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ORIGINAL PAPER

Using distance sampling and occupancy rate to estimate abundance of breeding pairs of Wilson's Storm Petrel (*Oceanites oceanicus*) in Antarctica

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Abstract Reliable population estimates are needed for the conservation management of seabird populations. Failing to account for detection probability in surveys often leads to underestimate population size and, if detection probability varies among surveys, to bias the estimated trends. This is particularly relevant for storm petrels, which are widespread small burrow- or cavity-nesting seabirds, which have low detection probabilities on land and at sea and whose population status and trends are the least known among seabirds. Here, we used the distance sampling method to estimate detection probability and breeding population size of the cavity-nesting Wilson's Storm Petrel (*Oceanites oceanicus*) in the Pointe Géologie archipelago, East Antarctica. Detection probability was 0.353 ± 0.053 and the average density of active nests was 45.53 ± 15.63 nests/ha. The proportion of nests occupied by breeders was estimated using an endoscope on a sample of nests and was 0.455 ± 0.053. The breeding population was estimated to be 793 (95% CI 344–1359) breeding pairs in January 2016. We advocate the distance sampling method as a robust approach to estimate abundance of breeding Wilson's Storm Petrels in Antarctica. Comparison with an earlier survey suggests that the population has decreased over the past 30 years, possibly partly due to a reduction in nesting habitat following the extension of the surface area occupied by penguin colonies.

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Introduction

Precise and accurate estimates of abundance of population size are essential to estimate population trends, to the study of population dynamics and for doing science-based conservation. Seabirds, which constitute a critical component of marine and terrestrial ecosystems (Montevecchi 1993; Frederiksen et al. 2006), are one of the most-threatened bird groups in the world (Croxall et al. 2012). Yet accurate estimates of many seabird populations are still lacking, limiting our understanding of their population dynamics and conservation status. This is particularly true for burrow- or crevice-nesting seabirds, a broad group of seabird species ($\approx$38% of all seabird species) spanning the globe, which frequently breed on sites hard to access, on remote islands, or inland far from the ocean (Brooke 2004). The most common technique to estimate the number of breeding burrow- or crevice-nesting seabirds is based on estimating the number of active burrows or crevices, assuming that each active burrow/crevice represents a breeding pair (e.g. Lawton et al. 2006; Reyes-Arriagada et al. 2007). However, in addition to breeding site accessibility, further complications for estimating abundance of burrow- or crevice-nesting seabirds are the detectability issue and nest occupancy (Lawton et al. 2006; Barbraud et al. 2009). When conducting population counts, all burrows or crevices are not always detected (Williams et al. 2002). A burrow or crevice present in the surveyed area may not be detected during the survey due to habitat characteristics, weather conditions or observer bias. If not accounted for, undetected burrows/crevices may result in an underestimate of population size (Anderson 2003). Similarly, active burrows or crevices may not always correspond to the presence of a breeding pair, and not accounting for burrow or crevice occupancy, i.e. the proportion of active burrows or crevices with a breeding pair may result in an overestimation of population size. Furthermore, if detection probability, i.e. the probability that a burrow/crevice is detected, or burrow/crevice occupancy varies over time and are not explicitly taken into account into repeated population estimates, the inferred population trends may be biased (Bart et al. 1998).

Few populations of polar (south of 60°S or north of 60°N) burrow- or crevice-nesting seabirds have been estimated while accounting for detection probability. Southwell et al. (2011) estimated detection probability of Snow Petrels (*Pagodroma nivea*) and Wilson's Storm Petrels (*Oceanites oceanicus*) in MacRobertson Land (East Antarctica) using the double observer approach (Nichols et al. 2000), but did not quantify the abundance of breeding pairs. Isaksen and Bakken (1995) estimated breeding densities of Little Auks (*Alle alle*) in Svalbard using capture-recapture methods and Chapman estimators (Chapman 1951). Since many burrow- or crevice-nesting polar seabirds nest in inconspicuous burrows or crevices and their numbers are poorly known, there is the need to obtain abundance estimates accounting for detectability and other forms of bias (Parker and Rexer-Huber 2016).

The Wilson's Storm Petrel is a small-sized flying seabird that nests on islands of the Southern Ocean and on ice-free areas of the Antarctic coast (Marchant and Higgins 1990). Nests are located in crevices situated under rocks and boulders on rocky slopes and cliff faces. While breeding localities are fairly well known, population sizes are not, and estimates found in the literature are highly conjectural and incomplete (Brooke 2004). The objectives of this study were to estimate abundance of breeding Wilson's Storm Petrels breeding in an Antarctic coastal locality while accounting for detection probability and nest occupancy. None of the existing local population estimates for the Wilson's Storm Petrel account for detection probability and nest occupancy (Beck and Brown 1972; Thomas 1986; Wasilewski 1986; Orgeira 1997; Olivier and Wotherspoon 2006; but see Copestake et al. 1988 for South Georgia). Therefore, our main objective was to propose the use of the distance sampling method, nest occupancy monitoring, and Geographic Information System to estimate breeding densities while accounting for nest detection probability and abundance of breeding pairs. A secondary objective was to compare our estimates relative to those from a previous survey (Thomas 1986) and to investigate the potential factors causing population changes.

Methods

Study area and species

The study was carried out on Ile des Pétrels (66°40′S–140°00′E, Fig. 1), Pointe Géologie archipelago, Terre Adélie, Antarctica, where Wilson's Storm Petrels nest in rocky crevices, cracks, and in between slabs (Thomas 1986). The archipelago consists of 52 islands and low-lying rocky islets and four nunataks. Four islands with breeding Wilson's Storm Petrels were destroyed during the construction of an airstrip during the late 1980s and early 1990s, on which Wilson's Storm Petrel do not breed anymore (Micol and Jouventin 2001). Wilson's Storm Petrels actually breed on six islands and one nunatak (Thomas 1986; Barbraud et al. unpublished data). All other islands and nunataks were visited several times during our survey and during previous surveys of the archipelago, and no breeding Wilson's Storm Petrel was ever recorded. Indeed, most islands and nunataks of the archipelago are small (less than 1 ha but most between and 0.02 and 0.30 ha), do not offer suitable habitat for Wilson's Storm Petrels to breed and are heavily covered by ice and exposed to waves. All islands and nunatak where Wilson's Storm Petrels breed has similar habitat types, of which Ile des Pétrels constitutes approximately 50% of the total area. These islands and nunatak are covered by rocks and snow without vegetation, and are inhabited by breeding colonies of Adélie Penguin (*Pygoscelis adeliae*), fulmarine petrels and South Polar Skuas (*Catharacta maccormicki*). At Terre Adélie, Wilson's Storm Petrels return to nest sites in the first two weeks of November and lay a single egg in December (Mougin 1968; Lacan 1971; Barbraud et al. unpublished data). Hatching occurs in mid-January and chicks fledge in early March (Mougin 1968; Barbraud et al. unpublished data).

Study design and fieldwork

We conducted the survey at Ile des Pétrels, by far the largest island of the archipelago, from 6 to 13 January 2016. The main difficulty to survey cavity-nesting species such as Wilson's Storm Petrels is that nests are not directly observable, but must be detected from signs at the surface using an appropriate method. Field observations indicate that on Ile des Pétrels and other islands of the Pointe Géologie archipelago, Wilson's Storm Petrel nests are often characterized by "stomach oil" deposits on nearby rocks. Petrels store oil derived from the birds' food in the proventriculus (Matthews 1949). This oil is primarily used to provide energy-rich meals to chicks (Warham et al. 1976), but is also regurgitated at the nesting sites for the purpose of intra-specific nests defense (Warham 1977). During the breeding season at Pointe

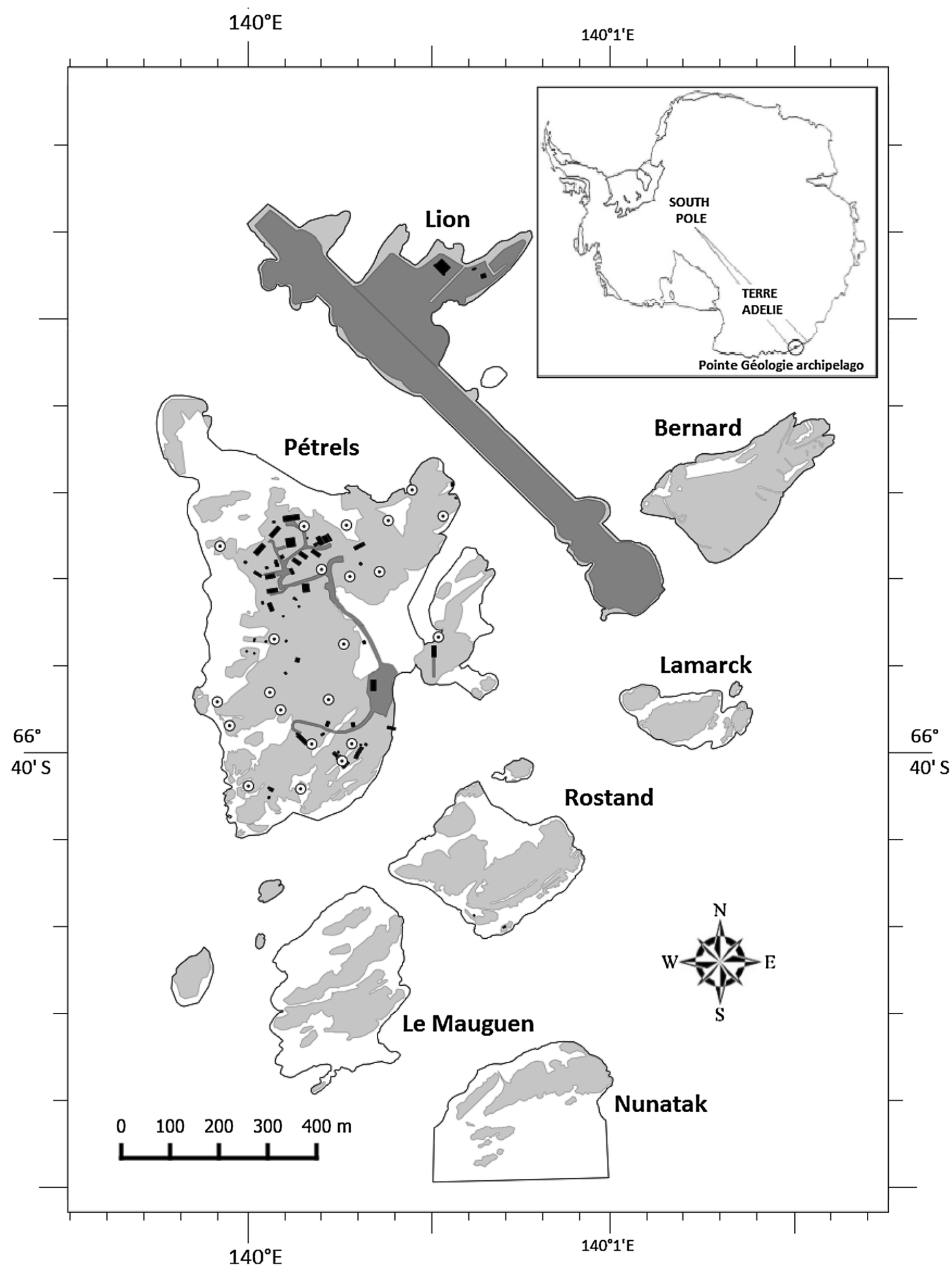

Fig. 1 Location of seven islands and nunataks of the Pointe Géologie archipelago where Wilson's Storm Petrels breed and of line transects on Ile des Pétrels, Terre Adélie, Antarctica. *White* snow and ice; *light grey* rocky areas, *dark grey* roads and airstrip, black: buildings. *Dotted circles* indicate sampling points

Géologie, Wilson's Storm Petrels can be observed interacting nearby nest entrances with occasional oil-spitting (CB, KD, JV, pers. obs.). The cold-arid Antarctic climate prevents a rapid biological degradation of this oil, and waxy organic deposits accumulate around nesting sites of petrels breeding in Antarctica, including Wilson's Storm Petrels (Pryor 1968). Since Wilson's Storm Petrel tend to use the same nesting site year after year (Roberts 1940; Beck and Brown 1972) and oil deposits remain on rocks, rocks with oil deposits potentially indicate the presence of active nest sites. Rocky crevices, cracks and slabs were thus considered as active (i.e. frequented by Wilson's Storm Petrels during the current year or during previous years) when "stomach oil" deposits were observed on nearby rocks. To test this assumption, we estimated the number of occupied nests that were not associated with oil deposits. In December 2017, we investigated all crevices and cracks in a restricted area to search for nests and noted whether nests were occupied or not and whether oil deposits were present on nearby rocks. Once this assumption was verified (see Results), a three-stage process was used to estimate breeding population size: the proportion of active crevices occupied by breeding Wilson's Storm Petrels was estimated by inspecting a sample of active crevices with a burrowscope (head diameter 8 mm, 1-m-long hose); the density of active crevices was determined using line distance sampling, and the rocky area calculated and multiplied by density and proportion of occupied crevices to obtain a population estimate for Ile des Pétrels.

To determine the density of active nests, we used the line distance sampling technique (Buckland et al. 2001). The method measures the distance to objects from a transect line and calculates the density based on the assumption that all objects are detected on the line and that the detectability of objects decreases as a function of distance from the line. Thus, when oil deposits were detected from the transect line, the observer measured the perpendicular distance between the line transect and the oil deposit and searched the nearby crevice for the presence of a nest. A nest was defined as a hole or fissure in rock walls lined with feathers or dry moss forming an obvious nest bowl (Beck and Brown 1972). If a nest was found it was recorded and included in the analysis. If no nest was found the crevice was ignored in the analysis and the observer continued the survey on the line transect. We overlaid ice-free land on Ile des Pétrels with a 50 $\times$ 50 m grid and selected a total of 17 grid cells at random for surveying (Fig. 1). For each selected grid cell, we determined the centroid and we sampled the density of Wilson's Storm Petrel nests across Ile des Pétrels using four 18-m-long transects starting at the centroid and oriented according to each cardinal point (north, east, south, and west). At each transect, a rope 18-m long was pegged along the ground to mark the line. Rocks with oil deposits either side of the line were then recorded by walking slowly along the line. Particular attention was made to thoroughly search the area immediately under the line. When a rock with oil deposit was detected, we inspected the nearby crevice to confirm the presence of a nest site. The perpendicular distance from the transect to each active crevice was measured to the nearest centimetre with a tape-measure. To avoid counting nests twice at the centroid of the four transects, each nest detected was marked. Because the four transects in a grid cell all started at the same grid centroid, the unit of replication was the grid cell and the data were analysed accordingly. A 18-m length was adopted for all line transects.

One of the key assumptions of distance sampling is that objects on the line are always detected. To evaluate this assumption, a sample of 5 transects randomly chosen were covered by pairs of observers walking one behind another. The first observer detected the nests from the line-transect and indicated all the detected nests to the second observer. The second observer recorded whether some nests were missed by the first observer paying particular attention to those potentially missed by the first observed within 10 cm of the line (see Buckland et al. 2004). No additional nest was detected by the second observer, so we considered $g(0) = 1$, i.e. the probability of detecting a nest at distance 0 from the transect was 1 .

To quantify nest occupancy, we inspected a sample of 88 nests using a 1-m-long endoscopic camera Somikon® for nests where the nest chamber was far from the entrance, and using a torch for other nests. Nest inspections were performed during the day. For each nest, we recorded the presence/absence of a bird and whether it was incubating an egg.

Analysis

We used the program DISTANCE 6.0 (Thomas et al. 2009) to compute the density of active nests. The probability of nest detection was estimated with models combining density functions (uniform, half-normal, and hazard-rate) with adjustments (cosine, simple, Hermite polynomials). The model with the lowest AICc was selected (Burnham and Anderson 2002). The adequacy of these models to the perpendicular distances was assessed by a Cramér-von Mises test with cosine weighting function and by verifying that coefficient of variation of the detection probability did not exceed 20% (Buckland et al. 2001). The Cramér-von Mises test with cosine weighting function is robust to detect departures from the fitted function near distance zero and at larger distances (Buckland et al. 2004).

Population numbers were estimated by multiplying snow-free areas by density and by nest occupancy. Nest occupancy was calculated as the proportion of nests occupied by a bird incubating an egg. A georeferenced map of the island was imported in the Geographic Information System program QGIS 2.8 (QGIS Development Team 2004–2013), which was used to estimate the total island area. The added area introduced by slope for each island was used to calculate the rocky surface areas. A mean slope was estimated for each island using GIS. Areas occupied by permanent snow, buildings of the scientific station and roads were estimated from a georeferenced map and subtracted from the island area. A combination of aerial photographs was used to identify the areas with permanent snow and buildings. Breeding colonies of Adélie Penguins were not subtracted from the island area, since our sampling design included line transects within part of some colonies. Area was used as a known constant rather than estimates. 95% confidence intervals were calculated incorporating uncertainty arising from the variance in nest density, the variance in detectability and the variance in nest occupancy using the methods described in Buckland et al. (2001).

We compared our estimates of the number of breeding pairs of Wilson's Storm Petrels with those from an earlier survey (Thomas 1986) and applied a linear regression to test whether the changes in breeding numbers of Adélie penguins (Thomas 1986; Barbraud et al. unpublished data) were related to changes in breeding numbers of Wilson's Storm Petrels. Estimates of the number of breeding pairs of Wilson's Storm Petrels and Adélie Penguins obtained in 1984 and 2014 were compared for five islands and one nunatak where Wilson's Storm Petrel breed (one group of four island was excluded since it was destroyed during the construction of an airstrip, Micol and Jouventin 2001). The number of breeding pairs of Adélie penguins was estimated using direct counts (see Jenouvrier et al. 2006 for further details), and we used the number of breeding pairs obtained in 2014 which corresponded to the maximum observed during the last 10 years.

Finally, using our survey as a pilot study, we provide specific recommendations about the total line length that need to be surveyed to achieve specific precision goals. To do this, we used the formula from Buckland et al. (2001, p. 242). We estimated total line length for different typical values of the dispersion parameters (2, 3 and 4) and for the estimated value given our data using the formula $n_0\left\{cv\left(\widehat{D}\right)\right\}^2$ where n_0 is the number of nests encountered in our study and $cv\left(\widehat{D}\right)$ is the coefficient of variation of nest density.

Results

A total of 93 nests were found in the restricted area surveyed for testing the assumption that occupied nests were associated with oil deposits. From these, 71 (76.3%) had oil deposits nearby and 22 (23.7%) had no oil deposit. Among nests with nearby oil deposits, 37 (52.1%) were occupied by a Wilson's Storm Petrel, but none of the nests without nearby oil deposits were occupied. Non-occupied nests with oil deposits were either obstructed by ice (22.5%) or were empty (25.4%). There was no bias in the proportion of nests according to line-transect orientation ($\chi^2 = 4.32, df = 3, p = 0.23$).

A total of 47 active nests (i.e. with oil deposits nearby) were detected on the 68 line-transects corresponding to a total distance of 1224 m. The average number of nest detections per unit length of transect was low (0.03 ± 0.06 nest/m). The average nest detection distance was 2.24 m and the maximum distance was 10.44 m (Fig. 2). Most (90%) nests were detected within 5 m of the line-transects. Competing models showed good fit ($p = 0.40$–0.60) and yielded similar density estimates (Table 1), except for the uniform distribution with simple and Hermite polynomial adjustments ($p = 0.001$–0.005). The coefficient of variation of the detection probability was 16% for the hazard rate function. Detection probability was 0.353 (95% CI 0.304–0.410) according to models with the half-normal function. Models with the hazard rate, half-

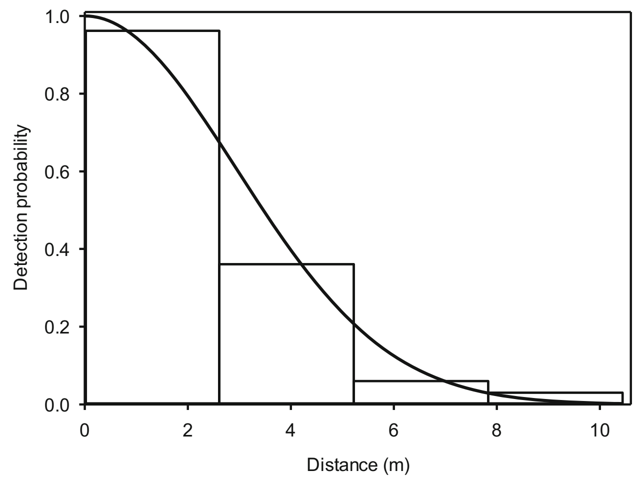

Fig. 2 Histogram of the Wilson's Storm Petrel data for Ile des Pétrels and best-fitting detection function (half-normal)

normal and uniform function with a cosine adjustment had the lowest AICc (AICc difference < 2). Due to model selection uncertainty between these models, we used a model averaging procedure to estimate densities and a bootstrap with 999 replicates to estimate confidence intervals. Accordingly, density on Ile des Pétrels corrected by detection probability was 45.53 active nests/ha (95% CI 17.77–80.65 nests/ha). Variance in density was mainly due to spatial variability in encounter rate (i.e. sampling variation), which contributed 74%, against 26% for the variance from estimating detectability.

The total area of the island taking into account the slope added area was 33.34 ha. The total area permanently covered by snow and occupied by buildings and roads was 13.68 ha, yielding an ice free and building free area of 19.66 ha. Therefore, we estimated the number of active nests of Wilson's Storm Petrels on Ile des Pétrels to be 895 (95% CI 349–1586). Out of a total of 88 active nests inspected, 40 were occupied by an incubating bird, yielding an occupancy rate of 0.455 ($se = 0.053$). We estimated the number of pairs of Wilson's Storm Petrels breeding on ile des Pétrels to be 404 (95% CI 176–691).

Assuming active nests densities on the other islands of the archipelago where Wilson's Storm Petrel are breeding were the same as those on Ile des Pétrels, there were an estimated 1763 (95% CI 703–3124) active nests of Wilson's Storm Petrel (Table 2). Assuming nest occupancies were also the same as those on Ile des Pétrels, there were an estimated 793 (95% CI 344–1359) breeding pairs of Wilson's Storm Petrels in January 2016.

The 1984 survey estimated 2298 active nest sites and 1328 breeding pairs of Wilson's Storm Petrels with an occupancy rate of 0.578 (Thomas 1986), corresponding to a 23 and 40% decrease relative to our estimates respectively.

Table 1 Competing models and associated Akaike's Information Criterion adjusted for small sample size (AICc) values, number of parameters (np) goodness-of-fit p values from Cramér-von Mises tests (GOF-CvM), detection probability (p, CV(p) = coefficient of variation), density estimates (D = density of active nests ha^{-1}, se(D) = standard error of D, 95% confidence interval)

Model	Adjustments	AICc	ΔAICc	np	GOF-CvM	p	CV(p)	D	se(D)	95% CI
Uniform	Cosine	170.1	0.8	3	0.500	0.318	0.108	45.12	13.31	24.96–81.56
Uniform	Simple polynomial	198.3	29.0	1	0.001	0.680	0.025	20.96	5.78	11.94–36.79
Uniform	Hermite polynomial	180.2	10.9	2	0.005	0.500	0.179	28.85	9.46	15.11–55.06
Half-normal	Cosine	171.3	2.0	1	0.400	0.353	0.075	40.61	11.56	22.83–72.23
Half-normal	Simple polynomial	171.3	2.0	1	0.400	0.353	0.075	40.61	11.56	22.83–72.23
Half-normal	Hermite polynomial	171.3	2.0	1	0.400	0.353	0.075	40.61	11.56	22.83–72.23
Hazard-rate	Cosine	169.3	0.0	2	0.600	0.318	0.161	45.20	14.43	24.03–85.02
Hazard-rate	Simple polynomial	169.3	0.0	2	0.600	0.318	0.161	45.20	14.43	24.03–85.02
Hazard-rate	Hermite polynomial	169.3	0.0	2	0.600	0.318	0.161	45.20	14.43	24.03–85.02

Table 2 Calculation of the number of active nests (N_{nest}) and breeding pairs (N_{pairs}) of Wilson's Storm Petrel in the Pointe Géologie archipelago

Breeding site	Rocky surface (ha)	N_{nest}	95% CI	N_{pairs}	95% CI
Pétrels	19.659	895	349–1586	404	176–691
Bernard	5.178	236	92–418	106	46–182
Lamarck	1.580	72	28–127	32	14–55
Rostand	4.058	185	87–327	83	36–142
Le Mauguen	3.083	140	55–249	63	27–108
Nunatak	2.116	96	38–171	43	18–74
Lion	3.054	139	54–246	62	27–107
Archipelago	38.728	1763	703–3124	793	344–1359

The added area introduced by slope for each island was used to calculate the rocky surface areas. A mean slope was estimated for each island using GIS

Applying our proportion of occupied burrows to the Thomas (1986) estimates, this corresponds to a 24% decrease in the number of breeding pairs. There was a positive correlation (Pearson's correlation coefficient: $r = 0.834$, $p = 0.039$) between the percentage of decrease in abundance of Wilson's Storm Petrel nests between 1984 and our survey and the percentage of increase in the number of breeding pairs of Adélie Penguin for the five main islands of the Pointe Géologie archipelago.

The total line length needed to achieve a specific level of precision of density increased non-linearly with the decreasing level of precision (Fig. 3).

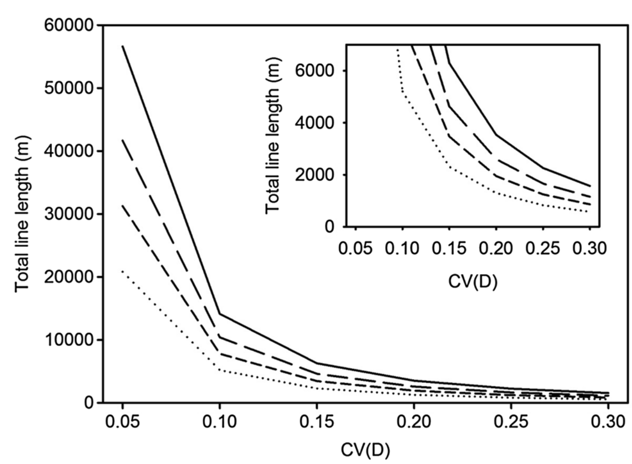

Fig. 3 Total line length to be surveyed to reach a stated level of precision in the estimator of density of Wilson's Storm Petrel nests. CV(D) indicates the coefficient of variation of nest density. The *different lines* represent different values of the dispersion parameter b (*plain line* $b = 5.4$ estimated form our data; *long-dashed line* $b = 4$; *short-dashed line* $b = 3$; *dotted line* $b = 2$). *Inset* represents a zoom for total line length less than 7000 m

Discussion

Evaluation of assumptions

The five key assumptions of distance sampling were met (Buckland et al. 2001). First, lines were placed randomly since we randomly selected a start point for transects. Only the direction of transects was arbitrary selected to fit with cardinal orientations at each point. This could have biased our sampling only if Wilson's Storm Petrel nests were distributed according to a particular orientation, which is unlikely given that no difference was detected in the proportion of nests according to line-transect orientation. Second, distances were measured accurately (±1 cm). Third, distances were measured prior to observer disturbance since the objects to which we measured (nests) were immobile. Fourth, we showed that all objects on the line were detected with two observers conducting samples on transects. Finally, the low number of nest detections per unit length of transect was low, suggesting that the independence of detection between perpendicular transects was not violated.

An important assumption was that rocks with oil deposits indicated the presence of active nest sites. Since we checked each crevice with oil deposits for the presence of a Wilson's Storm Petrel nest, it is unlikely that we overestimated the number of active nests. However, if nest sites were not systematically accompanied by oil deposits on nearby rocks, then we might have underestimated the number of active nests. Therefore, our abundance estimates should be interpreted as minimal estimates. We speculate that this underestimation was low since in Antarctica Wilson's Storm Petrel often eject stomach oil for defense of nest (Pryor 1968) and oil deposits remain on rock year after year, some deposits being several centimetres thick.

The number of breeding pairs was probably underestimated since nest attrition from average laying date in late December to the survey period was not estimated and taken into account. Hatching success recorded for Wilson's Storm Petrels breeding at other Antarctic localities can be highly variable between years, but suggest that the number of breeding pairs could have been underestimated by 7–17% assuming a constant hatching failure probability during the incubation period (Beck and Brown 1972; Quillfeldt 2001).

Although we estimated the proportion of nests occupied by Wilson's Storm Petrels to obtain an estimate of the breeding population, this proportion has been reported to vary from year to year in burrow-nesting seabirds and Wilson's Storm Petrels due to changes in food availability, age structure or environmental changes (Warham 1990; Quillfeldt 2001). In addition, temporary inaccessibility of breeding sites due to snow cover may also affect the proportion of nests occupied such as in the Snow Petrel (Chastel et al. 1993). Nest occupancy rate in Wilson's Storm Petrels can vary from 0.45 to 0.70 (Thomas 1986; Quillfeldt 2001). Thus, our estimate was in the lower range of the observed variation suggesting that our breeding population size estimate was conservative. Since our estimate was based on a single year survey, multiple years of monitoring of the proportion of nests occupied are needed to obtain more accurate estimates.

Areas used by Adélie Penguins were not removed from the total snow-free area used to estimate the number of nests of Wilson's Storm Petrels since we found several nests within Adélie Penguin colonies. However, nest detection probability may be lower within Adélie Penguin colonies due to frequent trampling of exposed rocks making it hard to identity fresh and old oil deposits. This could have biased our estimates and future surveys could use a stratified design aiming at estimating nest detection probability separately within and outside Adélie Penguin colonies.

Alternative methods

Using the double observer method in 50 × 50 m plots, Southwell et al. (2011) reported nest detection probabilities from 0.27 to 0.50 for Wilson's Storm Petrels in MacRobertson Land, Antarctica. Although we used a different method, nest detection probability was also low at Pointe Géologie. Together, these results demonstrate that small cavity-nesting seabirds such as storm petrels can remain undetected at sites when they are present and available for detection, and that their abundance needs to be estimated using methods accounting for detection probability. The double observer and distance sampling methods provide practical approaches for estimating detection probability and abundance for cavity-nesting seabirds. However, both methods have a limitation by assuming that all objects are available to be detected at the time of the survey (Diefenbach et al. 2007). This constraint is not an issue for burrow surveys such as ours, since burrows are always available for detection unlike individual birds which may be absent from the survey are at the time of the survey. The double observer method may also be more time consuming and costly since two observers are required, whereas distance sampling can be conducted by a single observer. Although capture-recapture approaches can be adequate to estimate abundance of storm petrels, they are often time consuming and have met mixed success primarily due to difficulties in obtaining adequate sample sizes of recaptures and meeting model assumptions (Beck and Brown 1972; Copestake et al. 1988; Sydeman et al. 1998; Sanz-Aguilar et al. 2009).

Acoustic playback has been used to survey storm petrels and other burrow-nesting Procellariiformes (e.g. Ratcliffe et al. 1998; Hounsome et al. 2006; Bolton et al. 2010). One of the main disadvantages of acoustic playback is that it requires estimating an additional parameter: the response rate to playback to obtain accurate estimates. Response rates to playback are often low and vary importantly due to effects of the environment, colony location, year, sex, breeding status or time of the day (Ratcliffe et al. 1998; Hounsome et al. 2006; Bolton et al. 2010; Soanes et al. 2012). This introduces an additional source of variation in abundance estimates and decreases precision. Estimating occupancy rate with a burrowscope assumes that all occupants were detected which may not be true when crevices are deep with complex entrances. In our study site, crevices with oil deposits were not very deep and the end of all crevices could be reached with our burrowscope.

Implications

This survey's result for Wilson's Storm Petrels population change on Ile des Pétrels suggests that the population appears to have decreased since 1984 (Thomas 1986). For the entire archipelago, our estimates are around 23% fewer number of nests, and 40% fewer number of breeding pairs. Although the occupancy rate was lower during our survey than during the 1984 survey, the decrease in the number of breeding pairs is outside the range of occupancy rate variation (~20–25%). Different survey methods were used in the two surveys and this population change should be treated with caution. The methods used by Thomas (1986) consisted in subdividing the areas of the archipelago into 136 sectors. Within each sector, a mean density of active nest sites was calculated by searching for active nests (using the same criteria than those used in our study) in small quadrats. The mean density for each sector was then multiplied by the surface of its corresponding sector to obtain an abundance estimate. Since detection probability was not accounted for by Thomas (1986) when searching for nests in small quadrats, his estimates were an underestimate of true abundance and we would have expected a lower abundance estimate in Thomas (1986) than ours. Therefore, despite these differences in survey protocols, we speculate that the decrease was real.

Several factors could explain a decrease in Wilson's Storm Petrels. First, the construction from 1982 to 1992 of an airstrip caused the destruction of three islands where Wilson's Storm Petrel were breeding totalling 309 nest sites (Thomas 1986). Second, the number of breeding pairs of Adélie Penguins increased by nearly 100% on the archipelago between the survey conducted by Thomas (1986) and recent years (Micol and Jouventin 2001; Jenouvrier et al. 2006). One direct consequence of this major increase was an extension of the surface area occupied by penguin colonies accompanied by important guano deposits potentially obstructing crevices and cracks used by breeding Wilson's Storm Petrels. The positive correlation between the percentage of decrease in abundance of Wilson's Storm Petrel nests between 1984 and our survey and the percentage of increase in the number of breeding pairs of Adélie Penguin support this hypothesis. However, the extension of the surface area occupied by penguins (assuming a mean density of 0.75 penguin nest per square meter, range 0.49–0.92, Ainley 2002) would correspond to a 3% decrease (range 2–4%) of the number of active nests of Wilson's Storm Petrels. Thus, other potential factors could also explain this possible decline such as changes in climate conditions on breeding and/or wintering grounds, but introduced predators can be ruled out as none was introduced in the archipelago.

Future surveys are needed to quantify population trends of Wilson's Storm Petrels in Antarctica and to infer the role of potential environmental factors. To detect changes in Wilson's Storm Petrel population size over time we recommend that burrow surveys incorporate monitoring of reference sites with corrections for burrow detection probability and burrow occupancy. We note that the confidence interval of the number of breeding pairs was large since it incorporated the variance in nest occupancy, the variance in nest detection probability and the variance in nest encounter rate. This uncertainty can be taken into account to estimate the power to detect change in the breeding population in the future (Gerrodette 1987). For example, the power to detect a 10% trend over a 10-year period varies from 74 to 98% depending on the relationship between sampling variation and population size (assuming an exponential model, a CV of 34%, and a α level of 0.05). Our results suggest that the large uncertainty associated with the number of breeding pairs was mainly due to the spatial sampling. Therefore, to improve precision, future surveys should aim at minimizing the variance contribution from sampling variation by using stratified sampling, ancillary habitat covariates and by increasing sample size (Williams et al. 2002). Based on our data and results from Fig. 3, achieving a level of precision of less than 10% we would require a large sampling effort (from about 10 to 60 km of transect). We would recommend that future surveys aiming at estimating nest densities of Wilson's Storm Petrels in Antarctica cover at least 2–5 km to achieve a level of precision of 15–20%.

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References

Ainley DG (2002) The Adélie Penguin: bellwether of climate change. Columbia University Press, New York

Anderson DR (2003) Response to Engeman: index values rarely constitute reliable information. Wildl Soc B 31:288–291

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. Anim Conserv 12:258–265

Bart J, Fligner MA, Notz WI (1998) Sampling and statistical methods for behavioural ecologists. Cambridge University Press, Cambridge

Beck JR, Brown DW (1972) The biology of Wilson's storm petrels *Oceanites oceanicus* (Kuhl) at Signy Island, South Orkney Islands. Br Antarct Surv Sci Rep 69:1–54

Bolton M, Brown JG, Moncrieff H, Ratcliffe N, Okill JD (2010) Playback re-survey and demographic modelling indicate a substantial increase in breeding European Storm-petrels *Hydrobates pelagicus* at the largest UK colony, Mousa, Shetland. Seabird 23:14–24

Brooke M (2004) Albatrosses and petrels across the world. Oxford University Press, Oxford

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2004) Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford

Burnham KP, Anderson DR (2002) Model selection and multinomial inference. Springer, New York

Chapman DG (1951) Some properties of the hypergeometric distribution with applications to zoological sample censuses. Univ Calif Publ Stat 1:131–159

Chastel O, Weimerskirch H, Jouventin P (1993) High annual variability in reproductive success and survival of an Antarctic seabird, the snow petrel *Pagodroma nivea*: a 27-year study. Oecologia 94:278–285

Copestake PG, Croxall JP, Prince PA (1988) Use of cloacal sexing techniques in mark-recapture estimates of breeding population size in Wilson's stormpetrel *Oceanites oceanicus*. Polar Biol 8:271–279

Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessement. Bird Conserv Int 22:1–34

Diefenbach DR, Marshall MR, Mattice JA, Brauning DW (2007) Incorporating availability for detection in estimates of bird abundance. Auk 124:96–106

Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J Anim Ecol 75:1259–1268

Gerrodette T (1987) A power analysis for detecting trends. Ecology 68:1364–1372

Hounsome MV, Insley H, Elliott S, Graham KL, Mayhew P (2006) Monitoring European storm-petrels Hydrobates pelagicus: a comparison of the results provided by mark/recapture and tape response methods. Atl Seab 8:5–20

Isaksen K, Bakken V (1995) Estimation of the breeding density of little auk (*Alle alle*). In Isaksen K, Bakken V (eds) Seabird populations in the Northern Barents Sea. Meddelelser 135, Norsk Polarinstitutt, Oslo, pp 37–48

Jenouvrier S, Barbraud C, Weimerskirch H (2006) Sea ice affects the population dynamics of Adélie penguins in Terre Adélie. Polar Biol 29:413–423

Lacan F (1971) Observations écologiques sur le pétrel de Wilson (*Oceanites oceanicus*) en Terre Adélie. Oiseau RFO 41:65–89

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 Biol 29:229–238

Marchant S, Higgins PJ (1990) Handbook of Australian, New Zealand and Antarctic Birds. Ratites to ducks, vol 1. Oxford University Press, Melbourne

Matthews LH (1949) The origin of stomach oils in the petrels, with comparative observations on the avian proventriculus. Ibis 91:373–392

Micol T, Jouventin P (2001) Long-term population trends in seven Antarctic seabirds at Pointe Géologie (Terre Adélie): human impact compared with environmental change. Polar Biol 24:175–185

Montevecchi WA (1993) Birds as indicators of change in marine prey stocks. In: Furness RW, Greenwood JJD (eds) Birds as monitors of environmental change. Chapman & Hall, London, pp 217–266

Mougin JL (1968) Etude écologique de quatre espèces de petrels antarctiques. Oiseau RFO 38:1–52

Nichols JD, Hines JE, Sauer JR, Fallon FW, Fallon JE, Heglund PJ (2000) A double-observer approach for estimating detection probability and abundance from point counts. Auk 117:393–408

Olivier F, Wotherspoon SJ (2006) Distribution and abundance of Wilson's storm petrels *Oceanites oceanicus* at two locations in East Antarctica: testing habitat selection models. Polar Biol 29:878–892

Orgeira JL (1997) Nidificacion y habitat del Petrel de Wilson (*Oceanites oceanicus*) en Puerta Cierva, Costa de Danco, Peninsula Antarctica. Ornithol Neotropical 8:49–56

Parker GC, Rexer-Huber K (2016) Guidelines for designing burrowing petrel surveys to improve population estimate precision. Agreement on the Conservation of Albatrosses and Petrels. http://www.acap.aq/en/resources/acap-conservation-guidelines. Accessed 13 Jan 2017

Pryor ME (1968) The avifauna of Haswell Island, Antarctica. Antarct Res Ser 12:191–212

Quillfeldt P (2001) Variation in breeding success in Wilson's storm petrels: influence of environmental factors. Antarct Sci 13:400–409

Ratcliffe N, Vaughan D, Whyte C, Shepherd M (1998) Development of playback census methods for Storm Petrels *Hydrobates pelagicus*. Bird Study 45:302–312

Reyes-Arriagada R, Campos-Ellwanger P, Schlatter RP, Baduini C (2007) Sooty shearwater (Puffinus griseus) on Guafo Isla, d: the largest seabird colony in the world? Biodivers Conserv 16:913–930

Roberts B (1940) The life cycle of Wilson's storm petrel Oceanites oceanicus (Kuhl). Scient Rep Br Graham Ld Exped 2:141–194

Sanz-Aguilar A, Massa B, Lo Valco F, Oro D, Minguez E, Tavecchia G (2009) Contrasting age-specific recruitment and survival at different spatial scales: a case study with the European storm petrel. Ecography 32:637–646

Soanes LM, Thomas RJ, Bolton M (2012) Evaluation of field and analytical methods for estimating the population size of burrow-nesting seabirds from playback surveys. Bird Study 59:353–357

Southwell DM, Einoder LD, Emmerson LM, Southwell CJ (2011) Using the double-observer method to estimate detection probability of two cavity-nesting seabirds in Antarctica: the snow petrel (*Pagodroma nivea*) and the Wilson's storm petrel (*Oceanites oceanicus*). Polar Biol 34:1467–1474

Sydeman WJ, Nur N, McLaren EB, McChesney GJ (1998) Status and trends of the ashy storm-petrel on southeast Farallon Island, California, based upon capture-recapture analyses. Condor 100:438–447

QGIS Development Team (2013) QGIS Geographic Information System. Open Source Geospatial Foundation. http://qgis.osgeo.org

Thomas T (1986) L'effectif des oiseaux nicheurs de l'archipel de Pointe Géologie (Terre Adélie) et son évolution au cours des trente dernières années. Oiseau RFO 56:349–368

Thomas L, Laake JL, Rexstad E, Strindberg S, Marques FFC, Buckland ST, Borchers DL, Anderson DR, Burnham KP, Burt ML, Hedley SL, Pollard JH, Bishop JRB, Marques TA (2009) Distance 6.0. Release 2. Research Unit for Wildlife population Assessment, University St Andrews, UK

Warham J (1977) The incidence, function and ecological significance of petrel stomach oils. Proc NZ Ecol Soc 24:84–93

Warham J (1990) The petrels: their ecology and breeding systems. Academic Press, London

Warham J, Watts R, Daintry RJ (1976) The composition, energy content and function of the stomach oils of petrels (order Procellariiforms). J Exp Mar Biol Ecol 23:1–13

Wasilewski A (1986) Ecological aspects of the breeding cycle in the Wilson's storm petrel, *Oceanites oceanicus* (Kuhl), at King George Island (South Shetland Islands, Antarctica). Pol Polar Res 7:173–216

Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations. Academic Press, San Diego