

An estimate of the South Georgia diving petrel *Pelecanoides georgicus* population at Ile de la Possession, Crozet archipelago

CHRISTOPHE BARBRAUD ¹, ADRIEN CHAIGNE², MAXIME LOUBON², OLIVIER LAMY² and FABRICE LE BOUARD²

¹Centre d'Etudes Biologiques de Chizé, CNRS UMR 7372, 79360 Villiers en Bois, France

²Réserve Naturelle Nationale des Terres Australes Françaises, TAAF, rue Gabriel Dejean, 97458 Saint-Pierre, France
barbraud@cebc.cnrs.fr

Abstract: Burrow-nesting seabirds constitute an important part of seabird diversity, yet accurate estimates of their abundance are largely lacking, limiting our understanding of their population dynamics and conservation status. We conducted a survey to estimate the number of South Georgia diving petrel (*Pelecanoides georgicus*) burrows during the 2013–14 breeding season on Ile de la Possession, Crozet archipelago, southern Indian Ocean. We used distance sampling and acoustic playback in order to estimate burrow densities in *a priori*-selected favourable nesting areas. A total of 855 burrows were detected. The mean altitude of burrows was 601.8 ± 69.4 m. The mean burrow detection distance was 1.77 ± 1.63 m. The burrow density was estimated at 15.649 burrows ha^{-1} (95% confidence interval (CI): 10.245–23.903) and the slope-corrected total favourable area was 2365.53 ha, which yielded an estimate 37 018 burrows (95% CI: 24 235–56 544). The playback response rate was $15.8 \pm 1.3\%$, and $40.8 \pm 1.7\%$ of burrows were occupied or showed signs of occupation. Occupancy rates were low compared to those measured by systematic burrow inspection in other studies. Assuming that laying occurred in 80–93% of the estimated number of burrows, as estimated by previous studies, gives an estimate of 29 614 (95% CI: 19 388–45 235) to 34 426 (95% CI: 22 538–52 585) breeding pairs.

Received 17 October 2019, accepted 12 February 2020

Key words: acoustic playback, burrowing petrel, detection probability, distance sampling, Procellariiformes

Introduction

Seabirds constitute a critical component of marine and terrestrial ecosystems (Montevecchi 1993, Frederiksen *et al.* 2006), but they are one of the most threatened bird groups in the world (Croxall *et al.* 2012, Dias *et al.* 2019). However, accurate estimates of many seabird populations are lacking, limiting our understanding of their population dynamics and conservation status. This is particularly true for burrow-nesting seabirds (~26% of all seabird species), which frequently breed at sites that are difficult to access, such as remote islands (Brooke 2004). The most common technique for estimating the number of breeding burrow-nesting seabirds is based on estimating the number of active burrows, assuming that each active burrow represents a breeding pair (e.g. Lawton *et al.* 2006, Reyes-Arriagada *et al.* 2006). However, in addition to breeding-site accessibility, further complications when estimating the abundance of burrow-nesting seabirds are determining burrow detectability and burrow occupancy rates (Barbraud *et al.* 2009, Lawton *et al.* 2006, Parker & Rexer-Huber 2016). When conducting a population census, not all

burrows are always detected by the observers (Williams *et al.* 2002). For example, a burrow within the survey area could go undetected due to habitat characteristics, weather conditions or observer bias. If not accounted for, detection probability (i.e. the probability that a burrow is detected) may result in an underestimate of population size. Similarly, active burrows may not always correspond to the presence of a breeding pair, and not accounting for burrow occupancy (i.e. the proportion of active burrows with a breeding pair) may result in an overestimate of the population size. Furthermore, if detection probability or burrow occupancy vary over time and are not explicitly taken into account in future population estimates, the inferred population trends may be biased (Bart *et al.* 1998).

Pelecanoididae (diving petrels) are small burrow-nesting seabirds that breed in the Southern Hemisphere and whose abundance and population trends are poorly known (Brooke 2004). Existing population-size estimates of diving petrels are based on various survey methods and have not always accounted for detection probability (Derenne & Mougin 1976, Croxall & Hunter 1982), potentially being inaccurate and poorly repeatable. As burrow detection probability can be relatively low and

variable in seabirds (Parker & Rexer-Huber 2016), there is a need to improve the accuracy of abundance estimates for diving petrels in order to infer their population trends and conservation status.

The South Georgia diving petrel (*Pelecanoides georgicus*) nests on islands of the Southern Ocean - mainly in the southern Indian Ocean and east of the Scotia Sea (Marchant & Higgins 1990). Nests are located in burrows dug in areas that are sparsely vegetated (loose soil or sand) or unvegetated, such as cinder scree. While breeding localities are fairly well known, population sizes are not, and estimates found in the literature are quite inaccurate, imprecise and incomplete (Brooke 2004). The objective of this study was to obtain a population estimate of South Georgia diving petrels on Ile de la Possession, Crozet archipelago, by estimating burrow densities while accounting for detection probability and burrow occupancy. None of the existing local population estimates for the South Georgia diving petrel account for detection probability and burrow occupancy (Croxall & Hunter 1982, Jouventin *et al.* 1984, Weimerskirch *et al.* 1989), except for the newly described Whenua Hou diving petrel (*Pelecanoides whenuahouensis*), previously considered conspecific to the South Georgia diving petrel (Fischer *et al.* 2020). Therefore, our main objective was to trial the combined use of distance sampling, burrow occupancy monitoring and geographic information system (GIS) data in order to estimate breeding densities.

Methods

Study area and species

Ile de la Possession (46°42'S, 50°90'E) is part of the Crozet archipelago, French Southern Territories. It is a volcanic island of ~150 km² in area, with steep mountainous terrain and large glacial valleys separated by relatively high plateaus. The highest point is Pic du Mascarin at 934 m above sea level (a.s.l.). Continuous vegetation cover is found up to 150 m a.s.l., dominated by bryophytes, *Acaena magellanica* and *Blechnum penna-marina*. Between ~150 and ~350 m a.s.l., there is a dominance of fell-field habitat composed of *Azorella selago* and *Agrostis magellanica*. Above 350 m, areas are sparsely vegetated or even unvegetated, mainly covered by loose soil, sand, cinder scree and lava rocks. There is a permanent research station, but no other habitation. Black rats (*Rattus rattus*) were inadvertently introduced to Ile de la Possession during the nineteenth century (Atkinson 1985, Johnstone 1985) and have a direct impact on breeding seabirds (Jouventin *et al.* 2003, Jones *et al.* 2008). Apart from rats, there are no other introduced predators on the island.

South Georgia diving petrels nest more or less colonially and dig their burrows in bare soil or where

plant cover is very low (Payne & Prince 1979, Brooke 2004). At Crozet, birds return to their colonies at the end of September. A single egg is laid in November (mean date 18 November) and the chick hatches in late December–early January and fledges in mid-February (Jouventin *et al.* 1985).

Sampling design and fieldwork

Fieldwork was conducted from 20 November 2013 to 14 January 2014 (i.e. during the incubation and brooding periods) (Jouventin *et al.* 1985). A three-stage process was used in order to estimate the number of active (i.e. occupied or apparently occupied) burrows. Occupied burrows were defined as burrows where an individual was present and apparently occupied burrows were defined as burrows with signs of occupation. First, burrow densities were estimated in a priori-identified favourable nesting habitats. Second, the proportion of occupied burrows was estimated by acoustic playback. Finally, the land area corresponding to favourable habitats where burrows were found was calculated for the entire island and multiplied by density in order to obtain island-wide estimates.

Estimating burrow density in favourable nesting habitats

In order to identify favourable habitats, Landsat satellite images (United States Geological Survey) and DigitalGlobe satellite images (available at www.bing.com/maps) were used. From these, favourable nesting habitats were delineated using the GIS program QGIS and their surfaces were calculated according to the following criteria, based on previous knowledge of the presence of burrows at Ile de la Possession and on literature knowledge (Payne & Prince 1979, Jouventin *et al.* 1985): 1) elevation > 250 m a.s.l., 2) slope < 45% and not exposed to strong winds (slopes facing WSW through WNW), and 3) areas sparsely vegetated or unvegetated (fine scree, sand, loose soil). Elevation and slope data were obtained from Shuttle Radar Topography Mission (SRTM) provided in a 90 m digital elevation model (available at <https://ers.cr.usgs.gov>). Areas with bare rocks were excluded from the analyses.

Burrow densities and their variances were estimated by line transects using distance sampling (Buckland *et al.* 2001). This method uses the distance from the line to the object (i.e. burrow) to correct for visibility bias and for estimating the detection probability and thus for correcting densities. Within the identified favourable nesting habitats, surveyed line transects were aligned parallel, 200 m or 400 m apart. Each transect line was covered by a single observer, and the perpendicular distance (constant elevation above ground) from the transect line to each burrow detected was measured to the nearest 10 cm with a 20 m decametre. Burrows to

either side of the line were recorded. Line transects were identified using a handheld GPS unit (Garmin GPSmap 60CSx). The observer walked in straight lines using the GPS unit navigation options. A total of 14 favourable habitat areas were delineated and 75 transects were performed (total length: 114 km).

Line-transect data were analysed using the *distance* and *mrd*s packages in *R* (Buckland *et al.* 2001, www.R-project.org). The truncation level was set following identification of outliers from box plots: outliers were values > 0.9 times the 90th percentile. Truncation allows for the detection of the outliers that make modelling the detection function difficult (Buckland *et al.* 2001). Histograms of the recorded distances showed a clear zero inflation, and as transects were randomly chosen, there was no biological reason for such a shape. The only explanation was observer bias as transects were not physically marked out in the field (e.g. there was no rope along the line transect). When an observer detected a burrow close to the line, it may have been attributed a distance of zero. In order to avoid any effect of this zero-inflation distribution in our analyses, data were pooled into equal distance intervals. The number of equal distance intervals varied between four and seven. The probability of burrow detection was estimated with models combining density functions (uniform, half-normal and hazard-rate) with adjustments (cosine, simple and Hermite polynomials). The adequacy of the selected model to the perpendicular distances was assessed by a χ^2 goodness-of-fit test on grouped data and by verifying that coefficient of variation of the detection probability did not exceed 20% (Buckland *et al.* 2001). The model with the highest goodness of fit and an acceptable coefficient of variation of the detection probability was selected. The four key assumptions of distance sampling are that: 1) objects on the line are detected with certainty ($g(0) = 1$), 2) objects are detected at their initial location, 3) measurements are exact and 4) detections are independent events. The first assumption was fulfilled in many other studies using the line-transect distance sampling method to estimate petrel burrow density (Lawton *et al.* 2006). Moreover, the low-lying and very sparse vegetation in the survey area did not conceal burrows. As burrows are by definition immobile, assumption 2 was satisfied. Given that distances were measured with a precision of 10 cm, we considered assumption 3 fulfilled. To satisfy the fourth assumption, additional burrows detected while walking from the line to the burrow initially detected, but not detected from the line, were not included in the analysis.

Estimating burrow occupancy

Occupant species was determined by looking at the burrow diameter and entrance characteristics (Derenne

& Mougin 1976, Marchant & Higgins 1990). Only small-diameter burrows (< 10 cm) in fine scree or sandy soil were counted. A similar species, the common diving petrel (*Pelecanoides urinatrix*), also breeds in the Crozet archipelago, but not at Ile de la Possession (Jouventin *et al.* 1984). No other species was found in the surveyed areas.

Detected burrows were recorded as apparently occupied when at least one sign of occupation was observed: presence of droppings, feathers, fresh footprints near the entrance, dead vegetation disposed of at the entrance by the birds, fresh scratch markings in the soil near or within the burrow entrance and/or fragments of new shell. Collapsed burrows and those where the entrance was obstructed by growing vegetation were not included in the analyses. In order to assess burrow occupancy, acoustic playback was used. As calls are sex specific in South Georgia diving petrels (Marchant & Higgins 1990), calls of both males and females were used. Vocalizations were played for 30 s down all burrow entrances and whether or not a bird responded was recorded. The initial plan was to use a burrowscope in order to check for the presence or absence of a bird inside the detected burrows and for the purpose of estimating a response rate to acoustic playback. However, burrow entrances are smaller in diameter, and the passage is often complex, consisting of several turns, and so the nest chamber could not be reached without damaging the burrows. Therefore, burrowscoping could not be used in order to assess response rate to acoustic playback.

In November 2017, we also used an infrared thermal camera (FLIR E40) on a sample of occupied burrows of South Georgia diving petrels at Ile de la Possession in order to test whether we could detect a heat signal, indicating the presence of birds in burrows. Tests were performed on a sample of 17 occupied burrows by pointing the camera towards the entrance of each burrow.

Estimation of area

Transect length, area of nesting habitats and slope were calculated in QGIS. The added area introduced by slope was used in order to calculate total field area. A mean slope was estimated using GIS data on the study area. Both transect length and area were corrected by slope before distance sampling analyses.

Results

Burrows of South Georgia diving petrels were found in 9 areas on 32 transects, and a total of 855 burrows were detected (Fig. 1). The mean altitude of detected burrows was 601.8 ± 69.4 m (minimum: 302 m, maximum: 751 m).

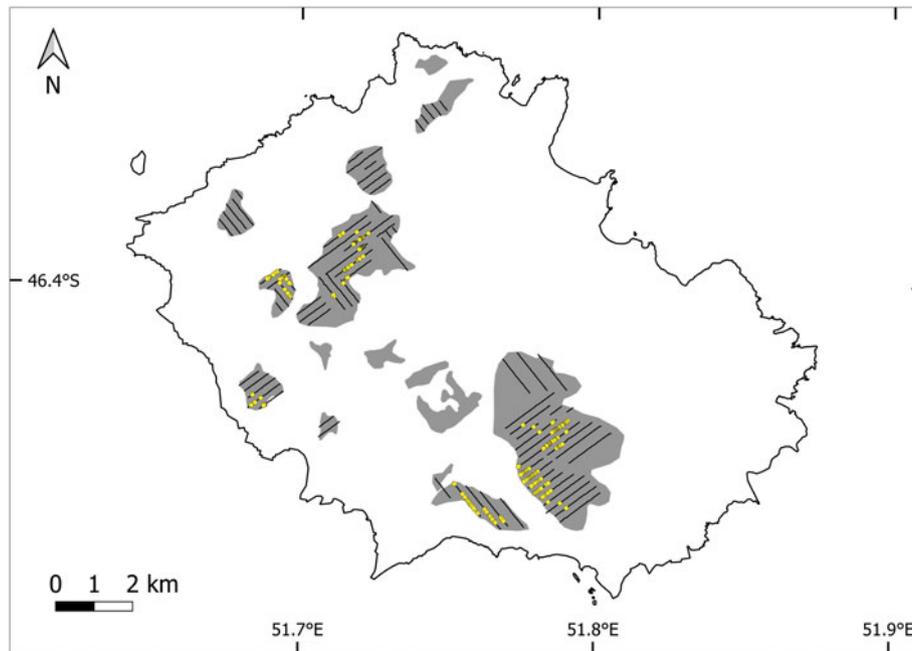


Fig. 1. Ile de la Possession (Crozet archipelago, southern Indian Ocean) showing the location of the areas favourable for breeding of South Georgia diving petrels that were surveyed (grey), the transects performed using distance sampling (black lines) and the detected burrows (yellow circles).

The mean burrow detection distance was 1.77 ± 1.63 m (minimum: 0, maximum: 10.10 m), and the distance data were truncated at 4 m for analysis (Fig. 2), which retained 437 detected burrows. The selected model (Table 1) showed a good fit and yielded a density of 15.649 burrows ha^{-1} (95% confidence interval (CI): 10.245–23.903). The total area, taking into account the area added by slope (mean slope $32.6 \pm 19.6\%$), was 2365.53 ha, which yielded an estimate of 37 018 burrows (95% CI: 24 235–56 544).

Acoustic playback was performed on 848 burrows, and a response to acoustic playback was recorded for 134 burrows, giving a response rate of $15.8 \pm 1.3\%$. For the remaining 714 burrows without a response to acoustic playback, signs of occupation were noted for 212 burrows. Therefore, the apparent burrow occupancy rate (including occupied and apparently occupied burrows) was $40.8 \pm 1.7\%$. These rates yielded 5812 (95% CI: 3805–8877) occupied burrows and 15 104 (95% CI: 9888–23 070) apparently occupied and occupied burrows, respectively. We failed to detect the presence of birds using an infrared thermal camera.

Discussion

The South Georgia diving petrel survey on Ile de la Possession using distance sampling allowed for the estimation of a mean burrow density of 15.649 burrows ha^{-1} (95% CI: 10.245–23.903), which yielded an estimate

37 018 burrows (95% CI: 24 235–56 544). The mean burrow detection distance was 1.77 ± 1.63 m and the mean altitude of burrows was 601.8 ± 69.4 m.

The estimated number of active (occupied and apparently occupied) burrows does not necessarily represent an estimate of the number of breeding pairs for several reasons. First, given the timing of the survey (incubation and brooding periods), it is probable that a proportion of burrows might have failed before our survey and were recorded as apparently unoccupied. At South Georgia, the hatching failure rates were 29–33% in scree areas (Croxall & Hunter 1982) and 22% at Ile de l'Est, Crozet (Despin *et al.* 1972). Second, the overall response rate to playback was low, and we suspect that some individuals present in burrows did not respond to acoustic playback. Out of the total number of burrows found without any sign of occupancy and without a response to acoustic playback, at least two (0.4%) were inadvertently found to be occupied when the burrow accidentally collapsed and an incubating bird was found. However, as the burrows are in fragile soils, inspection of burrows with a burrowscope in order to estimate a response probability was not possible without damaging the burrows. Third, some birds responded to acoustic playback despite there being no sign of occupancy at the entrance of the burrows ($n = 101$). This represented 75.4% of the total number of responses to acoustic playback recorded. Thus, given that the response rate to acoustic playback was low, it is probable that among

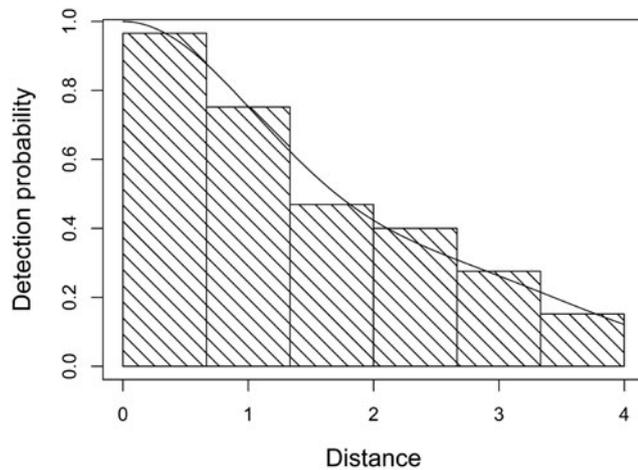


Fig. 2. Histogram of the South Georgia diving petrel burrow detection data at Ile de la Possession. Histogram bins have been modified from the original data by the *distance* package. The best-fitting detection function is represented. The truncation distance is 4 m.

burrows without signs of occupancy and no response to acoustic playback, some were indeed occupied. These three factors make it probable that we underestimated the number of breeding pairs using the number of occupied burrows. Fourth, only a proportion of burrows with signs of occupation may have ultimately contained an incubating bird. Chastel *et al.* (1995) found that, among burrows frequented by common diving petrels, 7.2% were occupied by non-breeding adults. Finally, the number of breeding pairs is probably lower than the overall number of burrows estimated, as it is probable that some burrows were not occupied during the breeding season. These last two factors tend to overestimate the number of breeding pairs. Assuming that laying occurred at between 80% and 93% of the estimated number of burrows, as was found by Jouventin *et al.* (1985) at Iles Crozet and by Chastel *et al.* (1995) at Iles Kerguelen, respectively, gives estimates of 29 614

(95% CI: 19 388–45 235) to 34 426 (95% CI: 22 538–52 585) breeding pairs during the breeding season of 2013–14.

Our abundance estimate of South Georgia diving petrels is more accurate and precise than the previous estimate of tens of thousands for Ile de la Possession (Jouventin *et al.* 1984). Burrow densities were lower than those obtained by previous surveys at Ile aux Cochons, Crozet (800–2600 burrows ha⁻¹, Derenne & Mougin 1976) or at Bird Island, South Georgia (260 burrows ha⁻¹, Croxall & Hunter 1982). However, these authors estimated burrow density by counting burrows individually over the surveyed areas or by only sampling areas occupied by diving petrels. South Georgia diving petrels breed on all of the islands of the Crozet archipelago except Iles des Apôtres, and abundance estimates for the archipelago are vague (Jouventin *et al.* 1984). Extrapolating our burrow density estimates to potentially favourable breeding areas for South Georgia diving petrels on other islands so as to obtain a global estimate for the entire Crozet archipelago seems unrealistic. Indeed, black rats were introduced on Ile de la Possession and probably had an impact on the abundance of small burrowing seabirds, including diving petrels (Jones *et al.* 2008). On Ile aux Cochons, feral cats (*Felis catus*) were also introduced, and are still present, and they may predate on diving petrels. The removal of introduced predators including the Pacific rat (*Rattus exulans*) on islands off the north-eastern coast of New Zealand's North Island resulted in an increased population of burrow-nesting seabirds, including common diving petrels (Buxton *et al.* 2015). At Marion Island, South Georgia, common diving petrels are scarce, probably affected by the introduction of cats in the 1950s (Dilley *et al.* 2017). The absence of breeding common diving petrels at Ile de la Possession, despite their high abundance on the other islands of the Crozet archipelago (Jouventin *et al.* 1984), suggests that this species may have been extirpated from Ile de la Possession by rats, which are absent from the other islands. At Ile de la Possession, rats occur at > 600 m a.s.l.

Table I. Modelling of burrow densities of South Georgia diving petrels at Ile de la Possession, Crozet archipelago.

Model	Adjustment	ΔAIC	\hat{D}	Lower(\hat{D})	Upper(\hat{D})	GOF	\hat{p}	$CV(\hat{p})$
Hazard-rate	Cosinus	0.7	0.00161	0.00106	0.00246	0.913	0.487	0.062
Half-normal	Cosinus	0.0	0.00156	0.00102	0.00239	0.679	0.503	0.066
Hazard-rate	Hermite	1.8	0.00151	0.00098	0.00232	0.352	0.521	0.078
Hazard-rate	Polynomial	1.8	0.00151	0.00098	0.00232	0.352	0.521	0.078
Half-normal	Hermite	3.1	0.00137	0.00091	0.00207	0.171	0.573	0.039
Half-normal	Polynomial	3.1	0.00137	0.00091	0.00207	0.171	0.573	0.039
Uniform	Cosinus	3.4	0.00136	0.00090	0.00205	0.154	0.579	0.030
Uniform	Polynomial	5.0	0.00141	0.00093	0.00215	0.113	0.556	0.061
Uniform	Hermite	9.5	0.00125	0.00083	0.00188	0.012	0.630	0.024

The best model is presented in bold.

ΔAIC = Akaike information criterion difference with the lowest Akaike information criterion model, \hat{D} = density estimate (burrows m⁻²), lower and upper = 95% confidence interval, GOF = *P*-value of the goodness-of-fit test, \hat{p} = detection probability estimate, CV = coefficient of variation.

(Terres Australes et Antarctique Françaises, unpublished data) and may negatively affect the abundance of South Georgia diving petrels up to this altitude. As South Georgia diving petrels breed at low altitude on islands free from introduced predators (Ile de l'Est, Despin *et al.* 1972; Heard Island, Barbraud, personal observation 1997), they may have been extirpated by rats at lower altitude on Ile de la Possession. Removing rats from Ile de la Possession would benefit South Georgia diving petrels, as well as other seabird species.

Future surveys are needed in order to estimate South Georgia diving petrel abundance at its main breeding sites in the Southern Ocean and to quantify population trends. The accuracy of burrowing petrel population estimates calculated by extrapolation of survey data is influenced by numerous sources of error (Parker & Rexer-Huber 2016), and in this study the 'uncertainty of burrow contents' was the most challenging source of error to address, something future South Georgia diving petrels surveys should focus on. The timing of the survey can be chosen in order to match with the laying and incubation period of South Georgia diving petrels, burrow detection probability can be estimated using a standard and repeatable method such as distance sampling in our study, availability bias (i.e. the proportion of South Georgia diving petrel habitat available for sampling) can be minimized as diving petrels do not nest in inaccessible cliffs and observer bias can be controlled for with multiple counts and observers. However, our and others' experiences (Parker & Rexer-Huber 2016) indicate that burrowscopes seem inadequate for determining the burrow occupancy of South Georgia diving petrels due to the small diameter of the burrow entrance and often complex shape of the tunnel, consisting of sharp turns. Direct inspection by hand would damage the burrows and may cause breeding failure. Acoustic playback has been used to survey other burrow-nesting Procellariiformes (Parker & Rexer-Huber 2016), but one of the main disadvantages of this approach is that it requires estimating an additional parameter: the response rate to acoustic playback, which, for the above reasons, is difficult to estimate in South Georgian diving petrels. In addition, even when acoustic playback reliably indicates occupancy, the presence of non-breeding birds can bias true breeding numbers. Other techniques such as camera traps (but see Fischer *et al.* 2017), heat sensors (but see our results) or CO₂ sensors require further testing (Parker & Rexer-Huber 2016). Thus, the most accurate method for estimating burrow occupancy is probably burrow excavation (Hunter *et al.* 1982), but this is a more intrusive method, causing damage to burrows and potentially affecting breeding success and future burrow occupancy.

To conclude, given the lack of knowledge on the abundance and population trends of South Georgia and

other diving petrel species and their importance in marine food webs, we recommend increasing population surveys and long-term monitoring. We also encourage studies aiming at improving non-disturbing methods for assessing burrow occupancy rates.

Acknowledgements

We thank S. Jeudi de Grissac and A. Bodin for their help in the field during the surveys. We thank B. Dilley and an anonymous reviewer for helpful comments that improved a previous version of the manuscript.

Author contributions

CB and FLB proposed the survey and developed the sampling design. Fieldwork was conducted by ML, OL and FLB. FLB, AC and CB conducted the analyses. All authors contributed to the writing.

Financial support

The project was supported by Terres Australes et Antarctiques Françaises (Cédric Marteau, RNN TAF) and the Institut Polaire Français Paul Emile Victor (IPEV program no. 109, PI Henri Weimerskirch).

References

- ATKINSON, I.A. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. In MOORS, P.J., ed. *Conservation of island birds: case studies for the management of threatened island species*. Cambridge: International Council for Bird Preservation, 35–81.
- BARBRAUD, C., DELORD, K., MARTEAU, C. & WEIMERSKIRCH, H. 2009. Estimates of population size of white-chinned petrels and grey petrels at Kerguelen Islands and sensitivity to fisheries. *Animal Conservation*, **12**, 258–265.
- BART, J., FLIGNER, M.A., NOTZ, W.I. & NOTZ, W. 1998. *Sampling and statistical methods for behavioral ecologists*. Cambridge: Cambridge University Press, 344 pp.
- BROOKE, M. 2004. *Albatrosses and petrels across the world*. Oxford: Oxford University Press, 552 pp.
- BUCKLAND, S.T., ANDERSON, D.R., BURNHAM, K.P., LAAKE, J.L., BORCHERS, D.L. & THOMAS, L. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford: Oxford University Press, 448 pp.
- BUXTON, R.T., ANDERSON, D., MOLLER, H., JONES, C.J. & LYVER, P.O. 2015. Release of constraints on nest-site selection in burrow-nesting petrels following invasive rat eradication. *Biological Invasions*, **17**, 1453–1470.
- CHASTEL, O., WEIMERSKIRCH, H. & JOUVENTIN, P. 1995. Body condition and seabird reproductive performance: a study of three petrel species. *Ecology*, **76**, 2240–2246.
- CROXALL, J.P. & HUNTER, I. 1982. The distribution and abundance of burrowing seabirds (Procellariiformes) at Bird Island, South Georgia: II. South Georgia diving petrel *Pelecanoides georgicus*. *BAS Bulletin*, No. 56, 69–74.
- CROXALL, J.P., BUTCHART, S.H.M., LASCELLES, B., STATTERSFIELD, A.J., SULLIVAN, B., SYMES, A., *et al.* 2012. Seabird conservation status,

- threats and priority actions: a global assessment. *Bird Conservation International*, **22**, 1–34.
- DERENNE, P. & MOUGIN, J. 1976. Les procellariiformes à nidification hypogée de l'Île aux Cochons (Archipel Crozet, 46°06'S, 50°14'E). *Comité National Français des Recherches Antarctiques*, **40**, 149–175.
- DESPIN, B., MOUGIN, J. & SEGONZAC, M. 1972. Oiseaux et mammifères de l'île de l'Est. *Comité National Français des Recherches Antarctiques*, **31**, 1–106.
- DIAS, M.P., MARTIN, R., PEARMAN, E.J., BURFIELD, I.J., SMALL, C., PHILLIPS, R.A., *et al.* 2019. Threats to seabirds: a global assessment. *Biological Conservation*, **237**, 525–537.
- DILLEY, B.J., SCHRAMM, M. & RYAN, P.G. 2017. Modest increases in densities of burrow-nesting petrels following the removal of cats (*Felis catus*) from Marion Island. *Polar Biology*, **40**, 625–637.
- FISCHER, J.H., DEBSKI, I., TAYLOR, G.A. & WITTMER, H.U. 2017. Assessing the suitability of non-invasive methods to monitor interspecific interactions and breeding biology of the South Georgian diving petrel (*Pelecanoides georgicus*). *Notornis*, **64**, 13–20.
- FISCHER, J.H., TAYLOR, G.A., COLE, R., DEBSKI, I., ARMSTRONG, D.P. & WITTMER, H.U. 2020. Population growth estimates of a threatened seabird indicate necessity for additional management following invasive predator eradications. *Animal Conservation*, **23**, 94–103.
- FREDRIKSEN, M., EDWARDS, M., RICHARDSON, A.J., HALLIDAY, N.C. & WANLESS, S. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, **75**, 1259–1268.
- HUNTER, I., CROXALL, J.P. & PRINCE, P. 1982. The distribution and abundance of burrowing seabirds (Procellariiformes) at Bird Island, South Georgia: introduction and methods. *BAS Bulletin*, No. 56, 49–67.
- JOHNSTONE, G. 1985. Threats to birds on subantarctic islands. In MOORS, P.J., *ed.* *Conservation of island birds: case studies for the management of threatened island species*. Cambridge: International Council for Bird Preservation, 101–121.
- JONES, H.P., TERSHY, B.R., ZAVALETA, E.S., CROLL, D.A., KEITT, B.S., FINKELSTEIN, M.E., *et al.* 2008. Severity of effects of invasive rats on seabirds: a global review. *Conservation Biology*, **22**, 16–26.
- JOUVENTIN, P., BRIED, J. & MICOL, T. 2003. Insular bird populations can be saved from rats: a long-term experimental study of white-chinned petrels *Procellaria aequinoctialis* on Ile de la Possession (Crozet archipelago). *Polar Biology*, **26**, 371–378.
- JOUVENTIN, P., MOUGIN, J.L., STAHL, J.C. & WEIMERSKIRCH, H. 1985. Comparative biology of the burrowing petrels of the Crozet Islands. *Notornis*, **32**, 157–220.
- JOUVENTIN, P., STAHL, J., WEIMERSKIRCH, H. & MOUGIN, J. 1984. The seabirds of the French subantarctic islands and Adélie Land, their status and conservation. In CROXALL, J.P., EVANS, P.G.H. & SCHREIBER, R.W., *eds.* *Status and conservation of the World's seabirds*. Cambridge: International Council for Bird Preservation, 609–625.
- LAWTON, K., ROBERTSON, G., KIRKWOOD, R., VALENCIA, J., SCHLATTER, R. & SMITH, D. 2006. An estimate of population sizes of burrowing seabirds at the Diego Ramirez archipelago, Chile, using distance sampling and burrow-scoping. *Polar Biology*, **29**, 229–238.
- MARCHANT, S. & HIGGINS, P.J. 1990. *Handbook of Australian, New Zealand and Antarctic birds*. Melbourne: Oxford University Press, 735 pp.
- MONTEVECCHI, W.A. 1993. Birds as indicators of change in marine prey stocks. In FURNESS, R.W. & GREENWOOD, J.J.D., *eds.* *Birds as monitors of environmental change*. London: Chapman & Hall, 217–266.
- PARKER, G.C. & REXER-HUBER, K. 2016. *Guidelines for designing burrowing petrel surveys to improve population estimate precision*. Agreement on the Conservation of Albatrosses and Petrels. Available at <http://www.acap.ac/en/resources/acap-conservation-guidelines> (accessed 12 August 2019).
- PAYNE, M.R. & PRINCE, P.A. 1979. Identification and breeding biology of the diving petrels *Pelecanoides georgicus* and *P. urinatrix* at South Georgia. *New Zealand Journal of Zoology*, **6**, 299–318.
- REYES-ARRIAGADA, R., CAMPOS-ELLWANGER, P., SCHLATTER, R.P. & BADUINI, C. 2006. Sooty shearwater (*Puffinus griseus*) on Guafo Island: the largest seabird colony in the world? *Biodiversity and Conservation*, **16**, 913–930.
- WEIMERSKIRCH, H., ZOTIER, R. & JOUVENTIN, P. 1989. The avifauna of the Kerguelen Islands. *Emu*, **89**, 15–29.
- WILLIAMS, B.K., NICHOLS, J.D. & CONROY, M.J. 2002. *Analysis and management of animal populations*. San Diego, CA: Academic Press, 817 pp.