

# ECOGRAPHY

## Research

### Generating unbiased estimates of burrowing seabird populations

Jeremy P. Bird, Aleks Terauds, Richard A. Fuller, Penelope P. Pascoe, Toby D. Travers, Julie C. McInnes, Rachael Alderman and Justine D. Shaw

J. P. Bird (<https://orcid.org/0000-0002-7466-1755>) ✉ ([jez.bird@uq.edu.au](mailto:jez.bird@uq.edu.au)), R. A. Fuller (<https://orcid.org/0000-0001-9468-9678>) and J. D. Shaw (<https://orcid.org/0000-0002-9603-2271>), School of Biological Sciences, Univ. of Queensland, St Lucia, Queensland, Australia. – JPB, P. P. Pascoe (<https://orcid.org/0000-0001-9586-1046>), T. D. Travers (<https://orcid.org/0000-0002-1218-6207>) and J. C. McInnes (<https://orcid.org/0000-0001-8902-5199>), Inst. for Marine and Antarctic Studies, Univ. of Tasmania, Battery Point, Tasmania, Australia. – JCM and A. Terauds (<https://orcid.org/0000-0001-7804-6648>), Australian Antarctic Division, Dept of Agriculture, Water and the Environment, Tasmania, Australia. – R. Alderman, Dept of Natural Resources and Environment, Hobart, Tasmania, Australia. JDS also at: School of Biological and Environmental Sciences, Queensland Univ. of Technology, Australia.

## Ecography

2022: e06204

doi: 10.1111/ecog.06204

Subject Editor: Nigel G. Yoccoz

Editor-in-Chief: Miguel Araújo

Accepted 12 February 2022



Maximising survey efficiency can help reduce the tradeoff between spending limited conservation resources on identifying population changes and responding to those changes through management. Burrow-nesting seabirds are particularly challenging to survey because nests cannot be counted directly. We evaluated a stratified random survey design for generating unbiased population estimates simultaneously for four petrel species nesting on Macquarie Island, Australia, where the survey cue, burrow entrances, is similar for all species. We also compared the use of design-based and model-based analyses for minimising uncertainty in estimates. We recorded 2845 Antarctic prion burrows, 306 white-headed petrel burrows and two blue petrel burrows while distance-sampling along 154 km of transects. For blue petrels and grey petrels, we completed nocturnal searches along a further 71 km and searched 249 km of tracks during follow-up ground searches. We failed to generate unbiased population estimates for two rare and localised species, blue and grey petrels, from our stratified random survey. Only for the most widespread and abundant species, Antarctic prion, did the estimate have reasonable power to detect a rapid population change. Model-based analyses of the stratified random survey data did not improve upon traditional design-based analyses in terms of uncertainty in population estimates, but they did provide useful spatial representation of current populations. Models that used the targeted survey data did not reflect current population sizes and distributions of the two rare and localised species. We found that when species ecologies, distributions and abundances vary, a multi-method approach to surveys is needed. Species with low abundance that occur patchily across large islands are likely to be best estimated using targeted surveys, whereas widespread and abundant species can be accurately and precisely estimated from randomised surveys using informative model-based analyses.

Keywords: density surface model, distance sampling, petrel, seabird, survey



[www.ecography.org](http://www.ecography.org)

© 2022 The Authors. Ecography published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

## Introduction

Seabirds are keystone species in ocean and island ecosystems. They provide top-down regulation of prey populations, drive primary production through nutrient deposition and support tourism and cultural harvests (Newman et al. 2009, Mulder et al. 2011, Danckwerts et al. 2014, Otero et al. 2018, Pagès et al. 2018). Today, numerous threats to seabirds at sea and on land result in their classification as one of the most threatened of all bird groups globally (Dias et al. 2019). As higher order predators in marine systems, seabirds' responses to anthropogenic impacts can indicate systemic environmental change and as such they have been adopted as 'essential ocean variables' for observing and managing our seas (Miloslavich et al. 2018). Monitoring seabirds can detect and track environmental changes, as well as the conservation status of individual species as they respond to anthropogenic threats and the effectiveness of conservation interventions being implemented to address those threats (Brooke et al. 2018, Dias et al. 2019).

About one third of all seabirds nest in underground burrows (Del Hoyo et al. 1992). Monitoring these species is particularly difficult because nests are hard to observe directly. Typically the number of burrows and the proportion that are occupied are measured separately and combined to obtain an estimate for a given area, often a whole island (Sutherland and Dann 2012). In most cases large uncertainty in these estimates prevents the detection of significant changes in seabird population sizes over time (Bird et al. 2021). Uncertainty is usually greater for burrow detection than burrow occupancy, since burrows are often distributed discontinuously across challenging terrain, and their entrances may be obscured by vegetation (Rayner et al. 2007, Rodríguez et al. 2019). While field and analytical methods are constantly evolving to improve the accuracy and precision of population estimates (Thompson 2013), further improvements are desirable, maximising efficiency during fieldwork and data analysis to deliver the most information within financial and practical constraints (Possingham et al. 2012).

Multiple burrowing seabird species often nest sympatrically on islands. In this study we test if unbiased estimators of several species' burrow numbers could be efficiently generated using a single randomised survey design given that the survey cue, burrow entrances, is similar across species. Alternatively, do morphological, phenological and ecological differences between species require targeted species-specific surveys as elsewhere (Dilley et al. 2019)? Determining the relevant survey design can be challenging. Stratified designs, where the area to be sampled is divided into homogenous sub-areas, or randomised designs where survey effort is distributed randomly across the area to be sampled, or a combination of the two, are recommended where the goal of surveys is to estimate populations and track changes over time (Buckland et al. 2015). However, for rare or highly localised species that can easily be missed within the landscape, randomised surveys can result in low precision (Thompson 2013, Pacifici et al. 2016). In such cases incorporating prior knowledge such as historical records,

pilot ground surveys and nocturnal surveys of aerial activity can improve results (Rayner et al. 2007, Arneill et al. 2019).

When analysing data, design-based or model-based analyses can be used. Design-based methods simply calculate abundance within the sampled area and extrapolate from this to the wider area. They make assumptions about the survey design, for example that sampling effort was allocated randomly. Model-based methods rely on the relationship between species abundance and spatial and environmental covariates to infer abundance in space and/or time. Models can improve precision in animal abundance estimates by eliminating biologically unlikely changes in density through smoothing (Camp et al. 2020). While design-based methods can require stratification of survey data to account for uneven sampling (possibly by design), model-based methods utilise data more efficiently through finer scale covariates. However, switching from design- to model-based methods requires a substitution of assumptions: from assuming sampling locations were chosen at random, to assuming the model accurately reflects a species' realised niche (Camp et al. 2020). Information is currently limited as to how well this assumption performs for different types of species, e.g. common or rare, and clustered or dispersed species (Pacifici et al. 2016, Dilley et al. 2019).

We studied four procellariiform petrels on Macquarie Island (54°30'S, 158°57'E), a remote oceanic island approximately 1500 km south-east of Tasmania, Australia. Our study system has many of the factors that make burrowing seabirds challenging to study. The island is large with most terrain only accessible by foot, so surveys require multi-day field trips. As a UNESCO World Heritage Site and Tasmanian Nature Reserve, access permits are required and the sub-Antarctic environment and island's terrain add logistical difficulty. The current distributions of our study species are poorly known as they are responding to staged eradications of introduced wekas *Gallinallus australis* (1988), cats *Felis catus* (2001), rabbits *Oryctolagus cuniculus*, black rats *Rattus rattus* and house mice *Mus musculus* (all 2011) following decades of impacts (Copson and Whinam 2001, Robinson and Copson 2014, Springer 2016). Antarctic prions *Pachyptila desolata* and white-headed petrels *Pterodroma lessonii* were previously widespread and relatively common, while blue petrels *Halobaena caerulea* and grey petrels *Procellaria cinerea* have only recently recolonised the island having been extirpated in the 1900s (Brothers 1984, Brothers and Bone 2008).

In this study we 1) compare the performance of a stratified random survey design with targeted species-specific surveys, and 2) compare design-based versus model-based analyses for estimating burrow numbers. We synthesize our findings into guidance on key considerations for surveying multi-species assemblages of burrowing seabirds.

## Methods

We estimated the sizes and distributions of our four study species' populations through five steps (Fig. 1).

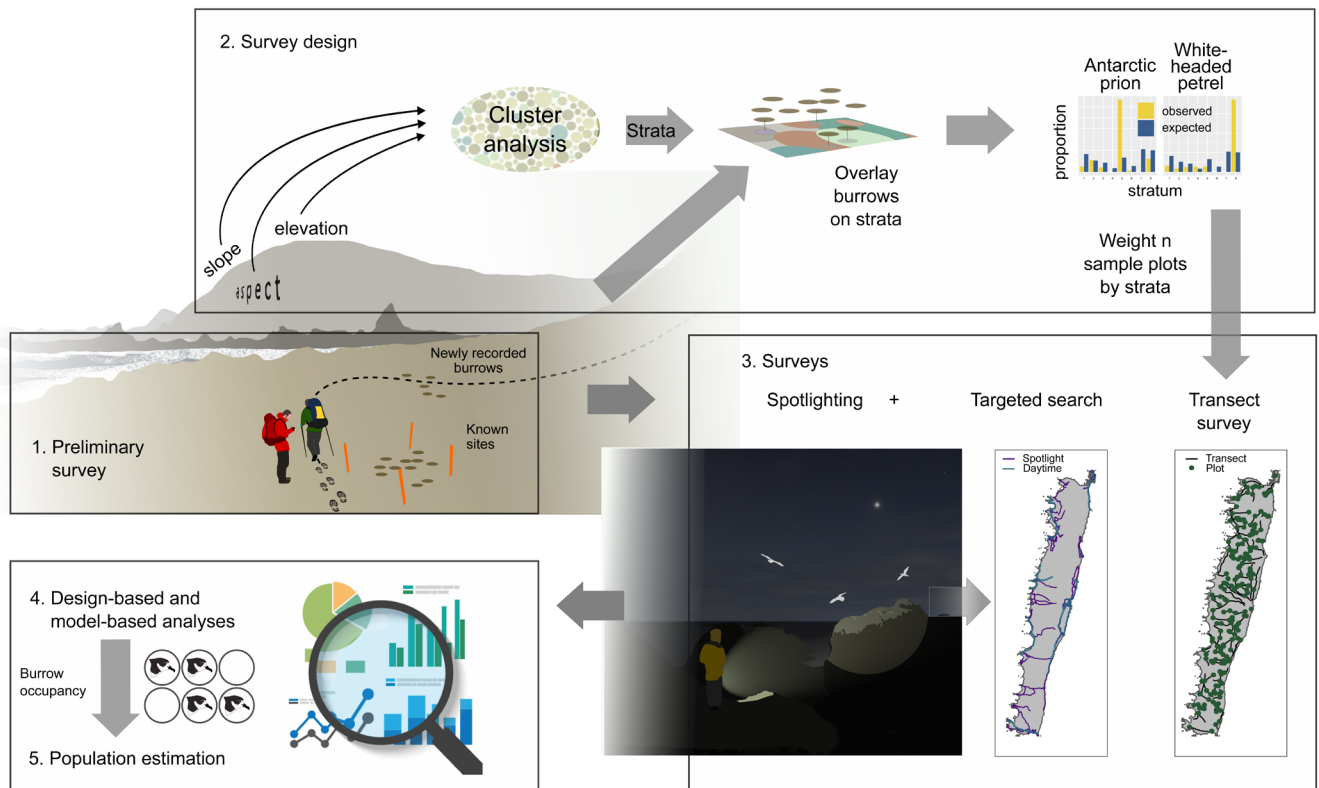


Figure 1. Petrel survey design and implementation on Macquarie Island. Burrows of different species were recorded at known sites and incidentally elsewhere (1). The frequency of incidental burrows in different modelled strata was used to assign numbers of random plots in different strata (2). Transect surveys were followed by targeted searches for localised species, informed by knowledge of existing sites and by spotlighting (3). Survey data were used to estimate burrow numbers using design- and model-based methods (4). Finally these estimates were adjusted for occupancy to give a final population estimate (5).

### Preliminary survey

We undertook a preliminary survey in November–December 2017 visiting known petrel colonies (Schulz et al. 2006, Brothers and Bone 2008) and opportunistically recording burrows across Macquarie Island. We recorded 1521 burrows in total during our preliminary survey. All burrows were identified to species level (Supporting information) and geo-referenced using a handheld Garmin 60 GPS.

### Environmental covariates, stratification and survey design

We used spatial environmental covariates and a clustering algorithm to classify eight strata across the island using the ‘cmeans’ function from the e1071 package in R (Meyer et al. 2019, <[www.r-project.org](http://www.r-project.org)>). The environmental covariates were aspect, elevation, proximity to ridgelines, slope, a topographic wetness index, topographically-deflected mean wind speed and a normalised difference vegetation index (NDVI), derived from a 5-m resolution digital elevation model and QuickBird satellite imagery (Bricher et al. 2013). All burrow locations from the preliminary survey were overlain on the eight strata and classified by species and stratum (Fig. 1). Antarctic prions and white-headed petrels were widespread

whereas blue and grey petrel burrows were not encountered away from known sites. Based on this we optimised effort in our stratified random survey for the two widespread species. When overlain on the strata Antarctic prions and white-headed petrels showed a strongly skewed distribution (Fig. 1). The observed frequency of each species’ burrows in each stratum was compared with expected frequency derived from track points extracted from our GPS tracks in Garmin BaseCamp ver. 4.7.0 (Garmin 2019) – a proxy for time spent surveying each stratum. The observed and expected frequency distributions (Fig. 1) were used to generate 200 stratified random points and 100 reserve points (as replacements when a target point was inaccessible) in QGIS ver. 3.6.3 (<<http://qgis.osgeo.org>>). One third ( $67 \times 2$ ) of the points were assigned to strata based upon the observed frequencies of Antarctic prion and white-headed petrel burrows in different strata, and the remaining third (66) were controls based upon the relative extents of the eight strata island-wide.

### Survey implementation

#### Stratified random transect survey

From 5 January to 24 April 2018 we distance sampled burrows along 158 km of transects navigated between our randomly generated points. Distance sampling is a way of

estimating density while explicitly accounting for uncertain detection (Miller et al. 2013), and has been used effectively to estimate petrel population sizes (Lawton et al. 2006, Rexer-Huber et al. 2017). In our survey, a lead person walked in a straight line, recording the exact route by handheld GPS. Waypoints were taken each time the transect transitioned from ‘short’ to ‘tall’ ( $\leq 70$  cm) vegetation so that the transect could be subdivided post hoc for analyses. A second person, walking directly behind the first, visually scanned left and right identifying all burrows observed from the transect line, recording them on a second GPS and measuring the perpendicular distance between the burrow and the transect line to the nearest 10 cm.

### **Targeted species-specific searches**

Because blue petrels and grey petrels were not encountered away from known colonies during the preliminary survey, we undertook targeted searches for those species. In 2017–2018 we surveyed all known colonies of blue petrels and grey petrels. To detect new colonies we adapted methods from Schulz et al. (2006) and Dilley et al. (2017), defining suitable habitat based upon descriptions in these two papers and our own experience of known sites (Supporting information). We conducted nocturnal surveys of suitable habitat by observing from vantage points, or traversing on foot, to identify birds vocalising or flying over colonies. Flying birds were readily observed to at least 100 m range with a Ledlenser P17.2 spotlight. Active daytime burrow searches were made in suitable habitats focusing on known sites, any areas identified during nocturnal surveys and around brown skua *Stercorarius antarcticus* territories where blue petrel remains were identified.

Burrows were found by looking for fresh droppings, feathers and trampled vegetation or soil at burrow entrances, and by listening for blue petrels responding to imitation calls (Schulz et al. 2006, Dilley et al. 2017). Colonies were defined as clusters of  $\geq 1$  burrow separated by  $> 50$  m from the nearest cluster. We attempted to census grey petrels, searching outwards from all located burrows to search the whole area of suitable habitat (Schulz et al. 2006). When surveying blue petrel colonies, we followed Dilley et al. (2017) to define the colony extent and estimate total burrows by sub-sampling circle plots and extrapolating to the colony area.

## **Analysis**

### **Design-based analyses**

#### *Colony counts*

For grey petrels we censused all burrows across the island, and for blue petrels we summed our colony estimates to generate a whole-island estimate of burrow numbers.

#### *Distance analyses*

We sub-divided our transects into sections by vegetation height and strata in QGIS. For Antarctic prions and white-headed petrels, we truncated the burrow observations, with the most distant 5% of observed burrows excluded from analyses. This resulted in truncation distances of 5.5 m for

analysis of Antarctic prion data and 11.10 m for white-headed petrel data. Using the distance package in R we then fitted half normal and hazard rate detection functions with cosine, hermite and polynomial adjustments and with stratum, observer and vegetation height as covariates (Miller 2017). To account for overdispersion of our distance data we used a two-step process to select a final detection function using an adjusted version of Akaike’s information criterion (QAIC) following Howe et al. (2019). We used the selected model to estimate abundance for each stratum within the area covered by transects (twice the truncation distance multiplied by transect lengths) and then scaled this to provide an overall burrow estimate and upper and lower confidence limits for the whole island (Miller 2017).

### **Model-based analyses**

We used a generalised additive model (GAM) and the selected detection functions described above to build density surface models (DSMs) in the dsm package for Antarctic prions and white-headed petrels from distance sampling data and environmental covariates (Miller et al. 2013, 2020). We clipped our transects into lengths  $2 \times$  the truncation distance in length. The lengths were then buffered by the truncation distance to create contiguous squares of strip transect. Observations were linked to their respective transect square to generate square-specific burrow counts. Mean values of the same environmental variables used to generate strata were calculated for each transect section using the tabularaster package (Sumner 2018). Models were fitted with estimated abundance – burrow count per transect square corrected for detection – as the response variable, spatial smooths of all seven environmental variables and a bivariate spatial smooth of x- and y-coordinates of burrow observations (Marshall et al. 2017). Three global models were fitted using quasipoisson, negative binomial and Tweedie distributions. The default basis complexity ( $k=10$ ) was used for all variables except the bivariate xy smooth which was assigned a basis complexity of  $k=60$  to allow a high level of spatial complexity and account for the spatial autocorrelated distribution of burrows (Marshall et al. 2017). We selected a probability distribution based upon diagnostic plots and adjusted  $r^2$  from the three global models and compared all subsets of the global model using AIC. The final model (lowest AIC score) was tested for concavity (Marshall et al. 2017, Bock 2018). The final model for each species was used to predict burrow abundance across the entire island at a  $20 \times 20$  m grid cell resolution. The predicted abundances from all cells were summed to produce an island-wide estimate of burrow numbers. If the selected detection function had no covariates we used the delta method for estimating 95% confidence intervals (CI). If the detection function included covariates we also used variance propagation to estimate CI (Miller et al. 2020, Bravington et al. 2021).

We also generated spatial models of blue and grey petrel abundance. Our data for these two species were derived from targeted surveys. Unlike in distance sampling where uncertain detection is explicitly accounted for, we assumed perfect detection of burrows during our targeted searches. We



extracted environmental covariates in the same way as above and fitted GAMs directly with the mgcv package (Wood 2017). We selected models in the same way as above, and used the selected model for each species to predict abundance island-wide.

### Power analyses

To evaluate the strength of our unbiased estimators of burrow numbers we simulated declines of 30, 50 and 80% over three generations for Antarctic prions and white-headed petrels following Bird et al. (2021) and assessed their power to detect significant differences between repeat estimates (Supporting information).

### Population estimation

We adjusted burrow estimates by species-specific occupancy from Bird et al. (in press) to generate population estimates. Estimates of occupancy were used to adjust burrow estimates: for colonies where colony-specific occupancy was available (blue petrels); or for the whole population (all other species). We multiplied burrow and occupancy estimates to estimate population size, and used the delta method to combine variances around the burrow and occupancy estimates before calculating confidence intervals.

## Results

### Survey implementation

During the transect survey we recorded 2845 Antarctic prion burrows, 306 white-headed petrel burrows and two blue petrel burrows. An additional 90 burrows (just under 3%) could not be identified to species-level and were excluded from analyses.

As only two blue petrel burrows and no grey petrel burrows were encountered during transect surveys, we walked 71 km during nocturnal surveys and searched 249 km of tracks

during follow-up ground searches. During these searches we found and surveyed 37 blue petrel colonies including 12 previously unrecorded colonies, and 74 grey petrel colonies including 31 at previously unrecorded sites.

Our stratified random transect surveys covered 48 ha and 60 ha, or 0.4 and 0.5% of the whole island for Antarctic prions and white-headed petrels respectively. This comprised  $2 \times$  effective strip half width (ESW) calculated during distance analysis (below)  $\times$  total transect length during transect surveys (Antarctic prions: ESW = 3.04, SE = 0.07, 95% CI 2.90–3.18; white-headed petrels: ESW = 3.82, SE = 0.21, 95% CI 3.68–3.96). The total areas searched for blue and grey petrels were 1192 and 1264 ha, or 9.3 and 9.9% of the whole island comprising the island-wide transect surveys plus buffered ground searches and nocturnal search tracks.

### Estimating burrow numbers

#### Design-based methods

Grey petrel abundance was low, so we counted all burrows in the colonies we located, totalling 630 burrows across the island. For blue petrels we estimated burrow density in each colony, extrapolated to the total area of the colony (Supporting information). The peak density recorded was 1.79 burrows  $m^{-2}$  and summed colony estimates gave a total of 11 900 burrows with a coefficient of variation of 8% (Table 1).

Distance analysis of the stratified random transect data identified a hazard rate key function with no adjustments and no covariates as the best detection function for Antarctic prion burrows and a half normal key function with observer as a covariate for white-headed petrel burrows (Supporting information). We recorded a peak density of 0.28 Antarctic prion burrows  $m^{-2}$  in the transect squares and 0.08 white-headed petrel burrows  $m^{-2}$ . Extrapolating to the full extent of each stratum, and summing these estimates returned total estimates of 288 000 Antarctic prion burrows and 29, 500 white-headed petrel burrows on the island, with CVs of 13% and 36% respectively (Table 1).

Table 1. Estimates of the total number of burrows, breeding occupancy and total population estimates for four burrowing petrel species on Macquarie Island. The upper and lower confidence limits are expressed as a range, with the coefficient of variation for each estimate. The most precise estimates for each species are highlighted in bold.

Species	Survey	Analysis	Burrow estimate	Range (95% CI)	CV (%)	Population estimate	Range (95% CI)	CV (%)
White-headed petrel	Transects	Design-based – distance analysis	29 500	20 800–41 700	36	13 464	9510–19 100	36
	<b>Transects</b>	<b>Model-based – DSM</b>	<b>28 000</b>	<b>20 200–38 700</b>	<b>34</b>	<b>12 769</b>	<b>9020–18 100</b>	<b>36</b>
Antarctic prion	Transects	Design-based – distance analysis	288 000	253 000–329 000	13	192 216	168 000–219 000	14
	<b>Transects</b>	<b>Model-based – DSM</b>	<b>239 000</b>	<b>212 000–271 000</b>	<b>13</b>	<b>159 575</b>	<b>141 000–181 000</b>	<b>13</b>
Blue petrel	<b>Targeted search</b>	<b>Design-based – extrapolation</b>	<b>11 900</b>	<b>11 000–12 800</b>	<b>8</b>	<b>5588</b>	<b>5040–6330</b>	<b>12</b>
	Targeted search	Model-based – DSM	1 610 000	312 000–2 910 000	82	902 443	402 000–2 030 000	92
Grey petrel	<b>Targeted search</b>	<b>Design-based – census</b>	<b>630</b>	<b>630–630</b>	<b>0</b>	<b>252</b>	<b>227–302</b>	<b>15</b>
	Targeted search	Model-based – DSM	230 000	112 000–347 000	52	91 190	53 900–154 000	56

### Model-based methods

Inspection of residual quantile–quantile (QQ) plots and AIC scores showed that the negative binomial distribution gave the best fit to the Antarctic prion data, and the Tweedie distribution for white-headed petrels (Supporting information). The selected models included terms for location, elevation, slope and NDVI for prions and location, elevation, slope, topographic wetness and NDVI for white-headed petrels.

Predicted burrow densities along transects peaked at 0.04 burrows  $m^{-2}$  for Antarctic prions and 0.01 burrows  $m^{-2}$  for white-headed petrels. Summing the predicted numbers of Antarctic prion and white-headed petrel burrows in all pixels island-wide returned estimates of 239 000 and 28 000 burrows respectively with CVs of 34% and 12% (Table 1). Model predictions, when plotted, also provide species distribution maps (Fig. 2).

To model blue petrel and grey petrel abundance, we included real absences from along transect and search tracks, and density estimates from within surveyed colonies. Initial attempts to run models with 30 000 absences failed

computationally, so a sub-sampled set of 3000 absences was used in the final models. The models predicted peak densities of 13.6 and 0.05 burrows  $m^{-2}$  for blue petrels and grey petrels, with whole-island estimates of 1 610 000 and 230 000 burrows respectively. Uncertainty around these estimates was high with coefficients of variation of 82% and 52% respectively.

### Estimating population size

Burrow inspections estimated 40% (95% CI: 36–48%) of grey petrel burrows, 46% of white-headed petrel burrows (44–55%) and 67% (55–79%) of Antarctic prion burrows to be occupied by breeding pairs (Bird et al. in press). For blue petrels occupancy was estimated at all colonies using playback (Bird et al. in press). Adjusting burrow estimates by occupancy gave us island-wide population estimates for each species (Table 1). Using the delta method to combine burrow and occupancy estimates did not dramatically inflate uncertainty in the final population estimates for prions and white-headed petrel.

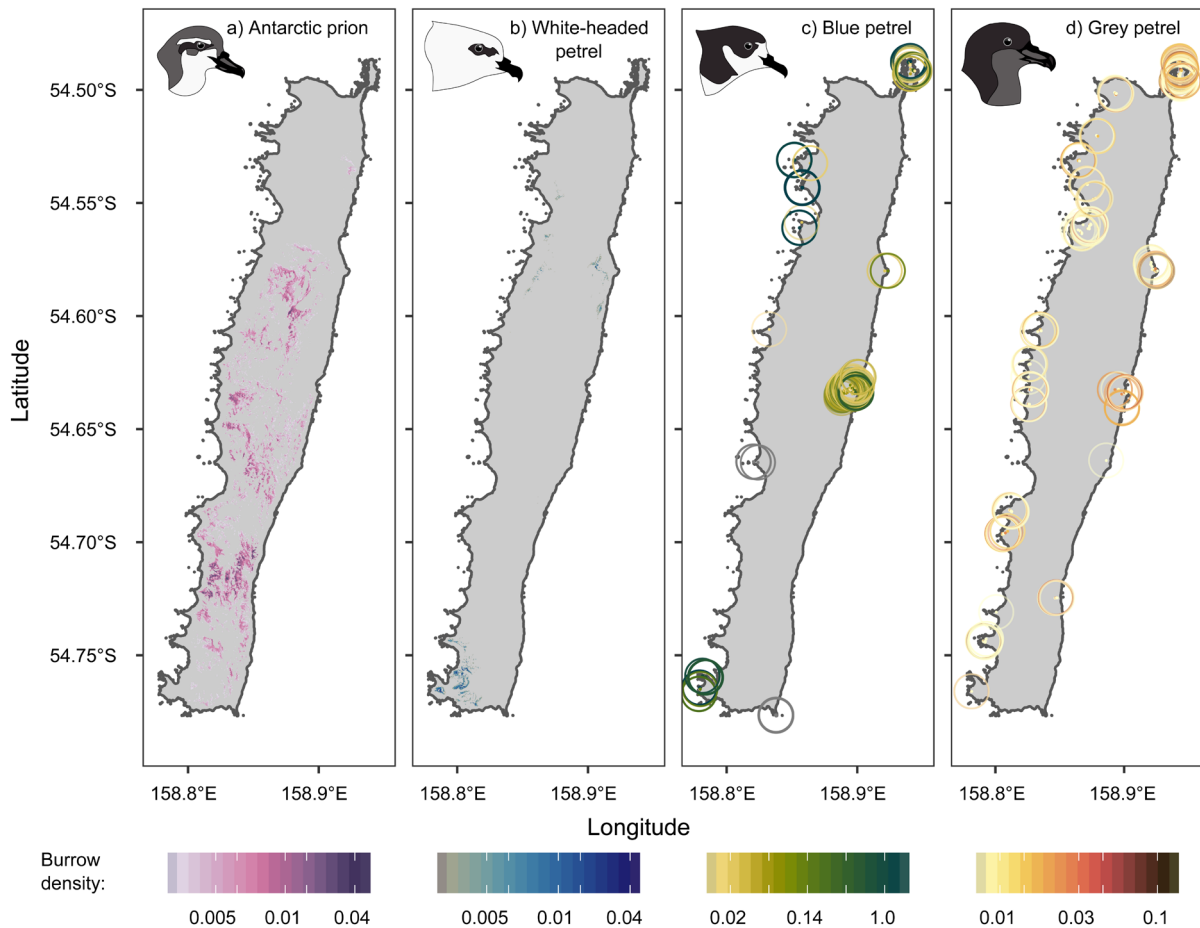


Figure 2. Island-wide burrow density (burrows  $m^{-2}$ ) plotted on a log scale for widespread species (a) Antarctic prions and (b) white-headed petrels, and recolonising species (c) blue petrels and (d) grey petrels. (a) and (b) are DSM predictions, (c) and (d) are from search surveys – circles are plotted around occupied pixels to increase visibility. Predicted densities in (a) and (b) were truncated below 1% of peak predicted density.

## Comparing methods

Sample sizes of Antarctic prions and white-headed petrels were large enough to generate burrow estimates using design-based distance analysis but were insufficient for blue petrels and grey petrels. The high number of Antarctic prion burrows encountered along transects resulted in lower uncertainty than for white-headed petrels. Censusing grey petrels and simple area-based extrapolation for blue petrels resulted in more precise estimates (lower CVs) than distance sampling, but our survey assumptions, such as finding all colonies/burrows and delineating colonies accurately, are untested.

There was negligible difference in uncertainty when estimating burrow numbers using the transect data and design-based distance analysis or model-based DSMs (Table 1). While the spatial predictions from the models (Fig. 2) and the partial effects plots (Supporting information) appear to be realistic, peak densities predicted by the models for the original sampling units (transect squares) were much lower than the raw estimates: 0.04 versus 0.28 burrows  $m^{-2}$  for

prions and 0.01 versus 0.08 burrows  $m^{-2}$  for white-headed petrels. This may be partially explained by model-smoothing, but it also suggests the models did not cope well with over-dispersion and zero-inflation in the data, which may be why the DSM-derived estimate for Antarctic prions is lower than the estimate from distance analysis.

Conversely, model-based estimates appear to substantially over-predict current blue and grey petrel burrow-densities, resulting in estimates two to three orders of magnitude above our direct estimates (Fig. 3). We overlaid our searched area – buffered nocturnal, transect and search survey tracks – on modelled blue and grey petrel abundance. This comparison indicates that habitat supporting 30% and 18% of the model-predicted populations of each species was surveyed, giving us confidence that the species were indeed absent from those areas, and that the models are over-predicting (Fig. 3).

Power analysis demonstrated that if the Antarctic prion population were increasing or decreasing rapidly (equivalent to a change of 30% over three generations as defined by the IUCN for Red List assessments) we would be able to detect

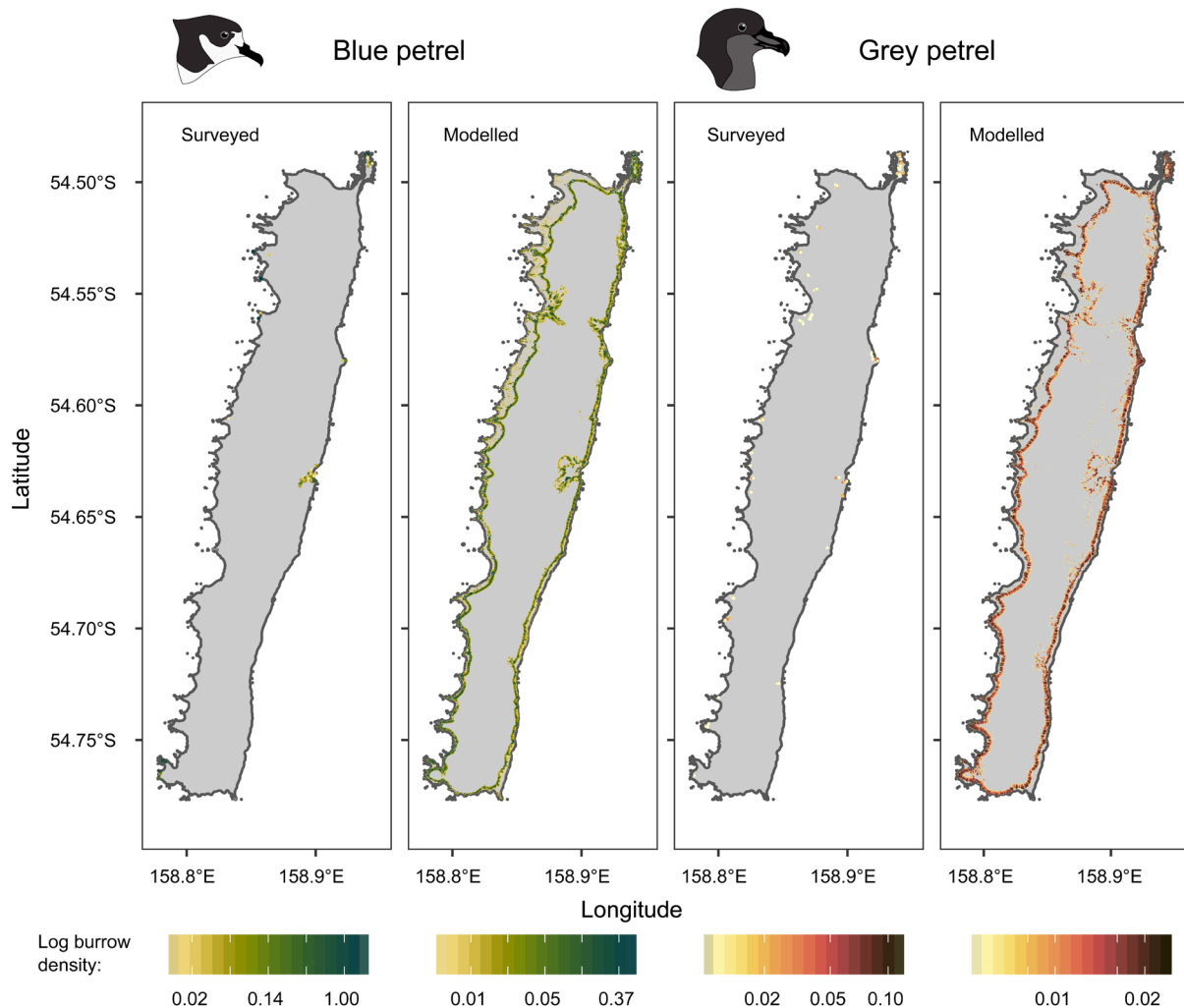


Figure 3. Surveyed and modelled densities of recolonising blue petrels and grey petrels illustrating that models currently over-predict the distributions of both species.

a significant difference between either our design-based or model-based estimates and an equivalent repeat estimate after approximately 15 years. The lower precision of our estimate of white-headed petrel burrow numbers means detecting such a rapid change would take more than 45 years (Fig. 4).

## Discussion

Our results show that a multi-method approach is needed to generate population estimates for multiple sympatric burrowing seabird species, even though their basic ecology is ostensibly similar. Furthermore, the most effective survey approach can vary for different species, even when the survey cue is similar and they occur within the same island ecosystem. Species habitat use, life histories, distributions and abundances are important factors in determining the survey approach. Below we summarise key considerations for designing burrowing seabird surveys (Fig. 5).

### Survey design

Most studies that estimate burrowing seabird population sizes aim to use their estimate to detect trends (Bird et al. 2021). For this, stratified and/or randomised survey designs are suitable for generating unbiased estimates (Buckland et al. 2015). We found, that given the patterns of occurrence of our study species our stratified random survey design was only suitable for generating unbiased estimates of two widespread species. It was unsuitable for the two localised species, blue and grey petrels. Furthermore, only our estimates of the most abundant species, Antarctic prion, had power to detect significant population changes in a moderate timeframe of ~15 years.

While targeted searches superficially appear to perform well, having lower coefficients of variation than estimates from our transect survey, they carry an unquantifiable bias which undermines their use for detecting trends. Mapping and censusing blue and grey petrel colonies provided a contemporary assessment of current distributions of both species, despite blue petrels being found to occur in just 0.05% and grey petrels in 0.03% of  $20 \times 20$  m pixels island-wide (compared with model predictions of  $> 1$  breeding pair of Antarctic prions in 16%, and white-headed petrels from 0.9% of all pixels). For rare and localised species, targeted searches can provide conservative estimators of population size for conservation assessments, and minimum occupied areas for inferring spatial change through time.

### Design-based versus model-based analysis

Given the high uncertainty in population estimates for burrowing seabirds to date, we assessed whether model-based approaches could reduce uncertainty in population estimates. We found that density surface models yielded marginally narrower confidence intervals for Antarctic prions and white-headed petrels than typical distance analysis, a

hybrid of design- and model-based methods (Table 1). The improvement in precision we observed was modest compared with Camp et al. (2020) who recently reported a 52% reduction in CI width using DSMs to estimate density over conventional distance analysis. There is no indication that a switch to model-based analyses will overcome the challenges associated with burrowing seabird population estimation and improve estimates for trend detection. Based upon our results and those of other recent studies (Buxton et al. 2016, Bird et al. 2021) we advocate that studies aiming to detect population trends should focus on constant-effort monitoring approaches rather than collecting intermittent whole-island population estimates.

In a landscape impacted by invasive species, whether currently or historically, native species do not occupy all suitable habitat (Smith et al. 2019). In our transect survey, this resulted in many zeros in otherwise suitable habitat. Consequently, the models for prions and white-headed petrels underestimated density because those high counts have been smoothed over all suitable habitat. The model compensated by overestimating occurrence, resulting in population estimates similar to those from distance sampling. In contrast, for blue and grey petrels for which our sample sizes were far lower, there was a big disparity between our design-based and model-based population estimates, with the models appearing to radically overestimate both density and occurrence (Fig. 3). This means it is difficult to test the assumption that our surveys detected all or nearly all colonies. While it's likely some colonies were missed, the history of field surveys on Macquarie Island (Schulz et al. 2006, Brothers and Bone 2008), and the fact we surveyed areas that supported 30% of total model-predicted blue petrel burrows and 18% of predicted grey petrel burrows, suggests our models failed to capture these species' realized niches accurately (Rayner et al. 2007, Camp et al. 2020). For highly localised species, the models were unable to accurately discriminate between suitable occupied habitat and apparently suitable unoccupied habitat.

Model-based analyses do have benefits. By providing information on distribution as well as abundance, models can: be more appropriate for communicating information to non-experts (Miller et al. 2013); inform spatially explicit management actions; inform monitoring design; and be used to reveal shifts in distribution through time. A limitation of monitoring colonial seabirds within established plots is that social attraction and density dependence can mask population growth and decline away from core ranges (Kildaw et al. 2005). Designing monitoring such that plots are positioned across a density gradient and include apparently suitable but unoccupied areas allows for the detection of wider population change. DSMs are an ideal tool to inform plot placement. For blue and grey petrels, the model predictions, while inadequate for abundance estimation, indicate apparently suitable habitat (Cianfrani et al. 2010), which, as with Antarctic prions and white-headed petrels, could be used to inform future searches and monitoring.



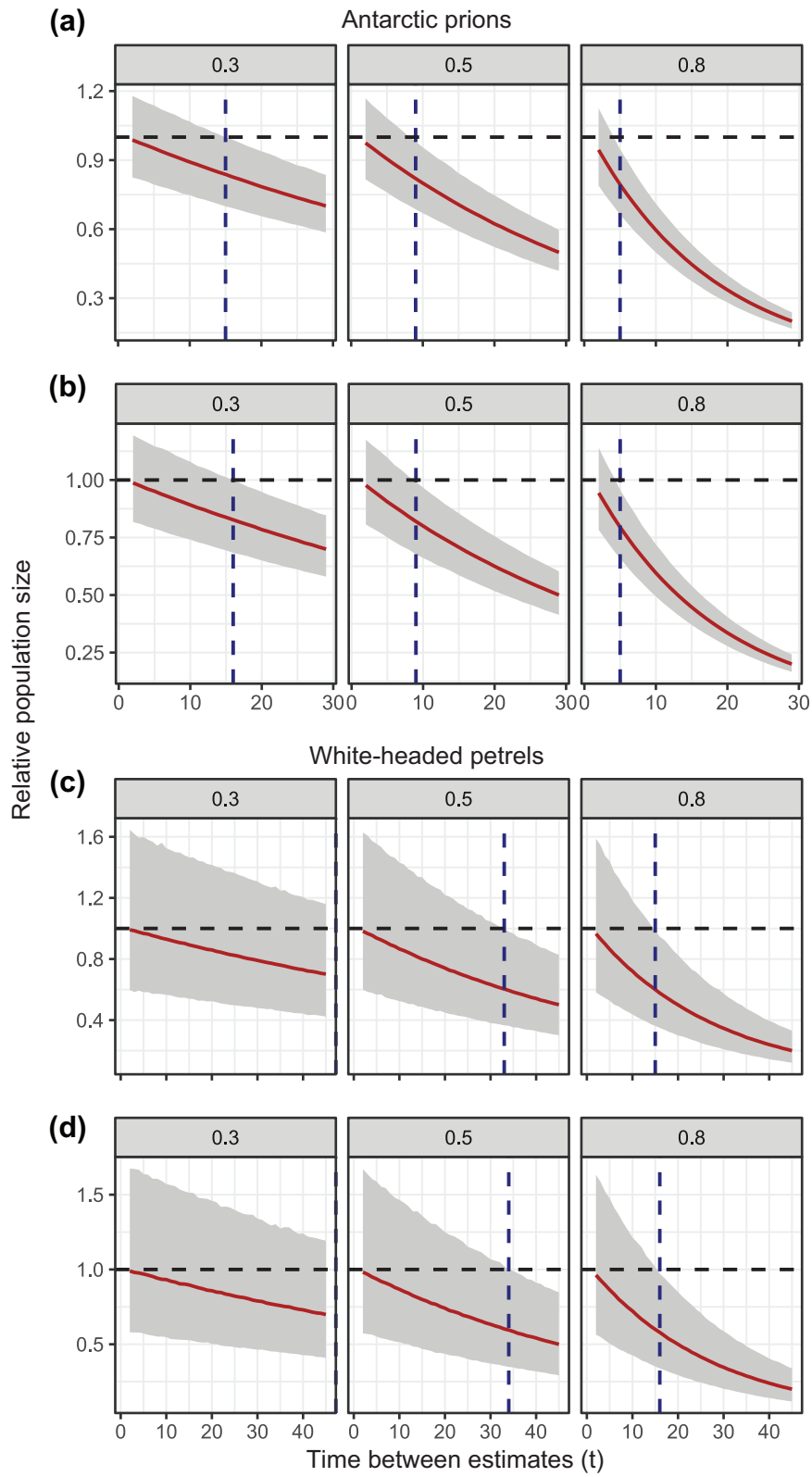


Figure 4. Time until differences between current and simulated future population sizes become significant from our distance analysis (a and c) and model-based analysis (b and d) of our stratified random survey data. We simulated rates of change of 30, 50 and 80% over three generations (sensu IUCN Red List criteria). The horizontal black dashed line represents no change ( $N_t/N_1 = 1$ ), and the vertical dashed line shows the first time-step at which the upper 95% CI excludes 1.

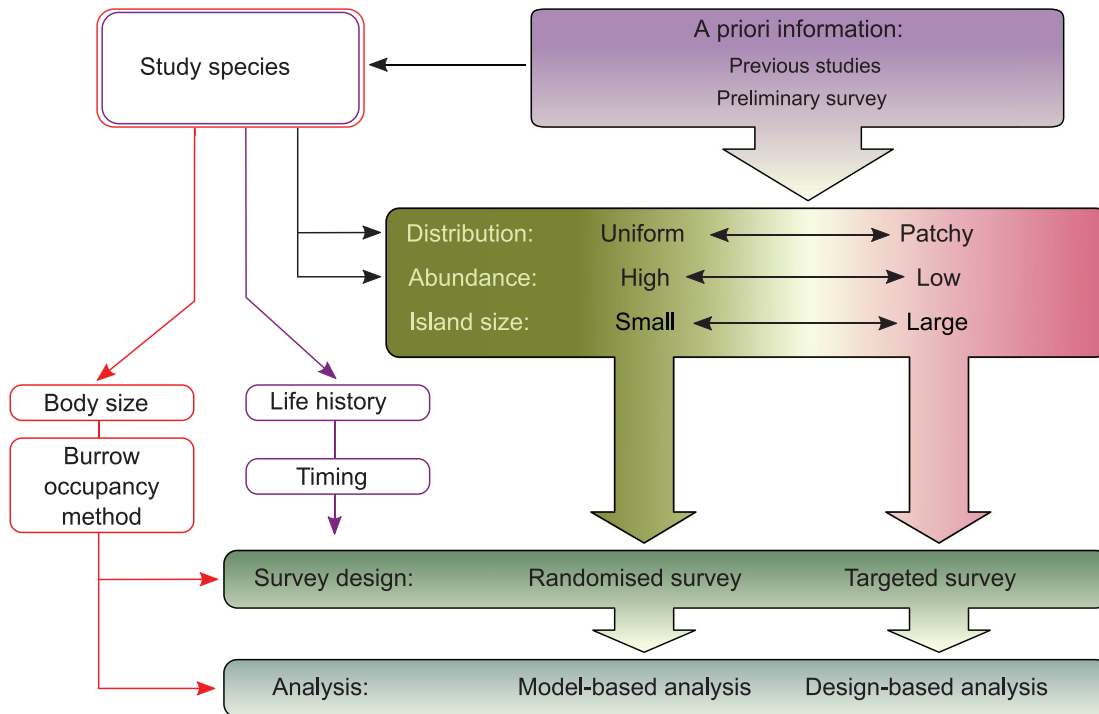


Figure 5. Key aspects of designing surveys and analyses for burrowing seabird populations.

### Recommendations for future studies

We had 12 months to complete multiple field surveys and compare a range of methods. Given this is not possible in most management scenarios, we consider how our results might help guide future burrowing seabird surveys that are more time-constrained.

First, defining the purpose for the survey and why a population estimate is needed (Lindenmayer et al. 2008, Possingham et al. 2012) is a fundamental step. This clarifies the importance of bias and precision, which informs survey design and analysis. For example, if the purpose is to provide one estimate for a time series that will be used to detect population trends, minimising bias and high precision are important (Bird et al. 2021). Similarly, if the aim is to inform spatially explicit management actions on the ground, or to communicate information about threats and actions, model-based analyses which provide a spatial representation of abundance may be most useful. Alternatively, if a population estimate is required for a conservation assessment, a design-based analysis that provides a high level of accuracy may be best.

Second, we recommend gathering any prior information about the island and study species and their approximate abundance and distribution. If previous surveys have occurred, consider repeating the same methods to allow comparisons to be made, even at the expense of increased precision from new methods. If methods cannot be repeated, prior information about species distribution and abundance can still be used to weight surveys, to choose the appropriate survey design, and to select between model-based and design-based analyses (Arneill et al. 2019, Camp et al. 2020).

Understanding the ecology and life history of the study species informs suitable timing for surveys and the best method for measuring burrow occupancy (Sutherland and Dann 2012, Bird et al. in press). Given the nocturnal activity of burrowing seabirds at colonies, spotlighting was a highly effective part of our survey strategy. We found only three species' burrows during daytime transect surveys, in contrast, we encountered flying/vocalising birds of 11 species while spotlighting at night. This directed daytime searches which led to the discovery of nesting burrows of three of these additional species during follow-up daytime searches, and the identification of many new colonies.

We have not been able to identify clear thresholds for choosing randomised versus targeted surveys or model-based versus design-based analyses, but in general prior consideration of island size and species distribution and abundance is helpful (Fig. 5). Species with low abundance that occur patchily across large islands are likely to be best estimated using targeted surveys, as these species are poorly captured by randomised survey design (Dilley et al. 2019). Model-based analyses of surveys for these species are also likely to overestimate distribution and abundance, so design-based analyses are typically better. At the other end of the spectrum, the populations of abundant, widespread species, especially on smaller islands, can be accurately and precisely estimated from randomised surveys using informative model-based analyses (Fig. 5). Distribution is typically the most important of these three parameters. Randomised survey designs perform better for widespread species, even at low abundance on large islands, than they do for patchily distributed, albeit more abundant species (Dilley et al. 2019).

In a rapidly changing world, seabird surveys will continue to provide information on the status and trajectory of threatened and recovering taxa, and highlight larger perturbations in marine and island ecosystems. We found that differences in species' ecologies, life histories, distributions and abundances require multiple survey methods. Given the cost of field surveys, defining the survey question is a fundamental first step in survey design. For assessing the conservation status of rare, patchily distributed taxa, targeted surveys that generate biased but inherently precautionary estimates are acceptable. For indicating large-scale change, randomised surveys of widespread and abundant species, which play the greatest functional role in ecosystems are preferred. Where it is important to derive trends from repeat measures, whole-island surveys, particularly of patchily distributed and rare species on larger islands, are better substituted with regular monitoring in a representative sample of sites.

**Acknowledgements** – The authors thank Noel Carmichael, Tasmania Parks and Wildlife Service and the Marine Conservation Team – Department of Natural Resources and Environment for their support facilitating this project. Thanks to Natalie Kelly, David Miller, Eric Rexstad, Simon Wotherspoon, Ben Raymond and Mike Sumner for suggestions for data manipulation and analysis, and to colleagues on Macquarie Island for support with data collection, in particular Melanie Wells and Andrea Turbett. We also thank Ecography Editor-in-Chief Prof. Miguel Araújo and Subject Editor Prof. Nigel Yoccoz and two anonymous reviewers for their exceptional help in improving the manuscript.

**Funding** – This study was supported by funding from the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub, the Australian Antarctic Science program (AAS 4305). JB was supported by a Research Training Program scholarship, an Antarctic Science International Bursary, National Environmental Science Programme Threatened Species Recovery Hub Research Support and a BirdLife Australia Stuart Leslie Bird Research Award.

## Author contributions

**Jeremy P. Bird:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Aleks Terauds:** Formal analysis (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Richard A. Fuller:** Project administration (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Penelope P. Pascoe:** Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Toby D. Travers:** Formal analysis (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Julies C. McInnes:** Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Rachael**

**Alderman:** Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Justine D. Shaw:** Conceptualization (supporting); Project administration (lead); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

## Transparent Peer Review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/ecog.06204>>.

## Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.sn02v6x2d>> (Bird et al. 2022).

## Supporting information

The supporting information associated with this article is available from the online version.

## References

- Arnell, G. E. et al. 2019. Sampling strategies for species with high breeding-site fidelity: a case study in burrow-nesting seabirds. – *PLoS One* 14: e0221625.
- Bird, J. P. et al. 2021. Uncertainty in population estimates: a meta-analysis for petrels. – *Ecol. Solut. Evid.* 2: e12077.
- Bird, J. P. et al. 2022. Data from: Generating unbiased estimates of burrowing seabird populations. – *Dryad Digital Repository*, <<https://doi.org/10.5061/dryad.sn02v6x2d>>.
- Bird, J. P., Fuller, R. A., Pascoe, P. P. and Shaw, J. D. Trialling camera traps to determine occupancy and breeding in burrowing seabirds. – *Remote Sens. Ecol. Conserv.* <<https://doi.org/10.1002/rse2.235>>.
- Bock, T. 2018. What is autocorrelation? | Autocorrelation examples. – <[www.displayr.com/autocorrelation/](http://www.displayr.com/autocorrelation/)>.
- Bravington, M. V. et al. 2021. Variance propagation for density surface models. – *J. Agric. Biol. Environ. Stat.* 26: 306–323.
- Bricher, P. K. et al. 2013. Mapping sub-Antarctic cushion plants using random forests to combine very high resolution satellite imagery and terrain modelling. – *PLoS One* 8: e72093.
- Brooke, M. de L. et al. 2018. Seabird population changes following mammal eradications on islands. – *Anim. Conserv.* 21: 3–12.
- Brothers, N. P. 1984. Breeding, distribution and status of burrow-nesting petrels at Macquarie Island. – *Aust. Wildl. Res.* 11: 113–131.
- Brothers, N. and Bone, C. 2008. The response of burrow-nesting petrels and other vulnerable bird species to vertebrate pest management and climate change on sub-Antarctic Macquarie Island. – *Pap. Proc. R. Soc. Tasman.* 142: 123–148.
- Buckland, S. T. et al. 2015. Distance sampling: methods and applications. – Springer.
- Buxton, R. T. et al. 2016. Monitoring burrowing petrel populations: a sampling scheme for the management of an island key-stone species. – *J. Wildl. Manage.* 80: 149–161.

- Camp, R. J. et al. 2020. Using density surface models to estimate spatio-temporal changes in population densities and trend. – *Ecography* 43: 1079–1089.
- Cianfrani, C. et al. 2010. Do habitat suitability models reliably predict the recovery areas of threatened species? – *J. Appl. Ecol.* 47: 421–430.
- Copson, G. and Whinam, J. 2001. Review of ecological restoration programme on subantarctic Macquarie Island: pest management progress and future directions. – *Ecol. Manage. Restor.* 2: 129–138.
- Danckwerts, D. K. et al. 2014. Biomass consumption by breeding seabirds in the western Indian Ocean: indirect interactions with fisheries and implications for management. – *ICES J. Mar. Sci.* 71: 2589–2598.
- Del Hoyo, J. et al. 1992. Handbook of the birds of the world. – Lynx edicions.
- Dias, M. P. et al. 2019. Threats to seabirds: a global assessment. – *Biol. Conserv.* 237: 525–537.
- Dilley, B. J. et al. 2017. The distribution and abundance of blue petrels *Halobaena caerulea* breeding at subantarctic Marion Island. – *Emu-Austral Ornithol.* 117: 1–11.
- Dilley, B. J. et al. 2019. Clustered or dispersed: testing the effect of sampling strategy to census burrow-nesting petrels with varied distributions at sub-Antarctic Marion Island. – *Antarct. Sci.* 31: 231–242.
- Garmin 2019. BaseCamp. – <[www8.garmin.com/support/download\\_details.jsp?id=4435](http://www8.garmin.com/support/download_details.jsp?id=4435)>.
- Howe, E. J. et al. 2019. Model selection with overdispersed distance sampling data. – *Methods Ecol. Evol.* 10: 38–47.
- Kildaw, S. D. et al. 2005. Formation and growth of new seabird colonies: the significance of habitat quality. – *Mar. Ornithol.* 33: 49–58.
- Lawton, K. et al. 2006. An estimate of population sizes of burrowing seabirds at the Diego Ramirez archipelago, Chile, using distance sampling and burrow-scoping. – *Polar Biol.* 29: 229–238.
- Lindenmayer, D. et al. 2008. A checklist for ecological management of landscapes for conservation. – *Ecol. Lett.* 11: 78–91.
- Marshall, L. et al. 2017. Intermediate distance sampling workshop – St Andrews 2017. – <<http://workshops.distancesampling.org/stand-intermed-2017/practicals/bookdown/index.html>>.
- Meyer, D. et al. 2019. Package ‘e1071’. Misc functions of the Department of Statistics, Probability Theory Group (Formerly: E1071), TU Wien. – <<http://sunsite2.icm.edu.pl/pub/unix/math/cran/web/packages/e1071/e1071.pdf>>.
- Miller, D. L. 2017. Package ‘Distance’ – distance sampling detection function and abundance estimation. – <<http://github.com/DistanceDevelopment/Distance/>>.
- Miller, D. L. et al. 2013. Spatial models for distance sampling data: recent developments and future directions. – *Methods Ecol. Evol.* 4: 1001–1010.
- Miller, D. L. et al. 2020. Package ‘dsm’. Density surface modelling of distance sampling data. – <<https://cran.rstudio.com/web/packages/dsm/dsm.pdf>>.
- Miloslavich, P. et al. 2018. Essential ocean variables for global sustained observations of biodiversity and ecosystem changes. – *Global Change Biol.* 24: 2416–2433.
- Mulder, C. P. H. et al. (eds) 2011. Seabird islands: ecology, invasion and restoration. – Oxford Univ. Press.
- Newman, J. et al. 2009. Estimating regional population size and annual harvest intensity of the sooty shearwater in New Zealand. – *N. Z. J. Zool.* 36: 307–323.
- Otero, X. L. et al. 2018. Seabird colonies as important global drivers in the nitrogen and phosphorus cycles. – *Nat. Commun.* 9: 246.
- Pacifici, K. et al. 2016. Occupancy estimation for rare species using a spatially-adaptive sampling design. – *Methods Ecol. Evol.* 7: 285–293.
- Page, M. et al. 2018. The dynamics of volunteer motivations for engaging in the management of invasive plants: insights from a mixed-methods study on Scottish seabird islands. – *J. Environ. Plan. Manage.* 61: 904–923.
- Possingham, H. P. et al. 2012. The conservation return on investment from ecological monitoring. – In: Lindenmayer, D. and Gibbons, P. (eds), *Biodiversity monitoring in Australia*. CSIRO, pp. 49–58.
- Rayner, M. J. et al. 2007. Predictive habitat modelling for the population census of a burrowing seabird: a study of the endangered Cook’s petrel. – *Biol. Conserv.* 138: 235–247.
- Rexer-Huber, K. et al. 2017. White-chinned petrel population estimate, disappointment Island (Auckland Islands). – *Polar Biol.* 40: 1053–1061.
- Robinson, S. A. and Copson, G. R. 2014. Eradication of cats *Felis catus* from subantarctic Macquarie Island. – *Ecol. Manage. Restor.* 15: 34–40.
- Rodríguez, A. et al. 2019. Future directions in conservation research on petrels and shearwaters. – *Front. Mar. Sci.* 6: 94.
- Schulz, M. et al. 2006. Breeding of the grey petrel *Procellaria cinerea* on Macquarie Island: population size and nesting habitat. – *Emu* 105: 323–329.
- Smith, A. et al. 2019. Modeling spatiotemporal abundance of mobile wildlife in highly variable environments using boosted GAMLSS hurdle models. – *Ecol. Evol.* 9: 2346–2364.
- Springer, K. 2016. Methodology and challenges of a complex multi-species eradication in the sub-Antarctic and immediate effects of invasive species removal. – *N. Z. J. Ecol.* 40: 273.
- Sumner, M. D. 2018. Package ‘Tabular Raster.’ – <<https://cran.r-project.org/web/packages/tabularaster/tabularaster.pdf>>.
- Sutherland, D. R. and Dann, P. 2012. Improving the accuracy of population size estimates for burrow-nesting seabirds. – *Ibis* 154: 488–498.
- Thompson, W. 2013. Sampling rare or elusive species: concepts, designs and techniques for estimating population parameters. – Island Press.
- Wood, S. N. 2017. Generalized additive models: an introduction with R. – CRC Press/Taylor & Francis Group.