POPULATION ESTIMATES OF BURROW-NESTING PETRELS BREEDING AT THE NIGHTINGALE ISLAND GROUP, TRISTAN DA CUNHA ARCHIPELAGO

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ABSTRACT

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Nightingale is a group of three small, uninhabited islands in the central South Atlantic Ocean. The islands are free of introduced mammals and are largely pristine, supporting two endemic land birds as well as globally important populations of several species of seabirds. Seven species of burrow-nesting petrels are known to breed on the islands, including roughly 40 % of the world's population of Great Shearwaters *Ardenna gravis*. We estimated burrow densities by systematically searching for their burrows in 5×5-m quadrats across the main island in the austral summer of 2015. A total of 1789 petrel burrows fell within the 75 sample quadrats with an average density of 0.95 burrows·m^{-2}, suggesting that upwards of four million petrels breed on the main island. Burrow densities and occupancy rates were extrapolated by species for each habitat type to generate population estimates: Great Shearwaters 2.34 million burrows (1.82 million pairs, 95 % CI 1.67–1.97 million); Broad-billed Prions *Pachyptila vittata* a minimum of 83000 burrows (with many more pairs breeding in rock crevices, total estimate 100000–500000 pairs), White-faced Storm Petrels *Pelagodroma marina* 17800 burrows (11700 pairs, 95 % CI 4700–16600), Soft-plumaged Petrels *Pterodroma mollis* 12100 burrows (estimated 8000–10000 pairs), Fregetta Storm Petrels *F. grallaria/tropica* 6600 burrows (estimated 5000 pairs), Common Diving Petrels *Pelecanoides urinatrix* 3900 burrows (estimated 5000 pairs), and Subantarctic Shearwaters *Puffinus elegans* an estimated 1000 pairs. Although Great Shearwater burrow densities and occupancies were lowest in the areas historically used for exploitation of chicks and eggs (ongoing, but now monitored), these results suggest the great shearwater population on Nightingale Island has remained relatively stable since the first estimates in the 1950s.

Key words: Great Shearwaters *Ardenna gravis*, burrow densities, petrel survey, seabird exploitation

INTRODUCTION

Nightingale Island and its two offshore islets, Middle and Stoltenhoff Islands, are located at 37°25′S, 012°28′W and are the smallest of a group of mountainous islands that comprise the Tristan da Cunha Archipelago in the central South Atlantic Ocean. The main island of Tristan (96 km^2) is inhabited by approximately 260 people, whereas neighbouring Inaccessible (14 km^2, 32 km to the southwest of Tristan) and Nightingale (2.6 km^2, 32 km to the south by southwest) Islands are uninhabited and largely pristine, supporting endemic land birds (e.g., *Nesospiza* finches) as well as globally important populations of seabirds (Ryan 2007). Despite its small size, Nightingale Island supports at least 40 % of the world's population of Great Shearwaters *Ardenna gravis* (BirdLife International 2018), and Middle Island, a small 10-ha (0.1 km^2) islet off the north coast of Nightingale, supports an estimated 36 % of the world's population of Northern Rockhopper Penguins *Eudyptes moseleyi* (Robson *et al*. 2011). The archipelago's birds have been documented in some detail following surveys in the 1930s (Hagen 1952), 1950s (Rowan 1952, Elliot 1957, Rowan 1965), 1970s (Wace & Holdgate 1976, Richardson 1984), 1980s (Fraser *et al*. 1998, Ryan & Moloney 1991), and more recently (e.g., Ryan & Moloney 2000, Robson *et al*. 2011). However, recent and accurate surveys of breeding populations of burrow-nesting petrels on the Nightingale group of islands are lacking.

Historic island estimates of the Great Shearwater population of Nightingale Island range from two to three million pairs (Rowan 1952, Richardson 1984, Ryan *et al*. 1990). Globally, the breeding population estimate is ~five million pairs (BirdLife International 2018), with an estimated ~two million pairs breeding on Inaccessible Island (Ryan 2007) and ~one million pairs breeding on Gough Island (situated 400 km southeast of the Tristan islands; Cuthbert 2004). Islanders collected tens of thousands of Great Shearwater eggs, chicks, and adults from Nightingale and Inaccessible Islands from the 1930s to the early 1950s, when up to 15000 eggs and 20000 chicks were collected annually (Hagen 1952, Rowan 1952). In the early 1970s, an estimated 40000–70000 adult Great Shearwaters were taken annually from Nightingale Island (Richardson 1984), but, in 1976, exploitation was restricted to the collection of eggs and chicks (prohibited elsewhere in the archipelago; Wace & Holdgate 1976). Currently, the Tristan da Cunha Conservation Ordinance of 2006 (St. Helena 2006) protects Great Shearwaters at all islands except Nightingale, where exploitation is still restricted to the collection of eggs and chicks. Tristan's Conservation Department now roughly monitors the numbers of Great Shearwater chicks and eggs that are taken, which in recent years has varied from zero (2008–2010) to ~5000 (2012) to a few hundred annually (2015–2019). Here, we present observations and population estimates of burrow-nesting petrels breeding on Nightingale Island recorded over the austral summers of 2015, 2016, and 2017.

STUDY AREA AND METHODS

The geography, vegetation, and history of the Tristan group of islands are described in detail by Wace and Holdgate (1976) and more recently in Ryan (2007). Nightingale's landscape is dominated by the 350–450-m high elongated ridge which rises steeply in the east. The central plateau (~250 m) is broken up into small hills and valleys, with four boggy ponds that have developed in shallow depressions on the western plateau, dominated by the sedge *Scirpus sulcatus*. Most of the island is covered with tussocks of *Spartina arundinacea* grass, which form dense, almost uniform stands that are 2–3 m high, broken only by copses of island trees *Phylica arborea* and small meadows of hummock-forming *Scirpus bicolor* that together cover ~5 % of the island (Fig. 1). Nightingale Island has two large, offshore islets: Middle Island (10 ha; 0.1 km^2), which is a relatively low-lying island dominated by tussock vegetation and rocky outcrops; and Stoltenhoff Island (8 ha; 0.08 km^2), a taller island with 70-m cliffs around much of its coastline and two rock stacks at its eastern end. Stoltenhoff is also dominated by tussock vegetation, but has a small copse of island trees at the highest point of the main islet (Ryan *et al*. 2011; Fig. 1). Nightingale and its islets are free of introduced mammals (e.g., house mice *Mus musculus* and ship rats *Rattus rattus*, which both occur on neighbouring Tristan da Cunha) and support millions of nesting seabirds (Rowan 1952, Ryan 2007). Nightingale has ~20 huts (each ~10 m^2) and a large Conservation hut (~150 m^2, Fig. 1), both of which are occasionally used by islanders for holidays and work.

Fieldwork

DD and BD stayed on Nightingale Island for >10 mo over three successive summers: 46 d between 16 September 2015 and 11 January 2016; and continuously from 07 October 2016–25 January 2017 and 15 September 2017–22 January 2018. The bulk of the dedicated survey fieldwork was completed in 2015, but in 2016 and 2017 we collected additional data and recorded ad hoc observations while in the field studying Nightingale's endemic finches.

Burrow survey

To estimate burrow-nesting petrel breeding densities, BD and DD systematically searched for burrows in 75 5x5-m quadrats across Nightingale Island (Fig. 1). The two islets, Middle and Stoltenhoff Islands, were not sampled. Burrows were sampled at eight sites (altitudes 20–350 m), where quadrats were arranged approximately 25 m apart in lines of five. These sites covered the three main habitat types: (1) *Spartina* tussock grass, which covers most of the island; (2) *Scirpus* meadows, known locally as 'lamb houses,' which are small clearings around the ponds and on gentle slopes on the central plateau; and (3) forests of *Phylica* trees with an understory of ferns (mainly *Asplenium* spp. and bracken *Histiopteris incisa*) and sedges (*Scirpus*, *Carex,* and *Uncinia* spp.). Because Broad-billed Prions *Pachyptila vittata* mostly breed in rock crevices found in the numerous rock stacks on Nightingale Island, only a subset of the population was sampled by the burrow survey.

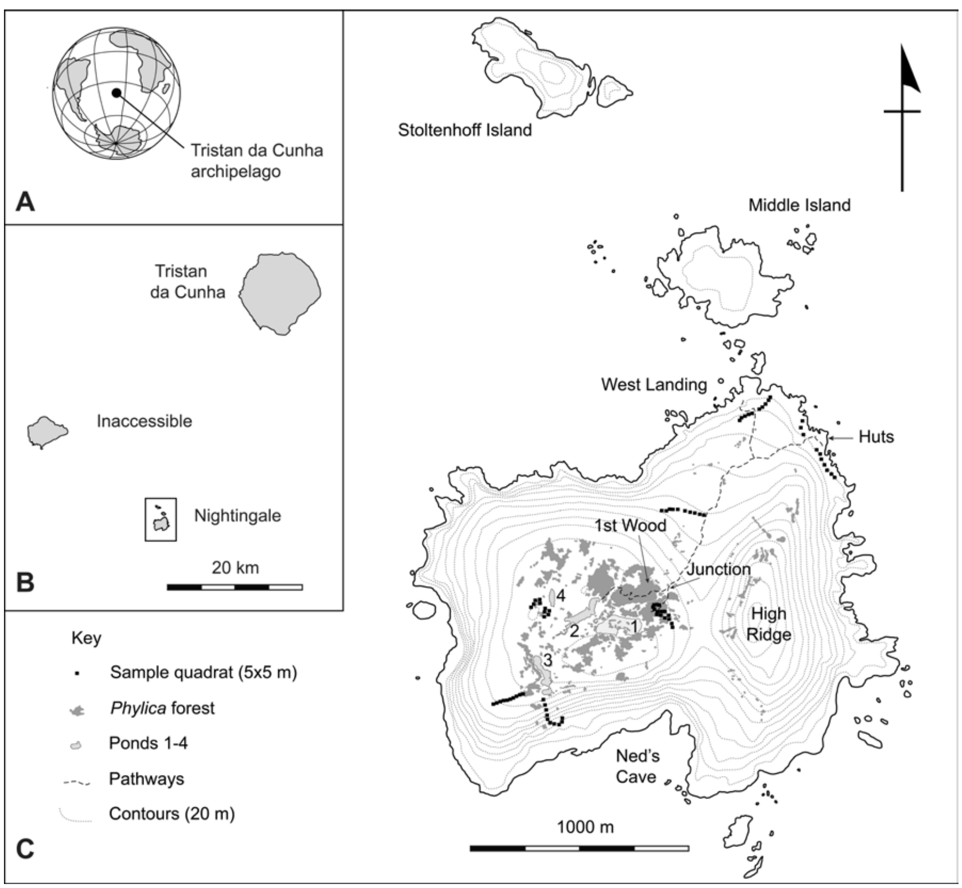

Fig. 1. (A) The location of the Tristan da Cunha Archipelago; (B) Nightingale and Inaccessible Islands relative the Tristan; (C) Nightingale Island and the outer islets, Stoltenhoff and Middle Islands, showing the locations of the 75 (5x5-m) quadrats (black squares not shown to scale) sampled in 2015.

The survey was completed from 07–29 November 2015 to coincide with the laying period of the most numerous petrel on the island, the Great Shearwater. At the time of the survey, Broad-billed Prions, White-faced Storm Petrels *Pelagodroma marina*, Subantarctic Shearwaters *Puffinus elegans,* and Common Diving Petrels *Pelecanoides urinatrix* were still breeding (see Fig. 2), but Soft-plumaged Petrels *Pterodroma mollis* and *Fregetta* Storm Petrels were not yet breeding (Fig. 2). Both Black-bellied *Fregetta tropica* and White-bellied Storm Petrels *F. grallaria* occur at Inaccessible Island (Robertson *et al*. 2016), and both have been recorded ashore on Nightingale Island (PGR unpubl. data). However, we did not extract birds from burrows to try to identify them to the species level.

All entrances to active burrows (with a bird present), and recently active burrows that fell within each 5x5-m quadrat, were identified and counted. Every burrow was inspected with a burrowscope (custom-made burrowscope with a high resolution conical pinhole camera, LED torch, and an 18×21-cm colour monitor) to determine the burrow status (empty, loafer, incubator). Large empty burrows were counted as Great Shearwater burrows because there are no other large burrow-nesting petrels on Nightingale Island. For smaller empty burrows, we used the relative shape and size of the burrow entrance and the physical burrow characteristics (Schramm 1986, Dilley *et al*. 2017) to infer which species previously occupied the burrow.

Data analyses

Burrow occupancy was defined as the proportion of burrows that contained a bird incubating an egg, and was recorded only for Great Shearwaters and White-faced Storm Petrels (at the start of our field seasons, Broad-billed Prions were already at hatching stage). Hatching success was calculated as the proportion of eggs that hatched, and fledging success was calculated as the proportion of hatched chicks that survived to fledge (i.e., fledglings alive at the last nest check). The overall breeding success was calculated as the proportion of eggs that produced a fledgling. However, the estimates we present are maximum estimates, given that some chicks may have died after observations ceased and before fledging. For nests found at the chick stage, approximate hatch dates were deduced based on the size of the chick (relative to chicks of known age at other study nests).

We aimed to survey the density of seven species of burrow-nesting petrels; however, for three of these species we recorded too few burrows to include in the extrapolation analyses. For these species,

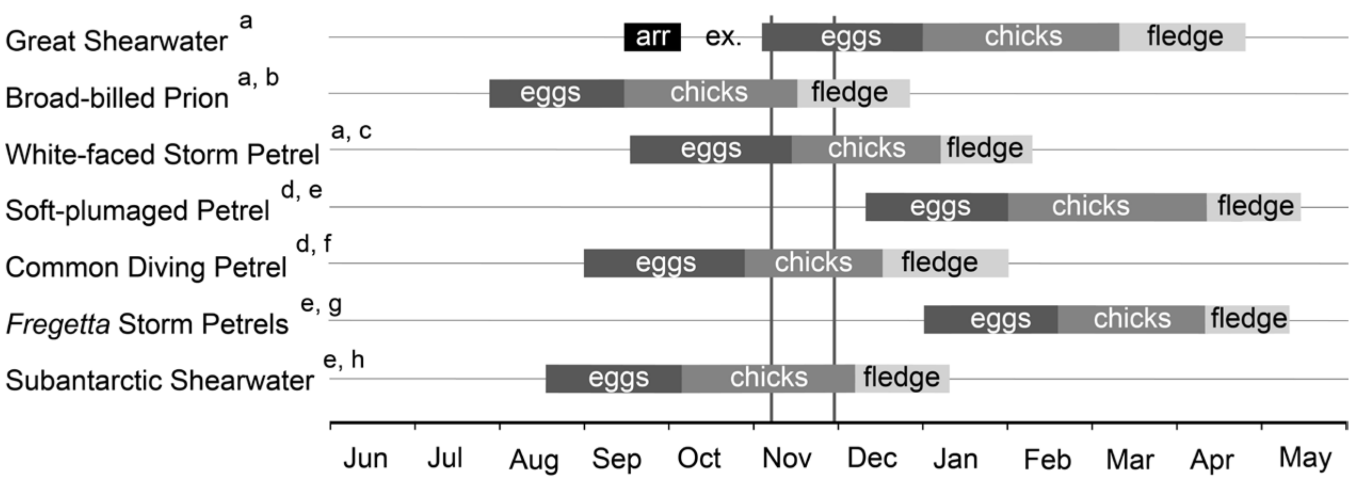

Fig. 2. Breeding months of seven species of burrow-nesting petrels at Nightingale Island. Vertical lines indicate the timing of the 2015 survey of 75 (5x5-m) quadrats. Data sources: [a] This study; [b] Berruti & Hunter 1986; [c] Campos & Granadeiro 1999; [d] FitzPatrick Institute unpubl. data; [e] Ryan 2007; [f] Payne & Prince 1979; [g] Quillfeldt & Peter 2000; [h] Booth *et al*. 2000.

TABLE 1
Population estimates of seven species of burrow-nesting seabirds breeding at Nightingale Island (excluding Middle and Stoltenhoff Islands) in 2015

Species	Burrows (95 % CI)	Pairs (95 % CI)	Method[a]
Great Shearwater *Ardenna gravis*	2 212 000 (2 034 000–2 391 000)	1 716 000 (1 573 000–1 860 000)	1
Broad-billed Prion *Pachyptila vittata*	83 600 (51 600–109 900)	*100 000–500 000*[b]	2
White-faced Storm Petrel *Pelagodroma marina*	17 800 (7 100–25 400)	11 700 (4 700–16 600)	1
Soft-plumaged Petrel *Pterodroma mollis*	12 100 (9 100–23 200)	*8 000–10 000*	2
Fregetta Storm Petrels *F. grallaria/tropica*	6 600 (4 500–15 700)	*5 000*	2
Common Diving Petrel *Pelecanoides urinatrix*	3 900 (1 100–12 500)	*5 000*	2
Subantarctic Shearwater *Puffinus elegans*	*1 500*	*1 000*	2

[a] Method: 1 = quadrats & density extrapolation; 2 = quadrats & *best estimate (italics)* based on field experience.
[b] Total estimates, including prions that breed in rock crevices and caves.

we report a 'best estimate' of the island population size based on our field experience (Table 1). For the remaining four species, we calculated burrow densities (n/25 m^2) for each quadrat plot. The standard errors (SE = SD/$\sqrt{n}$) and 95 % confidence intervals (CI = mean ± 2SE) were calculated from the mean burrow densities of each species for the three habitat types. Where data produced a negative CI (White-faced Storm Petrels, Broad-billed Prions, Soft-plumaged Petrels, *Fregetta* Storm Petrels, and Common Diving Petrels), these data were bootstrapped using library *boot* (Canty and Ripley 2014) in R (R Core Team 2018) with 5000 iterations.

The areas occupied by the Northern Rockhopper Penguin colonies on Nightingale and Middle Islands were excluded from the analyses. Although some burrow-nesting petrels do breed in these areas, they occur at lower densities than in other areas; burrow densities were not measured to avoid disturbance to the breeding penguins. The main penguin colony areas on Nightingale and Middle Islands were calculated in 2015 by walking the perimeter with a handheld GPS set to record a waypoint every five seconds. The edge of the main *Phylica* copse '1st Wood' was also calculated by walking the perimeter with a GPS. Because these areas are relatively flat, no correction for slope was needed. The remaining habitat perimeters and planar surface areas were captured remotely using Google Earth imagery and QGIS (version 2.18.11). Means are presented as mean ± SD, unless stated otherwise. Breeding years refer to austral seasons (i.e., 2015 for the 2015/16 summer breeding season).

RESULTS

A total of 1789 petrel burrows were found within the 75 sample quadrats (Fig. 1), suggesting upwards of four million petrels (1.95 million pairs; Table 1) breed on Nightingale Island with an average density of 0.95 burrows·m^{-2}.

Great Shearwater

A total of 1551 Great Shearwater burrows occurred within the 75 sample quadrats (Table 2) at Nightingale Island, where Great Shearwater burrows were found in 100 % of the quadrats sampled. Average burrow density for tussock habitat was 1.02 ± 0.25 (SD) burrows·m^{-2} and across all habitat types was 0.83 ± 0.30 burrows·m^{-2}. Assuming the same density occurs on the offshore islets, this suggests a total of 2.34 million burrows. Given burrow occupancies of 49 % to 78 % (by habitat, see Table 2), this equates to 1.82 million breeding pairs (95 % CI 1.67–1.97 million) of Great Shearwaters on Nightingale, Middle, and Stoltenhoff islands in 2015 (Table 2). The average density of Great Shearwater burrows sampled in tussock around the huts (5720 ± 905 burrows·ha^{-1}; 5720 ± 905 burrows·0.01 km^{-2}) was nearly half the density of burrows sampled in tussock across the rest of the island (10220 ± 2517 burrows·ha^{-1}; 10220 ± 2517 burrows·0.01 km^{-2}; Table 2, Fig. 1). Burrow occupancy (incubators) was also lowest around the huts (49 %) and in the *Phylica* copses (60 %), with an overall mean occupancy for all 75 quadrats of 70 % ± 13 %.

Breeding phenology and breeding success

Great Shearwaters returned to Nightingale from mid-September to renovate their burrows and mate. By the last week in September, huge rafts of birds were offshore in the afternoons. Birds were very vocal at their burrows, especially at dusk and at night, when many birds were calling from outside their burrow entrances. In 2017, we estimated the peak return period for new birds arriving on the island

TABLE 2
The estimated number of Great Shearwater burrows and breeding pairs on Nightingale, Middle and Stoltenhoff islands

Island Great Shearwater habitat (ha)	Number of quadrats	Total burrows	Empty burrows	Adult loafer	Adult incubator	Average burrows per ha ± SD	Estimated number of burrows (95 % CI)	Breeding pairs (95 % CI)
Nightingale								
Tussock around huts (1.9)	10	143	50 (35 %)	23 (16 %)	70 (49 %)	5720 ± 905	10819 (9736–11902)	5296 (4214–6378)
Rest of the island tussock (211.0)[a]	40	1022	156 (15 %)	68 (7 %)	798 (78 %)	10220 ± 2517	2154577 (1986794–2322361)	1682341 (1547857–1816826)
Phylica copses (12.2)	10	82	26 (31 %)	7 (9 %)	49 (60 %)	3280 ± 1012	40051 (32236–47866)	23933 (17511–30355)
Scirpus meadows & pathways (0.9)	15	304	62 (20 %)	20 (7 %)	222 (73 %)	8107 ± 3643	7277 (5588–8965)	5314 (3937–6691)
Middle[b]								
Tussock (5.2)[a]	-		-	-	-	-	53462 (49299–57625)	41744 (38407–45081)
Stoltenhoff[b]								
Tussok (7.6)	-		-	-	-	-	78097 (72015–84179)	60980 (56105–65855)
Total	**75**	**1551**	**294 (19 %)**	**118 (8 %)**	**1 139 (70 %)**	**8272 ± 3 518**	**2344283 (2155669–2532897)**	**1819 608 (1668031–1971186)**

[a] Excluding the penguin colony areas (2015).
[b] Islets not sampled; burrow densities assumed to be the same as on Nightingale.

to breed as 26 September (25–28 September, based on daily checks of 70 marked burrows from 19 September to 03 October; Fig. 3).

By early October, the island was noticeably quieter at night because most pairs had left on their pre-laying exodus, returning from late October to early November. The timing of laying was highly synchronous, with a peak in mid-November in all three study years (13 November ± 2.5 d in 2015, *n* = 50 eggs; 15 November ± 4.4 d in 2016, *n* = 44; 11 November ± 3.1 d, *n* = 47 in 2017; Fig. 4). No birds were found incubating an egg on the surface (a common practice at Inaccessible Island, where the tussock is denser; PGR pers. obs.), although occasional eggs were found abandoned under the tussock around laying time. The incubation period averaged 53 d (range 52–55 d) at five nests where laying and hatching dates were noted accurately (daily checks) in 2017. Eggs measured an average of 78.0 ± 2.8 mm (74.0–86.4 mm) × 49.3 ± 1.4 mm (46.9–52.1 mm, *n* = 21); mean hatching date in 2017 was 03 January ± 3.9 d (26 December 2017 – 09 January 2018, *n* = 34 chicks). Hatching success was 72 % (*n* = 50 burrows), 64 % (44), and 74% (47) for the three consecutive study years. Survival to fledging could not be recorded because we left the island well before the chicks fledged. However, in January 2018, two of 34 chicks disappeared within a week of hatching, but no further chick failures were seen on the final check, two weeks after peak hatching.

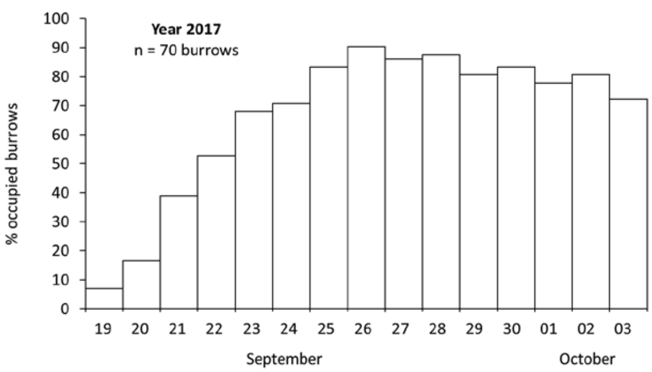

Fig. 3. The peak return period for Great Shearwaters arriving at Nightingale Island to breed in 2017.

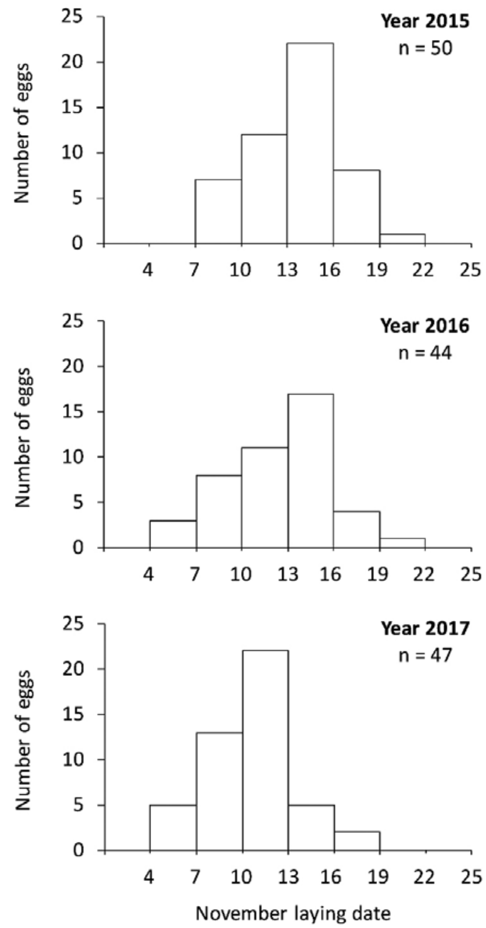

Fig. 4. Great Shearwater laying dates at Nightingale Island over three successive years.

TABLE 3
The number of petrel burrows found in 75 (5×5-m) quadrats at Nightingale Island in 2015[a]

Nightingale habitat types (ha)	Number of quadrats	Great Shearwater	Broad-billed Prion	White-Faced Storm Petrel	Soft-plumaged Petrel	*Fregetta* Storm Petrels	Common Diving Petrel	Subantarctic Shearwater	Total burrows
Tussock around huts (1.9)	10	143 (100 %)	51 (100 %)	4 (30 %)	8 (60 %)	1 (10 %)	4 (30 %)	1 (10 %)	212
Rest of the island tussock (211.0)[b]	40	1 022 (100 %)	34 (48 %)	5 (8 %)	2 (3 %)	0	1 (3 %)	0	1 064
Phylica copses (12.2)	10	82 (100 %)	16 (70 %)	13 (70 %)	14 (70 %)	13 (90 %)	3 (30 %)	0	141
Scirpus meadows & pathways (0.9)	15	304 (100 %)	10 (33 %)	25 (67 %)	21 (40 %)	10 (47 %)	2 (13 %)	0	372
Total	**75**	**1 551**	**111**	**47**	**45**	**24**	**10**	**1**	**1 789**

[a] Numbers in parenthesis indicate the percentage of quadrats which had burrows in each habitat.
[b] Excluding the penguin colony areas (2015).

Broad-billed Prion

Broad-billed Prions are abundant on Nightingale Island and are the most numerous seabird after Great Shearwaters. Estimating the population size is very difficult because they nest in a wide range of habitats, often with complex twisted burrows that can have multiple nest chambers from a common entrance. They also favour rocky stacks, caves, and crevices, which are abundant on the island. We recorded 111 burrows (39 with large chicks, 3 loafers, 69 unoccupied) within the 75 quadrats, suggesting a total of 83 000 burrows (95 % CI 51 000–109 000). Broad-billed Prion burrows were most common in coastal tussock (100 % of these quadrats contained prion burrows) and *Phylica* (70 %) habitats (Table 3). However, this burrow estimate is a minimum estimate of the island population, as it excludes the estimated thousands of prions that breed in rocky stacks and caves on Nightingale, Middle, and Stoltenhoff Islands (which have very high densities of prions; PGR pers. obs. 2009). We therefore estimate that 100 000–500 000 pairs breed on the three islands.

Eggs measured 37.7 ± 1.7 mm (36.0–42.0 mm) × 51.5 ± 1.6 mm (47.8–53.4 mm, n = 11). Average bill width of prions was 21.0 ± 1.0 (range 19.0–23.1, n = 79). On 18 September 2017, four of 11 active burrows had newly hatched chicks. Egg shells and depredated small prion chicks seen outside burrows in late September suggest that hatching time was approximately mid-late September. Small chicks (<5 d of age) were frequently killed by Tristan Thrushes *Turdus eremita*, which removed the chicks through the burrow entrance before bludgeoning their heads with their powerful bills (Ryan & Ronconi 2010). We only observed this behaviour once, but small chicks (1–2 weeks old) were found dead with head wounds on numerous occasions in early October 2016 and 2017, and it is likely that these were also killed by thrushes. Skuas *Catharacta antarctica* targeted fledglings in late November through to early December by excavating burrows or killing fledglings on the ground.

White-faced Storm Petrel

White-faced Storm Petrels were commonly encountered on Nightingale Island, and burrows were found under tufts of *Scirpus* sedge as well as under the introduced farm grass *Holcus lanatus* in the pathways, in the understory of *Phylica* copses and to a lesser extent under tussock grass (Fig. 5, Table 3), usually close to an open area for easy access. We recorded 47 burrows (four with incubating adults, 26 with chicks, 17 unoccupied) within the 75 quadrats. Burrows had a small, neat entrance (average 70 mm wide × 50 mm high, n = 6) with a narrow dry passage (mean length 500 ± 200 mm, 300–900 mm), often in an 'S'-shape, leading to a fist-sized chamber with a sparse nest lining of *Scirpus* or *Spartina* leaves. On two occasions, we found an active burrow leading off a Great Shearwater burrow passage. Burrow densities were highest in the *Scirpus* meadows and pathways (mean density of 0.06 burrows·m^{-2}; 25 of the 47 burrows found within the quadrats). Mean occupancy across all habitat types was 65 % ± 22 %, with the lowest occupancy rates in the tussock around the huts (25 %) and the highest in the *Phylica* copses (77 %). Some cryptic burrows were inevitably overlooked; thus, we estimate a minimum total of 17 800 burrows (95 % CI 7 100–25 400) and 11 700 (95 % CI 4 700–16 600) breeding pairs on Nightingale.

Eggs were white with red speckles concentrated around the broad end, measuring 38.7 ± 0.5 mm (38.1–40.0 mm) × 26.6 ± 0.4 mm (26.1–27.1 mm, n = 16). We marked 25 active nests during 09–13 November 2015; 15 already had small chicks when found (identified as White-faced Storm Petrels by their yellow toe webs), and those with eggs (10) were monitored every three days until hatching. Thereafter, nests were only checked once more, on 11 January 2016. Peak hatching time was approximately mid-November (average 11 November, range 29 October–24 November, n = 6 observed and 15 deduced); peak laying period was likely mid-late September (estimated as 05–30 September, using an incubation period of 54 d; Campos & Granadeiro 1999). Hatching success was not assessed because most nests were found at the late incubation or small chick stage. On 11 January 2015, 12 chicks had <20 % down feathers and three had up to 50 % down, suggesting a fledging period of mid-late January and a fledging success of 60 % (15/25). Chicks and adults were particularly vulnerable to predation by skuas, which excavated into burrows through the ceiling of the nest chambers. Although we did not observe any direct predation at a storm petrel burrow, a Tristan Thrush was seen killing a live ~two-day-old chick on 12 November 2015, and another was seen with a newly hatched chick in its bill on 19 November 2015.

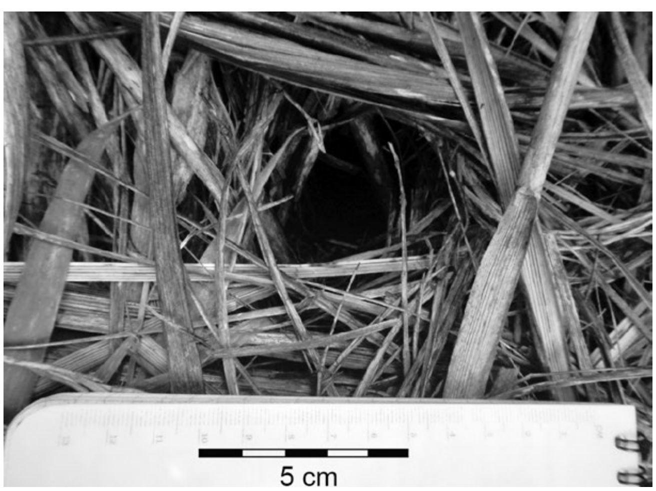

Fig. 5. Entrance of a White-faced Storm Petrel burrow in dead grass stems of *Spartina* tussock.

Fig. 6. A pair of Soft-plumaged Petrels in a burrow in the 1st Wood, Nightingale Island, on 11 January 2016.

Soft-plumaged Petrel

Soft-plumaged Petrel calls (especially flight calls) were heard at night, especially from November onwards. Our quadrat survey was completed before Soft-plumaged Petrels started to lay; however, a total of 45 burrows of Soft-plumaged Petrel-size fell within the 75 sample quadrats: four contained pairs, while 41 (of which 34 were newly renovated) were unoccupied. These figures indicate a minimum of 12 100 (95 % CI 9 100–23 200) burrows and a crude estimate of 8 000–10 000 breeding pairs. Six of the unoccupied forest burrows were revisited after the survey on 11 January 2016, of which four contained incubating birds (Fig. 6), lending some confidence to our identification of these unoccupied burrows.

Fregetta Storm Petrels

Fregetta Storm Petrels were present on the island from September, but were more commonly seen and heard as their January breeding season approached. A total of 24 burrows was recorded as *Fregetta* Storm Petrels within the 75 sample quadrats, indicating a minimum of 6 600 (95 % CI 4 500–15 700) burrows. Although the burrow characteristics were similar to those recorded for White-faced Storm Petrels, it seems unlikely that *Fregetta* Storm Petrels would share burrows with White-faced Storm Petrels because there is some overlap in their breeding cycles. We considered these 24 burrows to be those of *Fregetta* Storm Petrels because the burrows showed no signs of recent use (we observed thick cobwebs in the entrance and passage with no soil scrapings or signs of occupancy).

Five active nests were found in 1st Wood on 06 January 2017; eggs were white-pink in colour with a concentration of red speckles at the broad end, measuring 35.3 ± 0.4 mm (34.9–35.7 mm) × 24.7 ± 0.2 mm (24.4–25.0 mm, n = 5). Based on the quadrat burrow densities and frequency of calls, and observations at night in December/January, we crudely estimate a minimum of 5 000 pairs.

Common Diving Petrel

Common Diving Petrels were often heard around the huts at night and frequently observed at sea (either singly or in groups of 5–25) when crossing by boat between Tristan and Nightingale. Diving petrels were also very abundant outside the kelp zone at Nightingale, where high densities of birds were seen on numerous occasions. A total of 10 burrows of diving petrel-size fell within the 75 sample quadrats, of which only two were active: one incubating adult (egg 39.2 × 29.7 mm) in a forest burrow south of Pond 4 on 11 November 2015 and one adult brood-guarding a small chick in a burrow in the steep coastal tussock slopes on 18 November 2015. This suggests a minimum of 3 900 (95 % CI 1 100–12 500) burrows and a crude estimate of 5 000 breeding pairs. On 29 December 2017, a newly fledged chick was found dead outside its earth burrow in 1st Wood, with 'bludgeon' head wounds similar to those inflicted by Tristan Thrushes on storm petrel chicks and adults (Ryan & Ronconi 2010).

Subantarctic Shearwater

Subantarctic Shearwaters were occasionally heard at night on the island, most commonly from the steep tussock coastal slopes. One occupied burrow was found in a quadrat in the coastal tussock slopes on 29 November 2017. The burrow was 1.2 m long, with a sharp curve ending in a small nest chamber and lined with *Spartina* leaves, where an adult was incubating an addled egg (53.3 × 36.2 mm). The burrow was empty one week later. JR found an incubating adult in the steep coastal tussock slopes above West

TABLE 4
The estimated number of Great Shearwater burrows and breeding pairs on Nightingale Island since the 1950s

Nightingale Island (excl. Middle & Stoltenhoff)	Rowan (1952)	Richardson (1984)	Ryan *et al.* (1990)	This study
Year	1949–1950	1972–1974	1989	2015
Sample plot/transect	15 x (25 yd^2)	none	2 x (2 m x 50 m)	75 x (25 m^2)
Planar area used (ha)	167	400	320	225
Burrow densities (burrows·m^{-2}) by habitat				
Scirpus meadows	1.79	-	-	0.81
Phylica	0.72	-	0.86	0.22
Tussock	1.20	-	1.06	1.02
Overall density	1.20	1.00	~1.00	0.98
Reported burrow estimate				
Burrows	~2 million	~4 million	~3 million	2.3 million
Occupancy	~1.00[a]	-	0.71[b]	0.70
Comparison using a standardised planar area of 225 h (2.25 km^2) of habitat				
Burrow estimate	2.7 million	2.2 million	2.1 million	2.3 million
Pairs	2.7 million	-	1.6 million	1.7 million

[a] Occupancy not reported, but assumed as ~1.00 since "each year many hundreds of birds fail to obtain burrows and deposit their eggs on the open soil" (*cf.* Rowan 1952).
[b] Occupancy from Inaccessible Island at same time.

Landing in September 2012; no additional active burrows were located over the three field seasons. We crudely estimate a breeding population of 1 000 pairs.

Grey-backed Storm Petrel

Grey-backed Storm Petrels *Garrodia nereis* were not seen or found in skua remains on the island, but were occasionally seen offshore during boat transfers. Their distinctive 'cicada cricket' call was heard from the hut at night on numerous occasions in November 2016/2017, but we did not locate a bird despite repeated searches through the *Spartina* tussock.

DISCUSSION

Based on comparison of historical estimates of the number of Great Shearwater burrows, there appears to have been a steady decrease in Great Shearwater numbers since the 1950s (Table 4). However, when estimates are compared using a standardised planar area of 225 ha (2.25 km^2) of habitat, the population appears to have been relatively stable since the 1980s. Rowan (1952) estimated that upwards of two million pairs bred on Nightingale in 1949, and that their burrows covered the island at a mean density of one burrow per square yard (i.e., 1.20 burrows·m^{-2}, Table 4). This is the highest burrow density recorded on Nightingale, suggesting that there may have been a decrease in numbers between the first (Rowan 1952) and the second estimate (Richardson 1984). Ryan *et al*. (1990) recorded slightly lower densities in tussock (1.06 burrows·m^{-2}), which are comparable to our 2015 tussock estimates (1.02 burrows·m^{-2}). Although based on only a few records, this apparent early decline is further supported by Rowan's statement that "each year many hundreds of birds fail to obtain burrows and deposit their eggs on the open soil" (*cf*. Rowan 1952, pp. 101), suggesting that burrow occupancy was close to 100 % (Table 4). By contrast, in 2015 we found that 20 % of the burrows were unoccupied, and we only observed a few abandoned eggs on the surface. Overall breeding success was not recorded in this study, but most petrel breeding failures on rodent-free islands tend to occur during the incubation and small-chick periods (Brooke 1990, Warham 1996). Therefore, it is likely that breeding success at our study nests would have been >60 %, which is above the normal range for most shearwaters (see Cuthbert 2005).

The Great Shearwater burrows sampled in the tussock around the huts had the lowest density (5 720 ± 905 burrows·ha^{-1}; 5 720 ± 905 burrows·0.01 km^{-2}) and the lowest occupancy rates (49 %) across the island (Table 2, Fig. 1); this is likely due to the ongoing exploitation of chicks from this area over the last few decades. Burrow densities in *Phylica* and *Scirpus* meadows also appear to have fallen since previous surveys (Table 4). Although exploitation is roughly monitored and the shearwater population at Nightingale Island appears to have been relatively stable since the 1980s, Nightingale and Inaccessible islands are the most important rodent-free breeding sites for this species (Gough Island also supports a large breeding population in the presence of house mice *Mus musculus*). We strongly recommend restricting the exploitation of shearwaters at Nightingale and introducing an annual quota.

Broad-billed Prions are the second-most abundant seabird species breeding on Nightingale Island. Although two species of prions breed on Gough Island (Broad-billed Prion and MacGillivray's Prion *P. macgillivrayi*; Ryan *et al*. 2014), which is 380 km to the southeast, the morphology and timing of breeding suggest that only Broad-billed Prions breed at Nightingale Island. The average bill width of MacGillivray's Prions on Gough Island is <19 mm (Ryan *et al*. 2014). However, the bill width of prions measured on Nightingale Island in 2015 was >19 mm (average 21.0 ± 1.0 mm, range 19.0–23.1 mm, n = 79), similar to those reported by Fraser *et al*. (1988) for prions from Inaccessible Island (average 21.6 mm, range 20–23 mm, n = 12). MacGillivray's Prions also breed three months later than Broad-billed Prions on Gough Island, but, on Nightingale Island, we found no signs of prions laying in late November, or of small prion chicks in January.

Nightingale Island and its two offshore islets are globally important breeding sites for more than four million seabirds. The islands are riddled with petrel burrows, and the safeguarding of these seabirds' breeding sites should remain a top priority for Tristan da Cunha. The Nightingale Island group currently has no conservation status (unlike Gough and Inaccessible islands, which are a single World Heritage Site, individual Ramsar sites, and Tristan Nature Reserves), and we encourage the Tristan Administration to proclaim the two islets as nature reserves. The accidental introduction of mice or rats from neighbouring Tristan da Cunha Island (where both currently occur) poses the greatest threat to these birds, and biosecurity measures need to be strictly enforced for visiting tourists, scientists, and islanders to avoid such a catastrophe.

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