# ASPECTS OF THE BREEDING BIOLOGY OF WILSON'S STORM PETREL OCEANITES OCEANICUS AT BIRD ISLAND, SOUTH GEORGIA

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ABSTRACT. Aspects of the biology and measurements of the breeding population of Wilson's storm petrel at Bird Island, South Georgia (54° S) are compared with data from elsewhere. The breeding timetable is similar to that at Signy Island (61° S) and significantly later than at the Argentine Islands (65° S) and Terre Adélie (67° S); possible reasons for this are discussed. At South Georgia, breeding females are significantly larger than males in all characters, and a discriminant analysis using wing, bill and tarsus length correctly classified 85% of females and 94% of males. South Georgia birds are smaller than those from further south, but the differences suggest clinal variation rather than a disjunct pattern and it may be inadvisable to recognize any subspecies, although more data are needed from the northernmost breeding populations.

## Introduction

Wilson's storm petrel *Oceanites oceanicus* has a circumpolar breeding distribution around the Antarctic continent. In the Indian Ocean it breeds north to Îles Kerguelen (49° S) and Îles Crozet (47° S) and in the Atlantic Ocean north to South Georgia (54° S), where it is common, and the Cape Horn region (54° S) and the Falkland Islands (52° S), where it is local and uncommon (Croxall and others, 1984; Schlatter, 1984). Detailed studies have been made at Terre Adélie (66° 40′ S; Mougin, 1968; Lacan, 1971), Argentine Islands, Antarctic Peninsula (65° 15′ S; Roberts, 1940) and Signy Island, South Orkney Islands (60° 40′ S; Beck and Brown, 1972) but data from more northerly areas are absent or anecdotal. In the course of a study designed to assess breeding population size at Bird Island, South Georgia, in the austral summer of 1982–83, some morphometric data and information on the timing of the breeding season were obtained. These are summarized here and compared with those for the other breeding populations, especially the southern ones.

# **METHODS**

Study area

Bird Island ( $54^{\circ}$  02′ S,  $38^{\circ}$  00′ W), described in detail in Hunter and others (1982), is an island, 6.5 km long by 1.5 km wide, off the north-western tip of South Georgia. At Bird Island, most Wilson's storm petrels breed in coarse scree, talus and other rocky debris slopes, but small numbers are found in burrows in moss banks, in stunted tussock grassland and in crevices in cliffs. The study area was a 1 ha scree slope on the north-west side of Stejneger Peak (see Copestake and others, in press, fig. 1), with an estimated breeding population of c. 2300 pairs (Copestake and others, in press).

# Nest sites and study birds

During the pre-egg period, birds return at night to their burrows, where one or both members of the pair intermittently utter a series of grating calls. It was often difficult to locate the exact source of calls amongst the labyrinth of crevices and it was usually necessary to move some rocks in order to reach the bird. Once an occupied nest site was found, the access route to the burrow was marked with paint, and a wooden stake (1 m) placed vertically nearby to assist relocation from a distance.

Between 13 and 30 December 1982, 40 nest sites were found and these were checked daily until laying. At least one partner was measured, ringed and individually marked (with a small spot of paint on the rump) on the day the egg was first recorded. Female and male cloacae are very different in size at this time and birds could be sexed without difficulty (Copestake and others, in press). The partner was caught and measured later during incubation. Storm petrels readily desert burrows during incubation (Beck and Brown, 1972). Nests were only checked when a measurement was required as part of the main study, but despite this precaution only four nests hatched. Daily checks were resumed from 40 days after egg laying until hatching.

# Measurements

The following measurements were made on the breeding adults: wing (maximum chord to 1 mm using a stopped rule), bill (exposed culmen) and tarsus (both to 0.1 mm using vernier calipers) and weight (to the nearest 0.5 g using a Pesola spring balance). Similar measurements were made on a large sample of birds caught in mist nets at the study site. Length, width (both to 0.1 mm with vernier calipers) and weight (to 0.5 g) of eggs were also recorded.

## RESULTS

## Arrival

Wilson's storm petrels (Fig. 1) return to the Bird Island breeding grounds in mid-November. First sightings in three seasons were 12, 15 and 25 November. Numbers build up gradually over the following few weeks and most breeders have probably returned by early December.

# Pre-egg period

Although nests were located during the night, subsequent daily checks were madduring the day. At this time birds were seldom found in the burrows. In a total of 425 burrows checked, single birds were found on 21 (4.5%) occasions and pairs on nine (1.9%) occasions. On 7 January one pair was observed copulating in their burrow, only a day before the egg was laid.

# Eggs and egg-laying

Measurements of eggs, in comparison with those from other sites, are given in Table I. Only 16 nest sites were found before the first egg was laid in the study area. At these, 13 pairs laid eggs (Fig. 2a) giving a mean laying date of 5.4 January (sp. 12.0 days, range 43 days from 15 December to 26 January). Fourteen eggs were laid at a further 24 sites which, because egg-laying had already started in the population, might be a biased sample. However, the data for these nests (Fig. 2b) are not significantly different



Fig. 1. Wilson's storm petrel near entrance to breeding site. (Photo: A. Sweetman.)

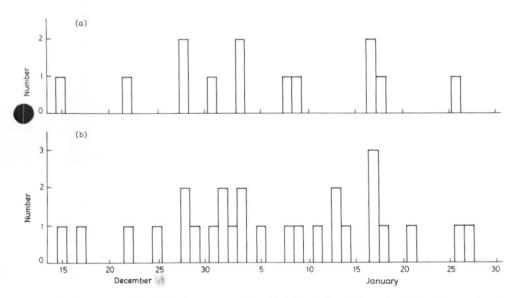


Fig. 2. Egg laying dates for Wilson's storm petrel at Bird Island, South Georgia; (a) for 13 nests found before 15 December, (b) for all nests (n = 27).

Location (Lat., Long.)	Length (mm)	Breadth (mm)	Fresh weight (g)	Reference
Îles Kerguelen	32.8 (n = 9)	23.5 (n = 9)		Beck and Brown, 1972
49° 21′ S. 70° 12′ E	(29.9-34.6)	(22.6-25.2)		
Bird Island, South Georgia	$33.3 \pm 1.0 (n = 19)$	$23.4 \pm 0.8 (n = 19)$	$9.9 \pm 0.9 (n = 13)$	This study
54° 00′ S, 38° 02′ W	(31.8-34.8)	(22.1-24.4)	(9.0-11.7)	
Signy Island	34.8 (n = 15)	24.7 (n = 15)	11.0 (n = 8)	Beck and Brown, 1972
60° 40′ S, 45° 38′ W	(33-36)	(24-26)	(10-12.5)	
Argentine Islands	$33.6 \pm 1.3 (n = 12)$	$23.5 \pm 0.7 (n = 12)$		This study
65° 15′ S, 64° 16′ W	(30.6-35.5)	(22.5-24.7)		
Terre Adélie	33.4 (n = 5)	23.6 (n = 9)	$10.1^{1} (n = 8)$	Mougin, 1968
66° 40′ S, 140° 01′ E	(32.1-35.3)	(22.0-24.4)	(8.5-11.0)	500 man ( 100 m ) 100 m )

Table I. Egg measurements (mean  $\pm$  standard deviation, with range in parentheses) of Wilson's storm petrel.

Table II. Laying and hatching data for Wilson's storm petrel at Bird Island, South Georgia.

Nest	Laying date	Hatch date	Incubation period (days)	Chick hatch weight (g)	
274	22 Dec.	14 Feb.	54	6.4	
289	3 Jan.	15 Feb.	43	7.0	
301	1 Jan.	18 Feb.	48	7.0	
353	18 Jan.	8 Mar.	49	6.5	
Mean	3.2 Jan.	20.7 Feb.	48.5	6.7	
sp (days)	11.1	10.3	8.5	0.3	

from the first sample ( $P \gg 0.1$ ) and both have median laying dates of 4 January. When combined they give a mean laying date of 6.4 January (sp 11.4 days, range 44 days from 15 December to 27 January). However, a female caught in a mist net on 4 February laid an egg overnight in the holding box, which increases the range to 52 days.

# Incubation period and hatching

Of the 27 eggs laid only four hatched, and data on incubation periods and hatchling weights are in Table II. The low hatching success was probably directly due to the handling necessary for determining changes in female cloacae size (Copestake and others, in press).

A mean incubation period of 48.5 days (range 43–54 days) is somewhat longer than that recorded at Signy Island of 44.5 days (sp 4.6 days, range 38–54 days, n = 19; Beck and Brown, 1972) and at the Argentine Islands of 43.4 days (sp 3.4 days, range 39–48 days, n = 9; Roberts, 1940) and significantly longer (Mann–Whitney 'U' test, P = 0.03) than that at Terre Adélie of 41 days (range 38–46 days, n = 4; Mougin, 1968). However, determination of true incubation periods in storm petrels is complicated by the prevalence of periodic, temporary, natural desertions known as egg neglect (Boersma and Wheelwright, 1979). In the South Georgia sample, the extra disturbance caused by the occasional handling of incubating birds may have increased the frequency of these temporary desertions. Alternatively, there may be a tendency for incubation period to decrease with increasing latitude and with decreasing egg size.

<sup>&</sup>lt;sup>1</sup> Stage of incubation not recorded.

Table III. Measurements of breeding male and female storm petrels at Bird Island, South Georgia.

		Mo	ale							
	Sample size	Mean	SD	Range	Sample size	Mean	SD	Range	t	P
Bill length (mm)	18	12.3	0.3	11.8-12.7	21	12.6	0.3	12.2-13.7	3.31	< 0.005
Tarsus length (mm)	17	34.2	0.9	32.1-35.6	21	35.5	1.1	33.2-37.3	3.50	< 0.005
Wing length (mm)	18	151	3	143-157	22	155	3	151-161	4.14	< 0.001
Weight (g)	16	33.5	2.0	30-38	18	36.0	2.75	31-43	3.17	< 0.005

Table IV. Arrival and laying dates for Wilson's storm petrels at different breeding localities.

	Date of first sighting			Egg-laying dates				Difference in lay date from South Georgia			
Location (Lat., Long.)	Mean	Range	Number of seasons	Mean	SD	Range	Sample	1	df	P	Reference
Îles Kerguelen 49° 21′ S, 70° 12′ E	21 Nov.	21 Nov.	1	25 Jan.	9.5	11 Jan7 Feb.	6	3.88	18	< 0.005	Beck and Brown, 1972
Heard Island 53° S, 73° 30′ E	1 Dec.	1 Dec.	1	15 Jan.	7.5	7 Jan.–22 Jan.	3	1.70	15	< 0.2	Downes and others, 1959
Bird Island, South Georgia 54° 00′ S, 38° 02′ W	17 Nov.	12-25 Nov.	3	6 Jan.	11.4	15 Dec27 Jan.	27				This study
Signy Island 50° 40′ S, 45° 38′ W	_	19 Oct13 Nov. (1951-69)	18	9 Jan.	7.8	28 Dec1 Feb.	68	1.38	80	< 0.2	Beck and Brown, 1972
	13 Nov.	8-18 Nov. (1978-84)	6								D. M. Rootes, pers. comm.
Argentine Islands	17.5 Nov.	11-24 Nov.	2	24 Dec.	6.4	14 Dec4 Jan.	16	3.38	28	< 0.005	Roberts, 1940 Beck and Brown, 1972
Terre Adélie 66° 40′ S, 140° 01′ E	6 Nov.	1–9 Nov. 4–5 Nov.	5 21	13 Dec.	9.8	25 Nov4 Jan.	28	6.63	40	< 0.001	Lacan, 1971 Mougin, 1968

<sup>&</sup>lt;sup>1</sup> Cape Denison, 67° 00′ S, 142° 40′ E (Falla, 1937).

The range of observed hatching dates is quite large (14 Feb.–8 March), but if hatching dates are estimated from known laying dates and the mean incubation period they range from 3 February to 16 March, with a mean of 23 February. The mean hatchling weight is very similar to that of 6.8 g (range 5.5–7.5 g) recorded by Lacan (1971) for four chicks at Terre Adélie.

## Adult measurements

The measurements from this study (Table III and Appendix 1) show that females are significantly larger than males in all characters measured. This is unusual in procellariforms but consistent with other data for Wilson's storm petrel (Murphy, 1936; Roberts, 1940) and apparently typical of storm petrels generally (Croxall, 1982; James, 1983). Identification of the sexes could not be reliably achieved using any single measure, and discriminant analysis (Green, 1982) was undertaken using wing, bill and tarsus length. Calculations were made using GENSTAT (4.03) (Alvey and others, 1980) implemented on a Honeywell 66/DPS-300 computer. Weight was excluded, as this is by far the most variable character (see Beck and Brow (1972) for the nature of seasonal changes) and its inclusion here did not significantly improve discrimination. The unstandardized discriminant function is:  $(bill \times -1.3510) + (tarsus \times -0.4781) + (wing \times 0.1420) - 60.0302$  (all measurements in mm) producing the individual discriminant scores (Appendix 1). The mean discriminant score for males is 0.9223 and for females -0.7839, a significant difference  $(F_{3,36} = 8.4477; P < 0.001)$ . The accuracy of sexing using this function is 85% for females (17 out of 20) and 94% for males (16 out of 17). This is close to, though a little better than, the results of a very similar analysis (using tarsus, wing and tail lengths) of British storm petrel Hydrobates pelagicus measurements (James, 1983).

### DISCUSSION

# Timing of breeding

Comparison of data on the timing of various events connected with breeding (Table IV) confirms Beck and Brown's (1972) suggestion that the date of arrival at the breeding grounds is more consistent between populations than the date of laying. Thus Wilson's storm petrels lay only three weeks after arrival at Terre Adélie but five to six weeks after arriving at South Georgia. The laying dates at Terre Adélie and Argentine Islands are significantly earlier than those at Signy, South Georgia and Heard Island (t = 12.8, DF = 128, P < 0.001), which are in turn significantly earlier than those at Îles Kerguelen (t = 4.2, df = 89, P < 0.001).

At sites on the Antarctic continent, the shortness of the summer season presumably favours laying as soon as possible after arrival, and the ensuing location of nest sites and re-formation of pair bonds. Even so, chicks do not fledge until 6–14 March (Terre Adélie, n = 3; Lacan, 1971) or 27 March–5 April (Argentine Islands, n = 4; Roberts, 1940) when climatic conditions (and probably food availability) are deteriorating rapidly. Why, however, do more northerly populations delay breeding to the extent that chicks do not fledge until 6 April–12 May (Signy Island, n = 12; Beck and Brown, 1972) and about 25 April (Bird Island), when in the climatically milder conditions one would expect that breeding could start much earlier than at the continental sites?

Of the 15 procellariform species breeding at Bird Island, Wilson's storm petrels are the latest to lay and only white-chinned petrels *Procellaria aequinoctialis*, northern giant petrels *Macronectes halli* and albatross chicks fledge later. In the South Georgia area, however, the rapid decrease in availability of zooplankton in surface waters does

not occur until May (Foxton, 1956), so the timing of chick rearing may still be consistent with adequate availability of food. At the time when most chicks fledge, however, food is unlikely to be particularly plentiful and it may be important that they should migrate north immediately. It may, therefore, be significant that, during growth, Wilson's storm petrel chicks may typically reach nearly twice adult weight (192%, range 163-213%, n=7, Signy Island; Beck and Brown, 1972) and are still 145% of adult weight at fledging (n=15; Beck and Brown, 1972), both the highest values recorded for any procellariform. Chicks thus fledge with large fat reserves to sustain their migration across the relatively unproductive tropical regions to the rich feeding grounds of the north-west North Atlantic.

In the few studies for which adequate data exist (Fisher, 1967; Harris, 1969; Brooke, 1978; Prince and others, 1981), breeding procellariforms lose weight during the chick-rearing period. Wilson's storm petrels, however, not only maintain their body weight but increase it before the end of chick rearing (Beck and Brown, 1972). Thus, during the lengthy chick-rearing period, breeding adults are ensuring that both they and their chicks acquire substantial fat reserves to help sustain them through at least the first part of their migration. This has presumably been achieved at the expense of rapid chick rearing – Wilson's storm petrels have a very long chick-rearing period for their size (see Croxall, 1984) – and if speed of rearing is not a main objective then there might be little advantage in starting breeding a few weeks earlier.

In terms of general availability and predictability of food resources, a late start to breeding means that a greater part of reproductive activity coincides with the main peak of food resources in February–March. It is possible that there may be a further advantage in delaying breeding. The small chicks of Wilson's storm petrel have a high daily energy requirement, and for their parents to meet this demand and to ensure that the chicks and themselves acquire large fat reserves will require intensive foraging effort. Their diet is principally Antarctic krill *Euphausia superba* and various amphipods (Falla, 1937; Roberts, 1940; Beck and Brown, 1972; BAS unpublished data), which are characteristically picked off the sea surface. Although Wilson's storm petrels can often be seen feeding during the day, most zooplankton tend to rise to the surface at night and are presumably most readily available at this time. The period of main food demand for Wilson's storm petrels is in March–April, and at this time the night is some 2–3 hours (50%) longer than one month earlier and lengthening rapidly. The advantage this represents in terms of additional nocturnal feeding time may well outweigh any disadvantage of delaying departure from the breeding grounds.

# Measurements

In his comprehensive review of geographical variation in Wilson's storm petrels, Roberts (1940) provisionally distinguished four populations worthy of subspecific rank, but later (see Beck and Brown, 1972) agreed with the views of Murphy (1960) and especially Bourne (1964) in recognizing only the nominate race *O. o. oceanicus* (all northern populations including South Georgia) and *O. o. exasperatus* (Antarctic continent, Antarctic Peninsula and associated island groups). South Orkney Island populations were potentially intermediate and, on the basis of fresh data from there and for some other southern populations, Beck and Brown (1972) proposed that *O. o. exasperatus* should include both South Orkney and South Georgia birds, restricting *O. o. oceanicus* to populations north of the Antarctic Convergence (i.e. effectively those at Îles Kerguelen, Îles Crozet, the Falkland Islands and the Cape Horn region). The status of the South Georgia population, the only available material of which had been 14 specimens collected in 1912–1914 (Murphy, 1918), was therefore uncertain.

Table V. Measurements (mm) and weights (g) of adult Wilson's storm petrels from breeding sites. Values are mean  $\pm$  standard deviation, with range in parentheses.

Sample <sup>1</sup>	Sex ratio M:F:unknown	Wing length	Tail length	Bill length	Tarsus length	Weight <sup>2</sup>	References
10*	7:1:2	144.5±3.5 (139–150)	59.3 ± 1.5 (57–62)	11.9 ± 0.5 (11.0–12.5)	33.5 ± 0.9 ((31.5–35.0)	25 (n = 1)	Roberts, 1940 Despin and others, 1972
4*	1:2:1	137.5 ± 3.4 (134–142)	63.7 ± 1.3 (62–64.5)	12.0 ± 0.4 (11.5–12.5)	$33.7 \pm 0.9 \; (34 – 34.5)$	_	Roberts, 1940
11*	9:2:0	139.6 ± 2.7 (136–143)	$59.0 \pm 2.4 \ (56.3 - 63.4)$	$11.5 \pm 0.5 \ (10.3 - 12.0)$	$34.9 \pm 0.9 \; (34 – 35.5)$	_	Roberts, 1940
39‡	18:21:0	153.1 ± 3.8 (143–161)		$12.5 \pm 0.3  (11.8 - 13.7)$	$34.9 \pm 1.2 (32.1 - 37.3)$	$34.9 \pm 2.7 (30.0 - 43.5)$ ( $n = 34$ )	This study
288†	_	$148.9 \pm 4.2 (139 - 164)$		_		31 4 + 2 0 (25 5 38 0)	This study
14*	8:5:1	$148.6 \pm 2.7 (144 - 159)$	$62.9 \pm 2.5 \ (60-68)$	$12.5 \pm 0.4 \; (12.0 – 13.0)$	$34.3 \pm 1.2 \ (32.0 – 36.0)$	- (23.5–36.0)	Murphy, 1918
69†	-	$151.4 \pm 3.9 (142 - 160)$ $(n = 155)$	69.6 ± 2.3 (61–75)	12.6 ± 0.7 (11.0–14.5)	34.2 ± 1.1 (31.5–36.5)	$38.1 \pm 2.3 (32-46)$ ( $n = 150$ )	Beck and Brown, 1972
13*		$146.7 \pm 2.6 (142 - 151)$	$66.8 \pm 2.1 \ (63-70)$	12.6 + 0.5 (12.0 - 13.5)	35.0 + 1.3 (32 - 36.5)	_	Beck and Brown, 1972
10*		152.4 ± 4.2 (142–156)	$69.9 \pm 2.7 (66-74)$	$12.3 \pm 0.3 \ (12.0 - 13.0)$	$34.5 \pm 0.8 (33-36)$	_	Roberts, 1940
17*	10:7:0	153.2 ± 4.3 (144–160)	$69.1 \pm 3.5 \ (61-73)$	$12.3 \pm 0.6 \; (11.0 – 13.0)$	$33.9 \pm 1.3 \; (32 – 36.5)$	_	Roberts, 1940
25‡		155.8 ± 4.0 (142–162)		$13.2 \pm 0.3 \; (12.8 – 13.6)$	$35.4 \pm 0.9 \; (34.3 – 37.1)$	$41.3 \pm 2.8 (34-37)$	This study
28‡		153 (137–163)	69 $(63-74)$ $(n=4)$	12.6 (12.0–14.0)	35.9 (33.5–39.0)	(n = 10)	Mougin, 1968
11*	7:4:0	153.4±3.7 (146–159)	$68.1 \pm 3.4 (63-74)$	$12.5 \pm 0.7 \; (11.0 – 13.0)$	33.3 ± 1.1 (32.0–35.0)	_	Roberts, 1940
10*	6:4:0	155.2 ± 3.6 (149–159)	$71.6 \pm 2.9 \; (66-75)$	$12.1 \pm 0.2\; (12.0 – 12.5)$	33.5 ± 0.9 (31.5–35)	_	Roberts, 1940
	10* 4* 11* 39‡ 288† 14* 69† 13* 10* 17* 25‡ 28‡	Sample1         M:F:unknown           10*         7:1:2           4*         1:2:1           11*         9:2:0           39‡         18:21:0           288†         —           14*         8:5:1           69†         —           10*         4:6:0           17*         10:7:0           25‡         —           11*         7:4:0	Sample¹         M. F. unknown         Wing length           10*         7:1:2         144.5±3.5 (139–150)           4*         1:2:1         137.5±3.4 (134–142)           11*         9:2:0         139.6±2.7 (136–143)           39‡         18:21:0         153.1±3.8 (143–161)           288†         —         148.9±4.2 (139–164)           14*         8:5:1         148.6±2.7 (144–159)           69†         —         151.4±3.9 (142–160)           (n = 155)         13*         —           10*         4:6:0         152.4±4.2 (142–151)           17*         10:7:0         153.2±4.3 (144–160)           25‡         —         155.8±4.0 (142–162)           28‡         —         153         (137–163)           11*         7:4:0         153.4±3.7 (146–159)	Sample <sup>1</sup> $M:F: unknown$ Wing length         Tail length $10^*$ $7:1:2$ $144.5 \pm 3.5 (139-150)$ $59.3 \pm 1.5 (57-62)$ $4^*$ $1:2:1$ $137.5 \pm 3.4 (134-142)$ $63.7 \pm 1.3 (62-64.5)$ $11^*$ $9:2:0$ $139.6 \pm 2.7 (136-143)$ $59.0 \pm 2.4 (56.3-63.4)$ $39^+_+$ $18:21:0$ $153.1 \pm 3.8 (143-161)$ — $288^+$ $ 148.9 \pm 4.2 (139-164)$ — $14^*$ $8:5:1$ $148.9 \pm 4.2 (139-164)$ $ 69^+$ $ 151.4 \pm 3.9 (142-160)$ $62.9 \pm 2.5 (60-68)$ $69^+$ $ 151.4 \pm 3.9 (142-160)$ $69.6 \pm 2.3 (61-75)$ $13^*$ $ 146.7 \pm 2.6 (142-151)$ $66.8 \pm 2.1 (63-70)$ $10^*$ $4:6:0$ $152.4 \pm 4.2 (142-156)$ $69.9 \pm 2.7 (66-74)$ $17^*$ $10:7:0$ $153.2 \pm 4.3 (144-160)$ $69.1 \pm 3.5 (61-73)$ $25^+_+$ $ 155.8 \pm 4.0 (142-162)$ $ 28^+_+$ $ 153 (137-163)$ $69 (63-74)$ $11^*$ $7:4:0$ $153.4 $	Sample¹         M:F:unknown         Wing length         Tail length         Bill length $10^*$ 7:1:2 $144.5 \pm 3.5 (139-150)$ $59.3 \pm 1.5 (57-62)$ $11.9 \pm 0.5 (11.0-12.5)$ $4^*$ 1:2:1 $137.5 \pm 3.4 (134-142)$ $63.7 \pm 1.3 (62-64.5)$ $12.0 \pm 0.4 (11.5-12.5)$ $11^*$ 9:2:0 $139.6 \pm 2.7 (136-143)$ $59.0 \pm 2.4 (56.3-63.4)$ $11.5 \pm 0.5 (10.3-12.0)$ $39^{\ddagger}$ $18:21:0$ $153.1 \pm 3.8 (143-161)$ — $12.5 \pm 0.3 (11.8-13.7)$ $288^{\dagger}$ — $148.9 \pm 4.2 (139-164)$ —         —         — $14^*$ $8:5:1$ $148.9 \pm 4.2 (139-164)$ —         —         — $14^*$ $14.5:1.4 \pm 3.9 (142-160)$ $62.9 \pm 2.5 (60-68)$ $12.5 \pm 0.4 (12.0-13.0)$ $69^{\dagger}$ — $151.4 \pm 3.9 (142-160)$ $69.6 \pm 2.3 (61-75)$ $12.6 \pm 0.7 (11.0-14.5)$ $11^*$ — $146.7 \pm 2.6 (142-151)$ $66.8 \pm 2.1 (63-70)$ $12.6 \pm 0.5 (12.0-13.5)$ $10^*$ $4:6:0$ $152.4 \pm 4.2 (142-156)$ $69.9 \pm 2.7 (66-74)$ $12.3 \pm 0.6 (11.0-13.0)$ $17^*$ $10:7:0$ $153.2 \pm 4.3 (144-1$	Sample¹ $M:F:unknown$ Wing length $Tail length$ $Bill length$ $Tarsus length$ $10^*$ $7:1:2$ $144.5 \pm 3.5 (139-150)$ $59.3 \pm 1.5 (57-62)$ $11.9 \pm 0.5 (11.0-12.5)$ $33.5 \pm 0.9 ((31.5-35.0)$ $4^*$ $1:2:1$ $137.5 \pm 3.4 (134-142)$ $63.7 \pm 1.3 (62-64.5)$ $12.0 \pm 0.4 (11.5-12.5)$ $33.7 \pm 0.9 (34-34.5)$ $11^*$ $9:2:0$ $139.6 \pm 2.7 (136-143)$ $59.0 \pm 2.4 (56.3-63.4)$ $11.5 \pm 0.5 (10.3-12.0)$ $34.9 \pm 0.9 (34-35.5)$ $39^{\frac{1}{4}}$ $18:21:0$ $153.1 \pm 3.8 (143-161)$ — $12.5 \pm 0.3 (11.8-13.7)$ $34.9 \pm 1.2 (32.1-37.3)$ $288^{\dagger}$ — $148.9 \pm 4.2 (139-164)$ —         —         —         — $14^{\bullet}$ $8:5:1$ $148.9 \pm 4.2 (139-164)$ —         —         —         — $14^{\bullet}$ $8:5:1$ $148.9 \pm 4.2 (139-164)$ —         —         —         — $14^{\bullet}$ $8:5:1$ $148.9 \pm 4.2 (139-164)$ —         —         —         —         — $14^{\bullet}$ $14.5$ $14.6 \pm 0.5 (12.0-13.0)$ $12.5 \pm 0.4 (12.0-13.0)$ $34.2 \pm 1.$	Sample*         M:F:unknown         Wing length         Tail length         Bill length         Tarsus length         Weight* $10^*$ 7:1:2 $144.5\pm3.5(139-150)$ $59.3\pm1.5(57-62)$ $11.9\pm0.5(11.0-12.5)$ $33.5\pm0.9(31.5-35.0)$ $25 (n=1)$ $4^*$ $1:2:1$ $137.5\pm3.4(134-142)$ $63.7\pm1.3(62-64.5)$ $12.0\pm0.4(11.5-12.5)$ $33.7\pm0.9(34-34.5)$ — $11^*$ $9:2:0$ $139.6\pm2.7(136-143)$ $59.0\pm2.4(56.3-63.4)$ $11.5\pm0.5(10.3-12.0)$ $34.9\pm0.9(34-35.5)$ — $39^+$ $18:21:0$ $153.1\pm3.8(143-161)$ — $12.5\pm0.3(11.8-13.7)$ $34.9\pm1.2(32.1-37.3)$ $34.9\pm2.7(30.0-43.5)$ $288^+$ — $148.9\pm4.2(139-164)$ —         —         —         31.4\pm2.0(25.5-38.0) $69^+$ — $148.6\pm2.7(144-159)$ $62.9\pm2.5(60-68)$ $12.5\pm0.4(12.0-13.0)$ $34.3\pm1.2(32.0-36.0)$ $31.4\pm2.0(25.5-38.0)$ $69^+$ — $151.4\pm3.9(142-160)$ $69.6\pm2.3(61-75)$ $12.6\pm0.7(11.0-14.5)$ $34.2\pm1.1(31.5-36.5)$ $38.1\pm2.3(32-46)$ $11^*$ — $146.7\pm2.6(142-151)$ $66.8\pm2.1(63-70)$ $12.6\pm0.7(11.0-13.0)$

<sup>&</sup>lt;sup>1</sup> Museum skins; † live adults, breeders and non breeders; ‡ live adults, breeders only.

<sup>2</sup> During mid-incubation, except for Kerguelen specimen.

Our additional South Georgia data permit the taxonomic status of its population to be reappraised (Table V).

Even when all birds caught away from breeding sites are excluded, there are still three potential problems in making realistic comparisons. First, it is difficult to compare measurements from museum skins with those from live birds. The former tend to shrink and, in certain characters, may do so to a very significant degree. Thus Kinsky and Harper (1968) calculated a 6–16% shrinkage in bill dimensions of prions Pachyptila. This probably explains why the museum specimens are consistently smaller than live birds in the samples from the Argentine Islands, Signy Island and South Georgia. Second, mist-net-caught samples of birds from a breeding site will normally include many non-breeders (see Copestake and others, in press). Many of these are likely to be immatures that may not yet have attained adult size. The differences between the mist-net and known breeding bird samples from Bird Island exemplify this problem. Third, because males and females differ significantly in size, a sample with a biased sex ratio (e.g. those from Îles Kerguelen and South America) will also have biased measurements when compared with samples of equal sex ratio. king all this into account, it appears that the extent of the differences in measurements between the populations at the Antarctic continent (67–71° S), Argentine Islands (65° S), Signy Island (61° S), South Georgia (54° S) and Îles Kerguelen (49° S) are of similar magnitude and that there is no clear evidence of any disjunction. With a regular cline in measurements from big birds in the south to smaller ones in the north of the breeding range it may be inadvisable to attempt to recognize any subspecies. However, more data, ideally from sexed, live birds of known status, are required from all the most northerly populations (Îles Crozet, Îles Kerguelen, Falkland Islands, Cape Horn) before this hypothesis can be adequately tested.

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## REFERENCES

- ALVEY, N. G., BANFIELD, C. F., BAXTER, R. I., GOWER, J. C., KRZANOWSKI, W. J., LANE, P. W., NELDER, J. A., PAYNE, R. W., PHELPS, K. M., ROGER, C. E., ROSS, G. J. S., SIMPSON, H. R., TODD, A. D., WEDDERBURN, R. W. M. and WILKINSON, G. N. 1980. GENSTAT: a general statistical program. Rothamsted Experimental Station, U.K.
- BECK, J. R. and Brown, D. W. 1972. The biology of Wilson's storm petrel, Oceanites oceanicus (Kuhl), at Signy Island, South Orkney Islands. British Antarctic Survey Scientific Reports, No. 69, 54 pp.
- BOERSMA, P. D. and WHEELWRIGHT, N. D. 1979. Egg neglect in the Procellariiformes: reproductive adaptations in the fork-tailed storm-petrel. Condor, 81, 157-65.
- BOURNE, W. R. P. 1964. On the occurrence and nomenclature of certain petrels in North America. *Bulletin of the British Ornithologists Club*, **84**, 114–16.
- BROOKE, M. DE L. 1978. Weights and measurements of the Manx shearwater, *Puffinus puffinus. Journal of Zoology, London*, **186**, 359–74.
- COPESTAKE, P. G., CROXALL, J. P. and PRINCE, P. A. In press. Estimation of breeding population size in Wilson's storm petrel *Oceanites oceanicus* using mark-recapture and cloaca sexing techniques. *Ornis Scandinavica*.

- CROXALL, J. P. 1982. Sexual dimorphism in snow petrels. Notornis, 29, 171-80.
- CROXALL, J. P. 1984. Seabirds (In Laws, R. M., ed. Antarctic ecology, Vol. 2. London, Academic Press, 533-619.)
- CROXALL, J. P., McInnes, S. J. and Prince, P. A. 1984. The status and conservation of seabirds at the Falkland Islands. (In Croxall, J. P., Evans, P. G. H. and Schreiber, R. W. eds. The status and conservation of the seabirds of the world. Cambridge, International Council for Bird Preservation Technical Series No. 2.)
- DESPIN, B., MOUGIN, J.-L. and SEGONZAC, M. 1972. Oiseaux et mammifères de l'île de l'Est, archipel Crozet, Comité National Français des Recherches Antarctiques. No. 31, 1–106.
- DOWNES, M. C., EALEY, E. H. M., GWYNN, A. M. and YOUNG, P. S. 1959. The birds of Heard Island. Australian National Antarctic Research Expedition Reports, Series B, 1, 1–135.
- FALLA, R. A. 1937. Birds. Reports of the British, Australian and New Zealand Antarctic Research Expedition, Series B, 2, 1–304.
- FISHER, H. I. 1967. Body weights in Laysan albatrosses Diomedea immutabilis. Ibis, 109, 373-82.
- FOXTON, P. 1956. The distribution of the standing crop of zooplankton in the Southern Ocean. *Discovery Reports*, **28**, 191–236.
- GREEN, P. T. 1982. Sexing rooks Corvus frugilegus by discriminate analysis. Ibis, 124, 320-24.
- HARRIS, M. P. 1969. The biology of storm petrels in the Galapagos Islands. Proceedings of the California Academy of Sciences, 37, 95–165.
- HUNTER, I., CROXALL, J. P. and PRINCE, P. A. 1982. The distribution and abundance of burrowing seabin (Procellariiformes) at Bird Island, South Georgia. I. Introduction and methods. British Antaro Survey Bulletin, 56, 49–67.
- JAMES, P. C. 1983. Storm petrel tape lures: which sex is attracted? Ringing and Migration, 4, 249-53.
- KINSKY, F. C. and HARPER, P. C. 1968. Shrinkage of bill width in skins of some *Pachyptila* species. *Ibis*, 110, 100-2.
- LACAN, F. 1971. Observations écologiques sur le pétrel de Wilson (Oceanites oceanicus) en Terre Adélie. L'Oiseau, 41, 65–89.
- Mougin, J.-L. 1968. Étude écologique de quatre espèces de petrels antarctiques. L'Oiseau, 38, 1-52.
- MURPHY, R. C. 1918. A study of the Atlantic Oceanites. Bulletin of the American Museum of Natural History, 38, 117–46.
- MURPHY, R. C. 1936. Oceanic birds of South America. New York, American Museum of Natural History.
- MURPHY, R. C. 1960. Oceanic birds. Proceedings of the Royal Society of London, Series B, 152, 642-54.
- PRINCE, P. A., RICKETTS, C. and THOMAS, G. 1981. Weight loss in incubating albatrosses and its implications for their energy and food requirements. *Condor*, 83, 238–42.
- ROBERTS, B. 1940. The life cycle of Wilson's petrel Oceanites oceanicus (Kuhl.). Scientific Reports of the British Graham Land Expedition, 1, 141–94.
- SCHLATTER, R. P. 1984. The status and conservation of seabirds in Chile. (In Croxall, J. P., Evans, P. G. H. and Schreiber, R. W., eds, The status and conservation of the seabirds of the world. Cambridge, International Council for Bird Preservation Technical Series No. 2.)

Appendix 1. Measurements of breeding male (M) and female (F) Wilson's storm petrels at Bird Island, South Georgia, together with individual discriminant scores.

Sex	Bill length (mm)	Tarsus length (mm)	Wing length (mm)	Weight (g)	Discriminant score	Sex as determined by score
M	12.5		151		_	
M	11.9	34.1	153	32.0	1.114	M
M	12.9	34.2	148	33.0	0.642	M
M	12.1	34.6	151	36.0	0.998	M
M	12.3	34.0	154	33.5	0.432	M
M	12.7	35.0	149.5	34.0	0.293	M
M	12.4	35.6	157	38.0	-0.943	F
M	12.0	34.0	149.5	32.7	1.667	M
M	12.6	32.6	153	31.5	0.811	M
M	11.8	35.6	149	_	1.344	M
M	11.9	32.1	152	33.0	2.155	M
M	12.3	34.5	154	34.5	0.217	M
M	12.3	34.3	151	35.0	0.857	M
) i	12.4	35.2	151	31.5	0.336	M
M	12.5	33.6	152	33.0	0.702	M
M	12.4	35.0	148	34.0	0.975	M
M	12.7	34.1	149	35.5	0.771	M
M	11.8	33.6	143	30.0	3.308	M
F	12.9	_	151	-	_	_
F	12.5	34.9	160	_	-1.331	F
F	12.6	35.0	156	_	-0.771	F
F	12.8	35.5	157	43.5	-1.440	F
F	12.8	34.8	153	35.0	-0.402	F
F	12.3	33.9	152	31.0	0.843	M
F	12.7	37.3	154	36.0	-1.522	F
F	12.6	35.9	153	34.5	-0.603	F
F	12.3	35.8	152	33.5	0.029	F
F	12.7	35.4	152	37.0	-0.340	F
F	_	36.8	158	39.6	_	_
F	12.2	35.6	153	34.5	0.066	F
F	12.3	34.6	153	_	0.359	M
F	12.4	35.7	159	36.5	-1.354	F
F	13.3	37.2	161	37.5	-3.382	F
F	12.9	34.5	151	38.5	-0.040	F
F	12.8	36.1	161	38.0	-2.435	F
F	12.9	35.3	157	35.0	-1.489	F
F	13.1	34.4	152	34.0	-0.452	F
	12.3	35.0	158	34.0	-0.735	F
	12.4	33.2	153	36.0	0.824	M
F	12.6	37.1	154	37.0	-1.302	F