Breeding and survival of Snares Cape Pigeons *Daption capense australe* at The Snares, New Zealand

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ABSTRACT

We studied Cape Pigeons *Daption capense* at The Snares, one of its northern most breeding sites, from pre-laying to fledging during 1985/86 and 1986/87, and compared our data with those from other localities. At The Snares, mean laying dates were 10 November 1985 and 8 November 1986, mean hatching date was 25 December 1985, mean fledging date was 14 February 1986, breeding success was 58.7% in 1985/86 and 50.0% in 1986/87, and adult male annual survival was 94%. Laying mainly begins later at higher latitude breeding sites and there are differences in pre-laying colony attendance between some populations. Incubation and nestling periods are similar throughout the species' range suggesting an inherent rather than environmentally-induced explanation for the relatively short nesting season of fulmars compared to other petrels.

KEY WORDS: Fulmarine petrels, Snares Cape Pigeon, breeding chronology, survival, Snares Islands

INTRODUCTION

Typically, petrels are long-lived and their breeding biology is characterised by low reproductive rates, a result of delayed maturity and the production of just one large egg per breeding attempt. Most breed annually, at the same site and with the same partner (Warham 1990). The fulmars comprise seven species of robust, medium to large petrels which do not burrow when breeding (Warham 1990). Most aspects of their breeding are similar to that of other petrels. However, a major difference is that the time taken to complete the breeding cycle is significantly shorter than it is for other petrels of similar sizes (Warham 1990).

Two subspecies of Cape Pigeons (*Daption capense*) are recognised. The nominate subspecies *D. c. capense* has the more southern distribution and breeds on the coasts and islands of Antarctica, including Crozet, Kerguelen and South Georgia Islands (Turbott 1990). The darker Snares Cape Pigeon (*D. c. australe*) breeds only in the New Zealand region on the Snares, Bounty, Antipodes, Auckland (Turbott 1990) and Campbell Islands (G. Taylor, pers. comm. & see Kinsky 1969). In 1987 it was found breeding on The Forty Fours and probably also on The Pyramid and The Sisters, Chatham Islands (Clark 1989, Tennyson *et al.* 1993). Although *australe* are generally considered to be smaller than *capense*, biometrics do not show significant differences between the two subspecies (Marchant & Higgins 1990).

Breeding biology of the nominate subspecies is well known from studies at Dumont d'Urville, Terre Adélie (Prévost 1953, 1964; Mougin 1968, Isenmann 1970), Casey (Cowan 1979); Heard Island (Downes *et al.* 1959); Signy Island, South Orkney Islands (Pinder 1966); Nelson Island, South Shetland Islands (Weidinger 1996a, 1996b); and the Crozet Islands (Despin 1977). Survival estimates of breeding birds were calculated by Hudson (1966). In contrast there has been only one study of the breeding of the Snares Cape Pigeon, at The Snares from after laying until the completion of fledging (Sagar 1979). The aims of the present study were to:

1 provide information about the complete breeding cycle of Snares Cape Pigeons at The Snares;

2 estimate nest-site retention, divorce rate and survival of established breeders; and

3 compare these data with those available from elsewhere.

STUDY AREA AND METHODS

The Snares (48° 02'S, 166° 36'E) consist of North East Island (280 ha), Broughton Island (90 ha) and numerous islets and rock stacks. Precipitous cliffs (up to 120 m a.s.l.), often with ledges and jumbles of rock comprise most of the coastline. Snares Cape Pigeons breed on several of the islands, the largest concentrations occurring on the Southwest and North Promontories of North East Island, and on North Daption Rock. In 1976, a study colony of Snares Cape Pigeons was established on the northwest face of the North Promontory, North East Island (Sagar 1979). We used this colony during the present study.

The study colony was between about 20 and 50 m asl on a cliff face. The upper part of the colony had large boulders on less precipitous slopes and these were surrounded by peat and *Poa astonii* tussock. Lower down, the colony was on a vertical face with ledges and fissures.

We were on The Snares from 2 November 1985 to 10 March 1986, 22 October 1986 to 20 February 1987, and 7 November to 8 December 1987. Observations spanned the breeding cycle from pre-laying to fledging during 1985/86 and 1986/87, and the laying and early incubation period in 1987. In each of the three seasons, searches were made of the entire North Promontory for banded birds, and a search of the Southwest Promontory was made during November 1987. In addition, observations of nest-site attendance were made during July 1992 and July 1994.

In 1985, before laying started, 50 nest sites were marked with numbered plastic squares placed under rocks adjacent to each site. Observations on the same sites were continued each year, even after discontinued use by any particular pair of Snares Cape Pigeons. Adults attending each of these 50 nests were captured, measured, weighed, and banded. The sex of each bird was determined by examination of the cloaca shortly before or after laying (Serventy 1956).

During 1985/86 daily visits were made to the colony from 4 to 18 November, 21 December to 2 January, and 6 to 24 February, with further occasional visits between

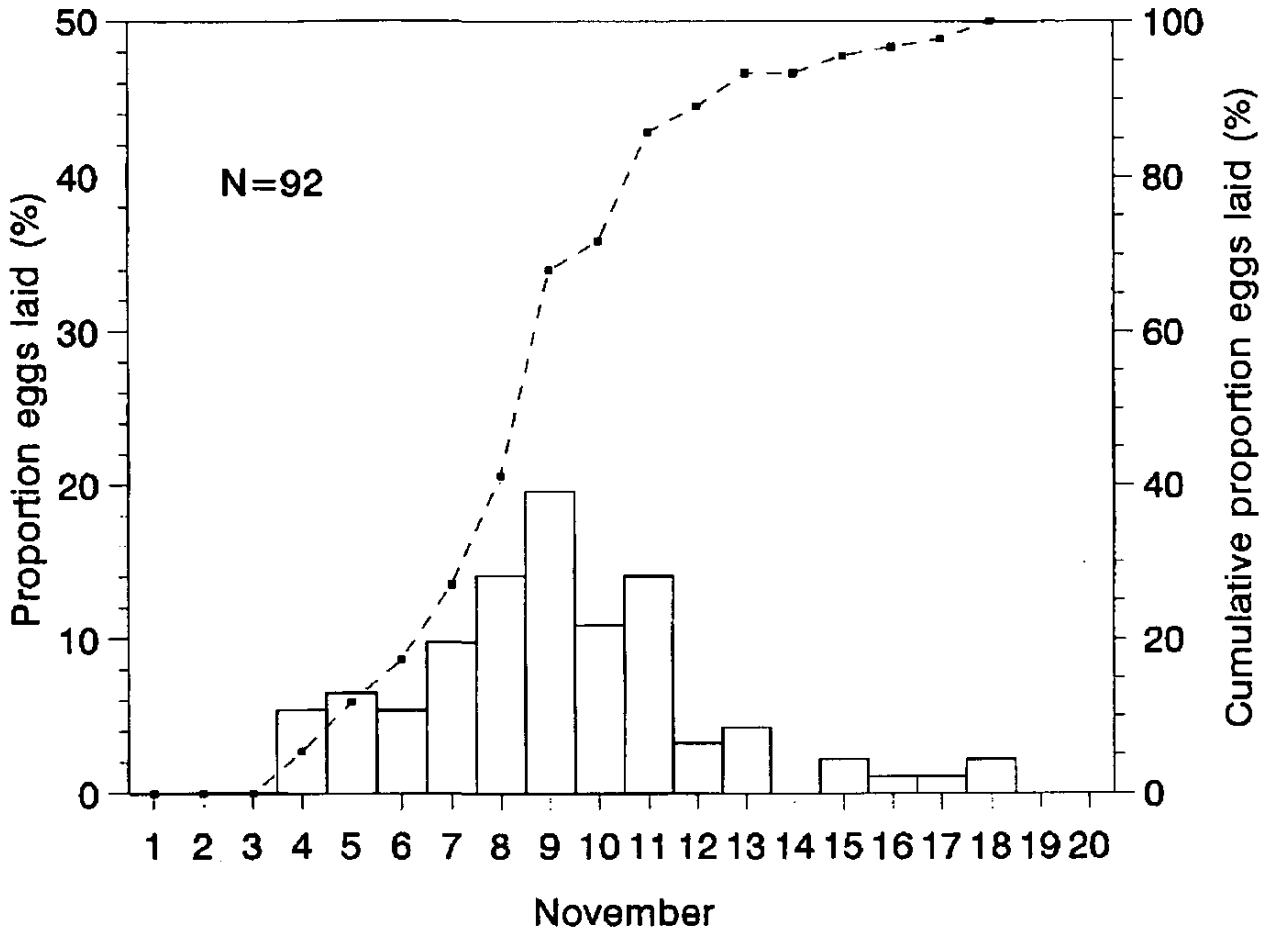

Figure 1 - Progression of egg laying by Cape Pigeons (*Daption capense*) at The Snares. Data from 1985 and 1986 are combined.

these periods. These visits enabled the days of laying, hatching and fledging at each nest to be recorded and chicks to be weighed prior to fledging. In 1986/87, the first visit to the study colony was made on 22 October. Daily visits were made from 4 to 15 November to record laying dates and then occasional visits were made until 31 January when all surviving chicks were banded. In 1987, visits to the colony were made every two days between 8 November and 6 December to monitor laying and recapture banded birds at marked nests.

Linear measurements of eggs were made using vernier calipers accurate to 0.1 mm. Eggs were weighed using a 100 g Pesola spring balance accurate to 1 g and egg volume index was calculated as length (mm) x breadth (mm) squared (LB^2); adults and chicks were weighed using a 1000 g Pesola spring balance accurate to 5 g.

Adult survival was calculated from the simple binomial expression of the minimum number known to be alive in the year(s) following banding. Statistics used are found in Zar (1984).

RESULTS

Pre-laying attendance at nest sites

There was a pre-laying exodus during late October. At the 50 nest sites checked on 22 October 1986, 23 (46%) were occupied by the male alone, 1 (2%) by

TABLE 1. Measurements (mean ± S.D., range) and tests of significance (ANOVA) of the eggs of Cape Pigeons (*Daption capense*) on The Snares.

Year & sample size	Length, mm	Breadth, mm	Mean egg volume index	Fresh mass, g
1985 (N=45)	61.4 ± 2.0	42.6 ± 1.1	111.4	61.0 ± 3.7
	56.4 - 62.3	40.6 - 44.7		54.0 - 68.5
1986 (N=42)	61.0 ± 2.0	42.5 ± 1.2	110.2	60.7 ± 4.0
	56.1 - 64.9	38.9 - 44.4		48.0 - 69.0
1987 (N=43)	61.4 ± 2.1	42.4 ± 1.2	110.4	60.3 ± 4.1
	56.6 - 65.6	39.2 - 44.6		47.0 - 70.0
	F=0.583, P>0.05	F=0.185, P>0.05	F=0.210, P>0.05	F=0.328, P>0.05

the female alone, and 1 (2%) by both birds; 25 (50%) of the nest sites were unoccupied. By 24 October, 35 (70%) of the nest sites were unoccupied, 12 (24%) were occupied by the male alone, and 3 (6%) by a pair of birds. On 26 October, 48 (96%) of the nest-sites were unoccupied and 2 (4%) were occupied by the male alone. On 4 November only nest sites where an egg had been laid were occupied and subsequently nest sites were occupied only as eggs were laid. Of those females that were seen at the site on 22 to 26 October the absence from the colony before laying averaged 13.6 days (S.D. = 3.7 days, range = 10-18 days, N = 5). On average, males were absent from the colony for 16.7 days (S.D. = 2.4 days, range 12-21 days, N = 28) before returning to undertake their first incubation shift.

Nest sites

Of the 50 nest sites, 21 (42%) were in the open on ledges or in fissures; 21(42%) were under rocks or in caves; and 8 (16%) were under overhanging *Poa astonii* tussock. Rainwater, draining off the rock face, flowed under three nests otherwise sheltered by rock overhangs.

Eggs and laying

Mean laying dates were 10 November 1985 (S.D. = 2.45 days, range 5-18 November, N = 46) and 8 November 1986 (S.D. = 3.18 days, range 4-18 November, N = 46), and so varied little between years. The laying period was short and extended over 13 days in 1985 and 14 days in 1986, with 93% of eggs laid within 10 days of the onset of laying (Figure 1). Egg dimensions and weight at laying were similar in all three years (Table 1). In 1985 there were four banded females in the study colony each with breeding experience extending back at least 15 years. For the three breeding seasons, the mean LB^2 and fresh mass of eggs of these older females were (114.7, 63.0 g) larger than those recorded for the study colony as a whole (111.4, 60.7 g), but the differences were not significant (ANOVA $F = 2.351$, $P > 0.05$; $F = 1.543$, $P > 0.05$ respectively).

TABLE 2 - Duration (in days) of completed incubation shifts in Cape Pigeons (*Daption capense*) on The Snares in 1985 and 1986.

Shift	Sex	Mean length, days	S.D.	Range	Sample size, N
1	Female	1.8	1.2	1 - 5	76
2	Male	5.0	1.9	1 - 9	33
3	Female	1.6	1.2	1 - 5	10
4	Male	1.7	0.9	1 - 3	3

TABLE 3 - Adult survival rates of Cape Pigeons (*Daption capense*) breeding on North East Island, The Snares. Birds at risk is defined as the number of banded birds known to be alive the previous breeding season (year n). Survival is the proportion of birds recaptured in year n+1.

Year	Variable	Males	Females	Total	G-test
1986	Birds at risk	50	48	98	
	Apparent deaths	3	4	7	
	Survival	0.940	0.917	0.928	0.003
1987	Birds at risk	49	48	97	
	Apparent deaths	3	11	14	
	Survival	0.939	0.771	0.856	4.424*
Total	Birds at risk	99	96	195	
	Apparent deaths	6	15	21	
	Survival	0.939	0.844	0.892	3.775*
G-test		0.005	4.002*		

*P<0.05.

Incubation and hatching

The incubation period in 1985/86 averaged 45.2 days (S.D. = 1.2 days, range 43-49 days, N = 33). Both adults shared incubation and, with the exception of the slightly longer first shift undertaken by the male, the duration of shifts was similar for both parents, at least during early incubation (Table 2).

The mean hatching date in 1985/86 was 25 December (S.D. = 3.1d; range 21 December - 4 January; N = 33). Starring of the shell surface began near the broader end of the egg. The chicks then took two to three days to emerge. For 30 eggs weighed freshly laid and at the first sign of starring, mean weight loss was 14.6% (S.D. = 4.5 range 7.9 - 27.6, N = 30).

Chick rearing period

In 1985/86, the mean duration of the nestling period was 50.1 days (S.D. = 2.4 days; range 45-54 days; N = 27). In 1985/86, the mean fledging date was 14 February (S.D. = 4.4d; range 5-24 February; N = 27). The mean mass of chicks declined from 488 g eight days before fledging to 382 g within a day of fledging (Figure 2).

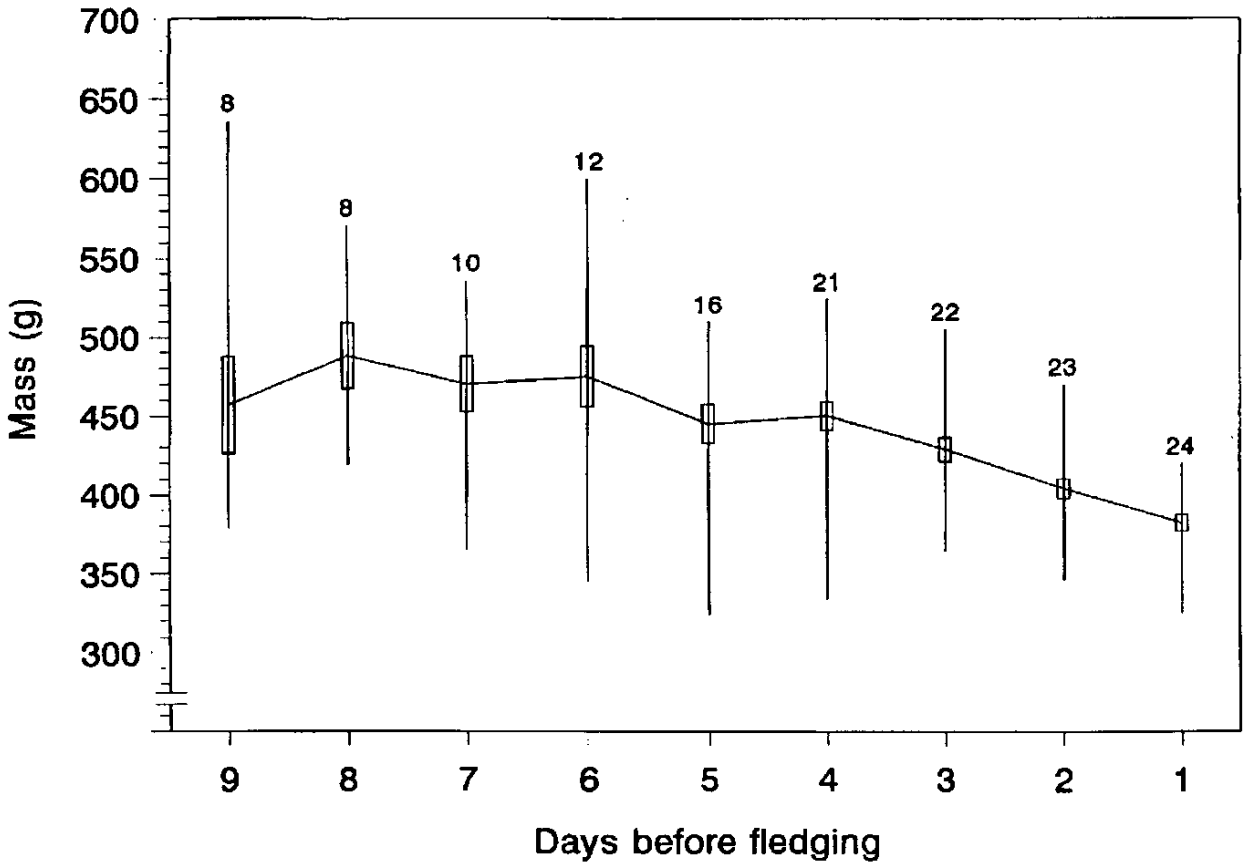

FIGURE 2 – Body mass of Cape Pigeon (*Daption capense*) chicks prior to fledging on The Snares, February 1986. Bar indicates one standard error, vertical line the range of body mass values.

Breeding success and causes of losses

In 1985/86, of 46 eggs laid in the study colony 33 (71.7%) hatched and 27 (81.2%) of these chicks fledged, an overall breeding success of 58.7%. Comparable figures for 1986/87 were 46 eggs laid, 39 (84.8%) hatched and 23 (58.9%) chicks fledged, an overall breeding success of 50.0%. Of the 20 eggs which did not hatch over the two seasons, 11(55%) failed to hatch after being incubated for >45 days, 3 (15%) disappeared, 3 (15%) were deserted early (<10 days) in incubation, and 3 (15%) chicks died after pipping the egg shell. Eggs which failed to hatch were incubated for up to 54 days before being deserted. In 1985/86 all chick deaths (N = 6) occurred within 26 days of hatching; 3 (50%) died 1-2 days after hatching. Observations at the study colony were too infrequent during 1986/87 to determine ages at which chicks died. However, three chicks in nests exposed to the weather died during a period of high (up to 20°C) temperatures in early January.

Divorce and nest site retention

During the period 1985-1987 there were 71 pair-years where the same partners were found breeding together. Two instances of divorce, where both previous partners were known to be alive, were recorded in the same period (one out of 42

pairs between 1985 and 1986 and one of 31 pairs between 1986 and 1987) which gives a minimum divorce rate of 2.7% (2/73) over the three breeding seasons. In some cases the disappearance of a partner does not necessarily indicate death, so actual divorce may be higher than this figure. There were ten instances where the male only was recorded again, five instances of the female only being recorded, and once neither partner was seen again.

Where the same partners were found breeding together in successive years they were always found at the same nest site (N = 71 pair-years). All 12 males which changed partners remained at the same nest site. Of seven females which changed partner, three (42.9%) retained the same nest site, but four (57.1%) changed nest site.

Adult survival and longevity

The two estimates of adult annual survival rate were 0.856 and 0.928 with an average rate of 0.892 overall (Table 3). However, there was a marked difference in annual survival rate by sex, with male survival higher than that of females (Table 3). Male survival was consistent in both years with a mean rate of 0.939 overall. In contrast, survival of females averaged 0.844 overall and was greater between 1985 and 1986 than between 1986 and 1987.

An adult female in the study colony had been banded originally at sea in Tory Channel (41° 14'S, 174° 15'E) in June 1961 as a bird of unknown age. This bird was last recaptured on 17 November 1987 when it was incubating, 26 years 5 months after it was first banded.

Non-breeding season activities

Winter observations at the study colony showed that pairs occupied nests and undertook nest construction (using pieces of granite, peat, or tussock) in July. On 31 July 1992 12 birds which had been banded as breeders in earlier years were recaptured; two of this total were known to be an established pair. Recaptures on 25 and 26 July 1994 included seven experienced breeders. Of the experienced breeders caught during these two years 11 were males and eight were females. In addition, six known-age birds, banded as pulli within the study colony, were recaptured at nests; these were 5 (2 birds), 7 (3 birds), and 9 (1 bird) years old (the timing of visits did not allow us to determine when known-age birds began breeding).

DISCUSSION

Breeding schedule of the Snares Cape Pigeon

Observations at The Snares during the 1976/77, 1985/86 and 1986/87 breeding seasons (Sagar 1979, this study) indicate that the breeding schedule of Snares Cape Pigeons varies little from year to year. In these three seasons the mean laying date varied from 8 to 11 November and laying extended over a maximum of 14 days. Synchronous laying between and within years is typical of highly migratory species and those which breed in high latitudes (Warham 1990).

The breeding timetable of Snares Cape Pigeons at its other breeding sites is poorly known, however, given that laying begins in early November at The Snares and all the recorded laying dates from more southerly colonies (noted below) are in mid-November, there is some indication of slightly later laying at higher latitudes. This latitudinal relationship has been noted for several other southern ocean seabirds (see Sagar 1979 & Tennyson 1991). At the Chatham Islands (44°26'S, 176°15'E) an incubating pair was seen on 28 November 1987 (Clark 1989). Laying at the Bounty Islands (47°46'S, 179°02'E) starts during the second week in November, with an egg noted on 9 November 1978 (Robertson & van Tets 1982). A chick was seen at the Bounty Islands on 12 January 1968 (Darby 1970). At the Antipodes Islands (49°40'S, 178°49'E) in 1995 one recently laid egg was found by A. Grant on 15 November and another was found on 17 November by A. MacIntosh (A. Tennyson unpubl.), "a freshly laid egg was recorded... between 19 and 20 November 1978" (Robertson & van Tets 1992), and many "occupied nests" were seen in late November 1978 (Imber 1983). At the Auckland Islands (50°50'S, 166°E) Wildlife Service staff found birds on eggs on 27 December 1972 (B.D. Bell, pers. comm.) and chicks were noted by G. Taylor (pers. comm.) on 8 February 1988. At Campbell Island (52°30'S, 169°11'E), an egg was laid between 16 and 18 November 1986 (G. Taylor, pers. comm.).

Egg size at The Snares

Egg size in petrels is affected by age (Warham 1990). For example, in Manx Shearwaters (*Puffinus puffinus*) egg size increased with the age of females until the birds were about ten years old, egg size then decreased in birds which were 15 years old or more (Brooke 1978). In contrast, in our study, the LB^2 and mass of eggs laid by females with experience extending back at least 15 years were not significantly different to eggs from the population as a whole. Egg measurements taken at The Snares in November 1976 (Sagar 1979) lie within the ranges recorded during this study.

Breeding success at The Snares

Breeding success in 1976/77 was 55.5% (Sagar 1979), similar to the 50.0% and 58.7% recorded during our study. As in 1976/77, weather conditions prevailing during the immediate post-guard stage appeared to affect the survival of chicks in exposed nests most. However, while in 1976/77 cool, wet conditions appeared to cause several chick deaths, in 1986/87 warm, sunny weather was associated with the death of chicks in exposed nests.

Mate & nest site retention

High retention rate of mates and/or nest sites is a feature of petrel breeding biology (Warham 1990). At Signy Island, 79% of *D. c. capense* nest sites were occupied by at least one member of the original pair in two successive seasons (Pinder 1966) and nest-site fidelity was 90% over two seasons at Nelson Island (Weidinger

1996b). During the three years of our study no male Cape Pigeons changed nest site, even though 12 had new partners in successive years. Although no females at The Snares changed nest site when they bred in successive years with the same partner, over 50% of those which changed partner also changed nest site. This behaviour probably reduces the chances of females being recaptured and may explain their lower estimated survival rates compared to males. For males at The Snares the estimated annual adult survival rate of 94% (this study) is the same as that calculated for male *D. c. capense* on Signy Island (Hudson 1966).

Timing differences between subspecies

The breeding biology of Cape Pigeons is similar throughout its range but there are some differences in the pre-laying behaviour between the population at The Snares and populations occurring further south. For example, at Signy Island and Terre Adélie males began reoccupying nest sites, following their pre-laying exodus, 5-6 days before the egg was laid (Pinder 1966, Mougin 1968), but at The Snares, males did not return until 1-2 days after laying. Consistent features in most populations include the short duration of the laying period, and little variation in laying dates from year to year (Prévost 1953, 1964; Pinder 1966; Mougin 1968, 1975; Despin 1977; Cowan 1979; this study).

Laying dates in the southern subspecies, even at the relatively northern Crozet Islands (46°S 52°E), are usually in the second half of November or first week in December (Prévost 1953; Downes *et al.* 1959; Pinder 1966; Mougin 1968, 1985; Isenmann 1970; Despin 1977; Van Franeker *et al.* 1990), compared to early to mid-November for the northern race. Pre-laying attendance at some southern populations is influenced by the break-out of ice and extent of snow cover at the nesting colonies (Prévost 1953, Pinder 1966), features which do not affect birds at New Zealand sites.

The short nesting season of Cape Pigeons

In petrels, incubation periods are highly correlated with egg size (Warham 1990). While following this trend, fulmarine petrels diverge from the general pattern by hatching their eggs more quickly than do similar sized non-fulmarine petrels (Warham 1990). Our calculations using data from three Cape Pigeon nesting sites support this conclusion. Mean fresh mass and LB^2 of eggs laid at The Snares are 60.7g and 110.7 respectively; 62g and 114.6 at Signy Island (Pinder 1966); and 67g and 116.6 at Terre Adélie (Mougin 1968). Incubation periods of 51.5 - 51.8d at The Snares, 51.6-52.1d at Signy Island and 52.2-52.3d at Terre Adélie are expected using the equations derived by Warham (1990) for petrel egg mass ($y = 26.68 \times ^{0.160}$) and LB^2 ($y = 25.32 \times ^{0.152}$). However, incubation periods at Signy Island (60° 40'S, 45° 38'W) and The Snares average 45 days (Pinder 1966, this study), while the average at Terre Adélie (67° S, 139° E) is reported as 44 or 45 days (Prévost 1964) and 47 days (Mougin 1968).

Nestling periods of Cape Pigeons are similar throughout their range with mean periods of *D. c. capense* ranging from 48 days at both Terre Adélie (Mougin 1968) and South Georgia (54° S, 38° W) (Croxall & Prince 1987) to 49 days at Signy Island

(Pinder 1966), while the average nestling period of. *D.c. australe* was 50 days. Warham (1990) has shown that fulmarine petrels raise their chicks much more quickly than do other petrels of a similar size.

The relatively short incubation and nestling periods of Antarctic populations of fulmarine petrels relative to other petrels of a similar size has been attributed to their access to dense concentrations of food and the continuous daylight which gives them more time to feed themselves and their chicks (Warham 1990). During the nestling period for Cape Pigeons nesting at The Snares the average daylength (taken as 30 minutes before sunrise to 30 minutes after sunset) is about 17 hours, substantially less than the continuous 24 hours daylight available to Antarctic populations. It is notable that despite this difference in daylength between Antarctic and Snares Cape Pigeon colonies, the incubation and nestling periods are very similar throughout their range. This suggests an inherent rather than environmentally-induced explanation for the relatively short nesting seasons of Cape Pigeons and possibly other fulmars.

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