesRecoge/DownloadDocument/4> on 24 February 2024.]
- MUÑOZ, D.M. 2011. *Áreas de Nidificación y Densidad de Nidos de Fardela de Vientre Blanco, Puffinus creatopus Coues en La Reserva Nacional Isla Mocha*. MSc thesis. Concepcion, Chile: Universidad de Concepcion.
- MURPHY R.C. 1936. *Oceanic Birds of South America*. Vol. 2. New York, USA: American Museum of Natural History.
- NAKAGAWA, S. & SCHIELZETH, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133–142. doi:10.1111/j.2041-210x.2012.00261.x
- NASA JPL. 2013. *NASA Shuttle Radar Topography Mission Global 1 arc second* [Data set]. NASA EOSDIS Land Processes Distributed Active Archive Centre. [Accessed online at <https://doi.org/10.5067/MEASURES/SRTM/SRTMGL1.003> on 23 November 2022.]
- OLIVIER, F. & WOTHERSPOON, S.J. 2006. Modelling habitat selection using presence-only data: case study of a colonial hollow nesting bird, the snow petrel. *Ecological Modelling* 195: 187–204. doi:10.1016/j.ecolmodel.2005.10.036
- PEARSON, S.F., HODUM, P.J., GOOD, T.P., SCHRIMPF, M. & KNAPP, S.M. 2013. A model approach for estimating colony size, trends, and habitat associations of burrow-nesting seabirds. *The Condor* 115: 356–365. doi:10.1525/cond.2013.110207
- PHILLIPS, R. A., GALES, R., BAKER, G. B. ET AL. 2016. The conservation status and priorities for albatrosses and large petrels. *Biological Conservation* 201: 169–183. doi:10.1016/j.biocon.2016.06.017
- R CORE TEAM. 2021. *R: A language and environment for statistical computing*. Vienna, Austria. R Foundation for Statistical Computing. [Accessed online at <https://www.R-project.org/> on 24 February 2024.]
- RAINE, A. F., DRISKILL, S., ROTHE, J. & VYNNE, M. 2022. Nest site characteristics of two endangered seabirds in montane wet forests on the island of Kaua‘i, Hawai‘i, USA. *Waterbirds* 44: 472–482. doi:10.1675/063.044.0408
- RAYNER, M.J., HAUBER, M.E. & CLOUT, M.N. 2007. Breeding habitat of the Cook’s Petrel (*Pterodroma cookii*) on Little Barrier Island (Hauturu): implications for the conservation of a New Zealand endemic. *Emu-Austral Ornithology* 107: 59–68. doi:10.1071/MU06038
- REXER-HUBER, K., PARKER, G.C., RYAN, P.G. & CUTHBERT, R.J. 2014. Burrow occupancy and population size in the Atlantic Petrel *Pterodroma incerta*: a comparison of methods. *Marine Ornithology* 42: 137–141.
- REYES-ARRIAGADA, R., CAMPOS-ELLWANGER, P., SCHLATTER, R.P. & BADUINI C. 2007. Sooty Shearwater (*Puffinus griseus*) on Guafo Island: The largest seabird colony in the world? *Biodiversity Conservation* 16: 913–930. doi:10.1007/s10531-006-9087-9
- RODRÍGUEZ A., ARCOS J.M., BRETAGNOLLE V. ET AL. 2019. Future directions in conservation research on petrels and shearwaters. *Frontiers in Marine Science* 6: 94. doi: 10.3389/fmars.2019.00094
- SERVICIO AGRÍCOLA Y GANADERO. 1998. *Reglamento de la Ley de Caza: Decreto Supremo n° 05 de Enero de 1998*. Santiago, Chile: SAG.
- SILVA, R., MEDRANO, F., TEJEDA, I. ET AL. 2019. Evaluación del impacto de la contaminación lumínica sobre las aves marinas en Chile: diagnóstico y propuestas. *Ornitología Neotropical* 31: 1–12.

- SCOTT, D., MOLLER, H., FLETCHER, D. ET AL. 2009. Predictive habitat modelling to estimate petrel breeding colony sizes: sooty shearwaters (*Puffinus griseus*) and mottled petrels (*Pterodroma inexpectata*) on Whenua Hou Island. *New Zealand Journal of Zoology* 36: 291–306.
- SUAZO, C.G., CABEZAS, L.A., MORENO, C.A. ET AL. 2014. Seabird bycatch in Chile: a synthesis of its impacts, and a review of strategies to contribute to the reduction of a global phenomenon. *Pacific Seabirds* 41: 1–12.
- SUTHERLAND, D.R. & DANN, P. 2012. Improving the accuracy of population size estimates for burrow-nesting seabirds. *Ibis* 154: 488–498. doi:10.1111/j.1474-919X.2012.01234.x
- TINKER, M.T., ZILLIACUS, K.M., RUIZ, D., TERSHY, B.R. & CROLL, D.A. 2022. Seabird meta-Population Viability Model (mPVA) methods. *MethodsX* 9: 101599. doi:10.1016/j.mex.2021.101599
- VEGA, R., L. OSSA, B. SUÁREZ, A. ET AL. 2019. *Informe Final - Convenio de Desempeño 2019. Programa de Observadores Científicos 2017–2018*. Programa de Investigación del Descarte y Captura de Pesca Incidental en Pesquerías Pelágicas 2018–2019. Valparaíso, Chile: Instituto de Fomento Pesquero.
- WHITEHEAD, A.L., LYVER, P.O.B., JONES, B. ET AL. 2014. Establishing accurate baseline estimates of breeding populations of a burrowing seabird, the grey-faced petrel (*Pterodroma macroptera gouldi*) in New Zealand. *Biological Conservation* 169: 109–116. doi:10.1016/j.biocon.2013.11.002
- ZEILEIS, A., KLEIBER, C. & JACKMAN, S. 2008. Regression models for count data in R. *Journal of Statistical Software* 27: 1–25.
- ZUUR, A.F., IENO, E.N., WALKER, N.J., SAVELIEV, A.A. & SMITH, G.M. 2009. *Mixed Effects Models and Extension in Ecology with R*. New York, USA: Springer.
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