

# TIMING OF BREEDING, BREEDING SUCCESS AND CHICK GROWTH IN SOUTH POLAR SKUAS (*Catharacta maccormicki*) IN THE EASTERN LARSEMANN HILLS, PRINCESS ELIZABETH LAND, EAST ANTARCTICA

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## ABSTRACT

Details are given of the breeding phenology, breeding success and growth of chicks, obtained during the 1989/90 summer in a small population of South Polar Skuas nesting in the Larsemann Hills (69°21'S, 76°00'E), Princess Elizabeth Land, east Antarctica. Eggs were laid from mid-November to mid-December (mean date 30 November), chicks hatched from mid-December to early January (mean date 26 December) and fledged from 5 February onwards (mean date 16 February). Breeding success in the 13 regularly monitored nests averaged 0.5 chicks fledged per pair, i.e. 0.26 per egg laid. Asynchronous hatching resulted in most first chicks (from first eggs) dominating their siblings; they grew faster and survived better than the second chicks, presumably as the result of more food. Second eggs were significantly smaller than first eggs, and egg size and volume gave rise to slight differences in mass at hatching; this did not appear to influence chick growth. Food availability, unfavourable weather conditions and predation by other skuas were the main factors influencing chick growth and successful chick rearing; the presence of sibling aggression may have reduced survival in second chicks. Breeding success in the Larsemann Hills is considered in relation to foods available from feeding territories or from station refuse; in the small samples available, those pairs with obvious territories or with access to refuse produced more chicks to the flying stage.

## INTRODUCTION

Aspects of the breeding ecology of the South Polar Skua (*Catharacta maccormicki*) have been studied at various sites within the Antarctic (e.g. Eklund 1961, Young 1963a, 1963b, Trillmich 1978, Peter *et al.* 1990). Such studies have shown that the timing of arrival at breeding sites varies, with those nesting at more southern sites appearing later (Le Morvan *et al.* 1967). Although egg-laying itself may vary only slightly throughout the species' range (Young 1977), being perhaps somewhat earlier at more southern sites (e.g. at Ross Island from 18-19 November to 27 December, Young 1963a, Spellerberg 1971) than at those further north (e.g. at Signy Island, from mid-December to early January, Hemmings 1984), it may be influenced by food availability (Jouventin & Guillotin 1979). There may also be a slight difference in the duration of the incubation period with latitude, those breeding further north showing 27 - 30 days (Hemmings 1984) whereas, further south, Young (1963a) gave an incubation duration of 28 - 29 days for most eggs at Cape Royd and Reid (1966) 24 - 35 days (mean of 29.5 days) at Cape Hallet. Near Davis, Hull *et al.* (1993) considered that the mean

incubation period was 28 days. Such minor differences may, however, reflect only observational variations. Nevertheless, breeding success itself differs from site to site, and between years (e.g. Young 1963a, Ensor 1979). Such variation may relate to local weather conditions, but may also reflect food availability and the influence of sibling aggression (Spellerberg 1971, Procter 1975, Ensor 1979). To date, there have been few studies of South Polar Skuas breeding away from Adélie Penguins (*Pygoscelis adeliae*) and details are generally lacking for areas where the skuas rely on other bird species for food.

In this paper, we report on results obtained during an examination of a small population of South Polar Skuas breeding in the eastern Larsemann Hills, Princess Elizabeth Land, east Antarctica. Details are given of breeding phenology, success, and the influence of egg size and hatching sequence on chick growth and survival. Results are discussed in relation to local conditions, including the availability of foods from stations within the area.

## METHODS

### Study area

The Larsemann Hills ( $69^{\circ}21'S$ ,  $76^{\circ}00'E$ ) is a relatively small, ice-free area south of Davis station ( $68^{\circ}35'S$ ,  $77^{\circ}58'E$ ), in east Antarctica (Fig. 1). Stuwe *et al.* (1989) and Gillieson *et al.* (1990) have provided details of the

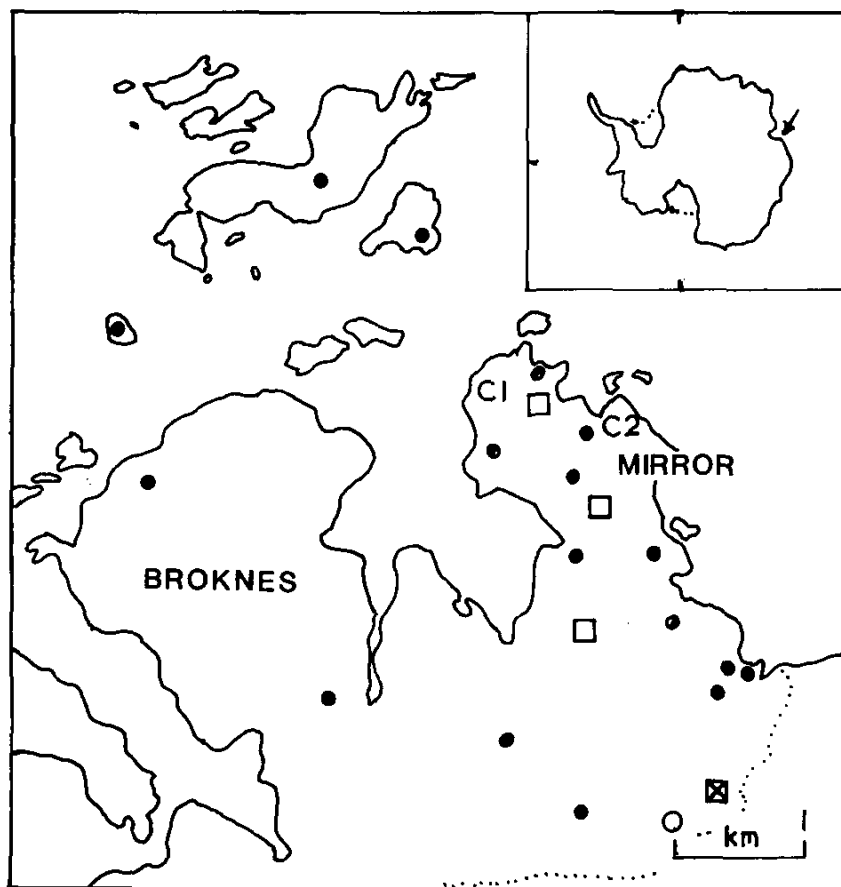


FIGURE 1 — The study area, Larsemann Hills, in relation to Antarctica generally. The approximate locations of nest sites are indicated (•), as are club sites (C1, C2) and the research bases (□).

physiography of the study area, which consists of a granitic country rock, deformed and considerably dissected by glacial and periglacial activity, resulting in an uneven landform incorporating valleys, hills, and icebound fjords. Lakes of varying size and salinity abound in the area. Weathering has caused bed rock fragmentation, crevicing, and unstable boulder slopes, in which Snow Petrels (*Pagodroma nivea*) and, less abundantly, Wilson's Storm Petrels (*Oceanites oceanicus*) nest (Wang & Norman 1993). The neighbouring polar ice sheet results in a stronger, more persistent katabatic wind, and temperatures are apparently lower than pertain at Davis (B. Lingen, pers. comm.). The study area presently (1991) supports two major (winter and summer) and one minor (summer) stations; a previous winter station, Progress 1, was abandoned in 1989, but all stations have been established on Mirror Peninsula since 1986 - 1987. Of relevance to this study is the absence of breeding populations of surface nesting petrels (e.g. Southern Fulmar *Fulmarus glacialisoides* and Antarctic Petrels *Thalassoica antarctica*) or penguins, although Adélie Penguins breed to the north and south of the Larsemann Hills, and there is a colony of Emperor Penguins (*Aptenodytes forsteri*) some 30 km away at Amanda Bay (Woehler & Johnstone 1991).

### Breeding and growth data

Initial surveys of the study area, bounded by Broknes and Mirror Peninsulas and the polar ice edge, were undertaken in the 1988/89 austral summer, during which period defended territories and some current nest sites were found. More detailed surveys of the area were made from October 1989 to late February 1990, and the area was briefly revisited in January 1991. In this period, 17 breeding pairs of South Polar Skuas were found on Broknes and Mirror Peninsulas and adjacent islands (Fig. 1). However, three nests (pairs 13, 16 and 17) were rarely visited; two sites (pairs 1 and 15, used in 1988/89) were not successfully resumed in 1989/90 and one site (pair 4) was first occupied in 1989. Data presented below relate primarily to 13 nesting pairs of skuas, at sites where both adults were marked before egg-laying in 1989/90. These nests were usually visited at 1 - 2 day intervals (except in bad weather) throughout the breeding period. Such visits were intensified around the expected hatching dates and before the expected first flying dates of young. Nesting pairs of skuas in the study area were classified as being associated with feeding territories which contained breeding Snow Petrels or as not having an obviously defended feeding territory (Wang & Norman 1993).

At the Larsemann Hills, skuas return to nesting areas mainly in mid-to late October (Wang 1991), as they do at other sites (e.g. Parmalee 1985), and observations on territory defence and reproductive behaviour were intensified around that time. In the study area there were at least two club sites (C1 and C2 in Fig. 1): these were frequently examined and birds present counted. Numbers at C1 were usually low (4 - 6 birds). Small numbers (5 - 8) were present at C2 in February 1989, and such totals then declined. In 1989/1990, skuas first appeared at C2 in mid-November and numbers increased in late November (maximum of 26); 20 - 28 skuas were present there from December to February. The club sites occasionally included birds which had lost eggs or chicks.

Lengths and breadths of eggs, once laid, were measured with vernier calipers (to 0.1 mm) and their internal volumes  $v$  (in mL) determined from  $v \# 0.00048 (\text{length} \times \text{breadth}^2)$  (e.g. Furness 1983). During nest checks, contents were noted and eggs were identified (and marked) as being laid first or second. Chicks were banded and weighed (to 1 g) when first found, and weighed at 3-4 days intervals thereafter, throughout the pre-fledging stage. As another measure of growth, the distance between the bill tip and the occipital condyles (condylo-basal length) was also obtained (to 0.1 mm) with calipers when chicks were weighed; this measure proved more reliable (and easier to obtain) in local field conditions than other parameters.

## RESULTS

### Egg parameters

The laying sequence was determined in 13 nests, and the hatching sequence for 21 eggs. On average, eggs were 70.02 ( $\pm$  s.d. 1.40, range 67.7 - 72.7,  $n = 21$ ) mm long and 49.91 ( $\pm$  0.87, 48.6 - 51.4) mm wide, and had a calculated internal volume of 83.81 ( $\pm$  4.51, 77.1 - 91.83) mL. First eggs were significantly longer and wider than second eggs (Table 1), and had greater internal volumes (paired  $t$ -tests,  $p < 0.01$  in each case,  $n = 8$ ). In individual nests, second eggs were on average 1.3 % shorter and 1.6 % narrower than first eggs, and were 3.9 mL less in volume. Regressions of length and breadth, for all first and second eggs (Fig. 2) indicate their general similarity, and first egg lengths and widths were strongly, and significantly, correlated with those measures for second eggs (e.g. for lengths, widths and volumes,  $r = 0.943, 0.891, \text{ and } 0.930, p = < 0.005, n = 8$ ).

### Breeding phenology and success

The first egg in the study area (pair 7) was found on 18 November, and the last egg was recorded (pair 4, second egg) on 18 December. For all eggs the mean laying date was 30 November  $\pm$  8.1 days ( $n = 21$ ); the mean laying date of 13 first eggs was 29 November  $\pm$  7.5 days (range 18 November - 12 December) and that for 8 second eggs 3 December  $\pm$  9.0 days (22 November - 18 December). In the eight nests where laying dates of both eggs were known, there was a mean of 4.6  $\pm$  1.6 (2 - 8) days between them. No relaying was recorded in any nest. The first chick (pair 7, first egg) was found on 14 December, and the last chick to be hatched was found on 11 January (pair 4, second egg). The first egg hatched 3.8  $\pm$  2.6 (2 - 8,  $n = 6$ ) days before the second. For first eggs, the mean hatching date of 25 December  $\pm$  7.1 days ( $n = 13$ ) was 25.8  $\pm$  1.1 days after laying; the incubation period for second eggs was 24.5  $\pm$  0.5 days resulting in a mean hatch date of 29 December  $\pm$  9.8 days. For all chicks found, the mean hatch date was 26 December  $\pm$  8.0 days (14 December - 11 January,  $n = 19$ ).

As last observations in the area were made on 22 February 1990, not all chicks were followed through to fledging (= flying). The first chick to fly, from nest 7, did so on 5 February; others were seen flying subsequently (and chicks present in nests on 22 February 1990 fledged; J.S. Burgess, pers. comm.). Fledging took an average of 53.2  $\pm$  1.0 days (range 52 - 55,  $n = 6$ ) for those chicks followed, with the mean date being 16 February  $\pm$  6.4

TABLE 1 — Length (mm), breadth (mm) and volume (mL) of first ( $n = 13$ ), second (8) and all (21) eggs ( $\pm$  s.d. and range) of South Polar Skuas measured in the Larsemann Hills, east Antarctica

		Length	Breadth	Volume
First egg	mean	70.48	50.28	85.6
	s.d.	1.31	0.84	4.3
	range	68.6 - 72.7	49.1 - 51.4	80.1 - 91.8
Second egg	mean	69.27	49.32	80.9
	s.d.	1.28	0.58	3.3
	range	67.7 - 71.7	48.6 - 50.2	77.1 - 86.7
All eggs	mean	70.02	49.91	83.8
	s.d.	1.40	0.87	4.5
	range	67.7 - 72.7	48.6 - 51.4	77.1 - 91.8

days. Assuming that two eggs were laid in each of the 13 nests (2 - 14) visited frequently, hatching success was 70.1%; this success was higher for first-laid eggs (92.3%) than for second (53.8%). Egg losses were not attributed, but most presumably were predated. Despite the relatively high hatching rate, chick survival to fledging was low; of the 19 losses (of eggs or chicks), 12 were of chicks and only seven (36.8%) fledged. First-hatched chicks (from first-laid eggs) were more successful (50%) than second-hatched chicks (14.3%). Three chicks were found dead (and eaten) in or around the nest sites (one had apparently starved, and at least one other died after a 3-day blizzard), and nine disappeared (one was killed, and one was eaten, by other skuas). The long blizzard may have caused the deaths of other chicks, left undefended afterwards while parents foraged for food. Success to fledging in this study was, therefore, 26.9% of eggs laid for the 13 study nests, i.e. 0.5 chicks per pair. The nesting area of pair 17, although defended, had no eggs or chicks in January 1989 but had a chick in January 1991; pair 16 had a chick in January 1991.

Sibling aggression may have resulted in deaths of some second chicks. In one instance (pair 4) the first chick, six days older than the second, pecked and chased its sibling away from the nest site. The second chick died seven days after hatching, with a body mass of only 77 g. At another site (pair

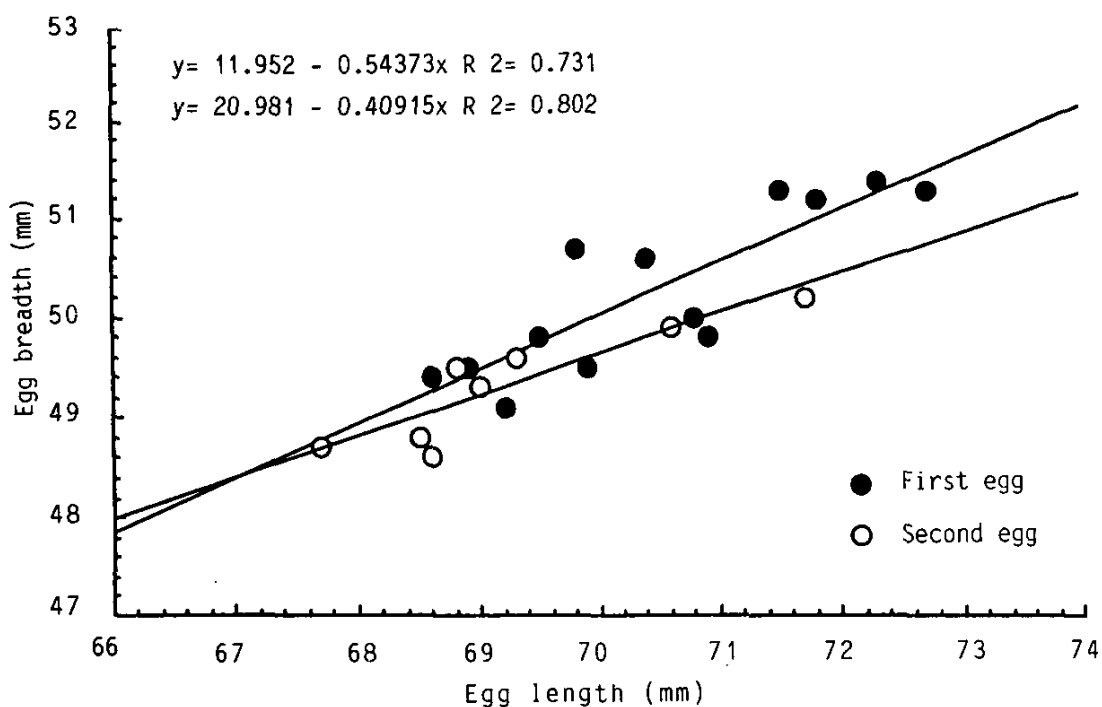


FIGURE 2 — Relationships between length and width (mm) in eggs of the South Polar Skua from nests in the eastern Larsemann Hills

5), the second chick was harassed away from the nest when 5 days old (108 g, i.e. only 70% of the sibling's mass) and moved some 80 m away. This chick had a substantially reduced body mass throughout its recorded life. Its body mass 19 days post hatching (23 January) was 273 g, 56% of its sibling's mass at the same age and 47% at the same time.

### Chick growth

Changes in body masses of known-age first and second chicks with time are summarised in Figure 3. Chicks from first eggs tended generally to have a higher absolute hatching mass ( $65.2 \text{ g} \pm 1.85$ , 62.0 - 68.0,  $n = 12$ ) than that of second chicks ( $62.7 \pm 1.75$ , 60 - 65,  $n = 6$ ), and the difference was significant (paired  $t$ -test,  $p = 0.0015$ ,  $n = 6$ ). Hatching body mass (g) in relation to calculated volume ( $v$ , in mL) was similar in both eggs (mean mass/volume for both series of eggs =  $0.76 \pm 0.02$ ), and the mass of the first chick at hatching was significantly correlated with that of the second chick ( $r = 0.881$ ,  $p = 0.02$ ,  $n = 6$ ). Nevertheless, the first chicks hatched were  $45.3 \pm 20.3 \text{ g}$  (28 - 80,  $n = 6$ ) heavier, and the condylo-basal lengths were some  $7.7 \pm 1.8 \text{ mm}$  (5.6 - 10.8) longer than that of the hatch mass or condylo-basal length of the second chick when it hatched  $3.8 \pm 2.6$  (2 - 8) days later; such differences between chicks increased with increasing chick age. Growth rates of either chick were not even throughout their development (Fig. 4). Fitting a logistic growth curve (Ricklefs 1967) to increasing body mass results in

$W$  (chick mass in g) =  $1255.4 / 1 + 22.6034 e^{-0.1518t}$  where  $t$  = chick age in days after hatching. The asymptotic mass of 1255.4 g is the mean

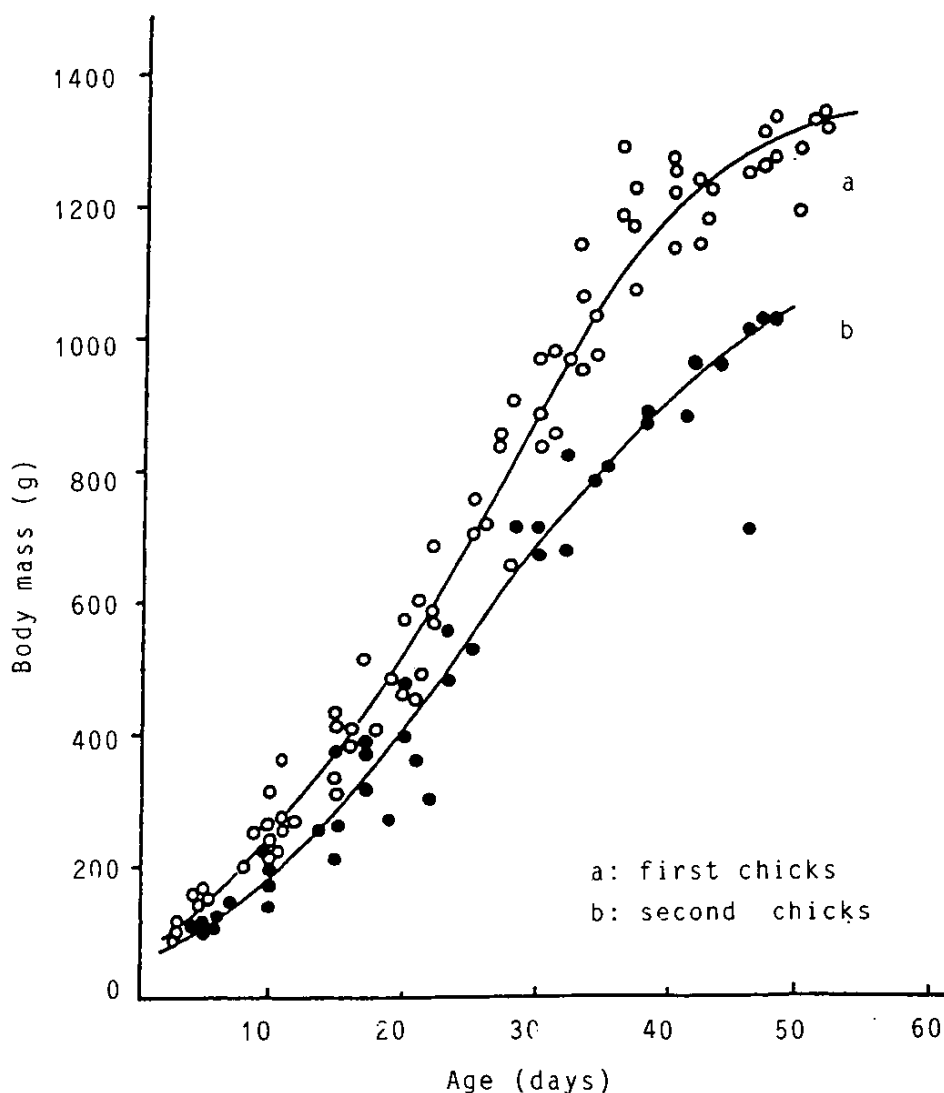


FIGURE 3 — Growth of known-age chicks, indicated by body mass (g), of South Polar Skuas hatched from first and second eggs (mean masses also indicated)

for fledging chicks at first flight. Mean daily body mass increased rapidly to about 20 days post hatching (and a mass of c. 628 g); daily incremental growth (mass) was then reduced. Thus body mass increased by a mean of  $22.5 \pm 4.1$  g/day ( $n = 10$ ) from 5 - 10 days of age and  $43.9 \pm 8.2$  g/day in the 20 - 30 day period post-hatching. However, this rate decreased to  $15.6 \pm 10.2$  g/day ( $n = 6$ ) when chicks were 40 - 50 days old, nearing the flying stage (Table 2). The changes in condylo-basal length in developing skua chicks also showed a similar pattern (Table 3). The increasing size of the condylo-basal length (Fig. 5) paralleled that of mass, to which it was well correlated for five chicks raised by pairs with ( $r = 0.976$ ,  $p = <0.0001$ ,  $n = 50$ ) or without feeding territories ( $r = 0.970$ ,  $p = <0.0001$ ,  $n = 56$ ).

Chick growth was apparently influenced by egg volume, and by the consequent hatching mass; calculated egg volume was significantly correlated with the chicks' initial body mass ( $r = 0.790$ ,  $p = 0.0022$ ,  $n = 12$  for first eggs;  $0.630$ ,  $p = 0.064$ ,  $n = 8$  for second eggs). Separation of the growth of chicks (indicated by increasing body mass or condylo-basal length) on the basis of original egg volume, i.e. those from eggs with volumes = >

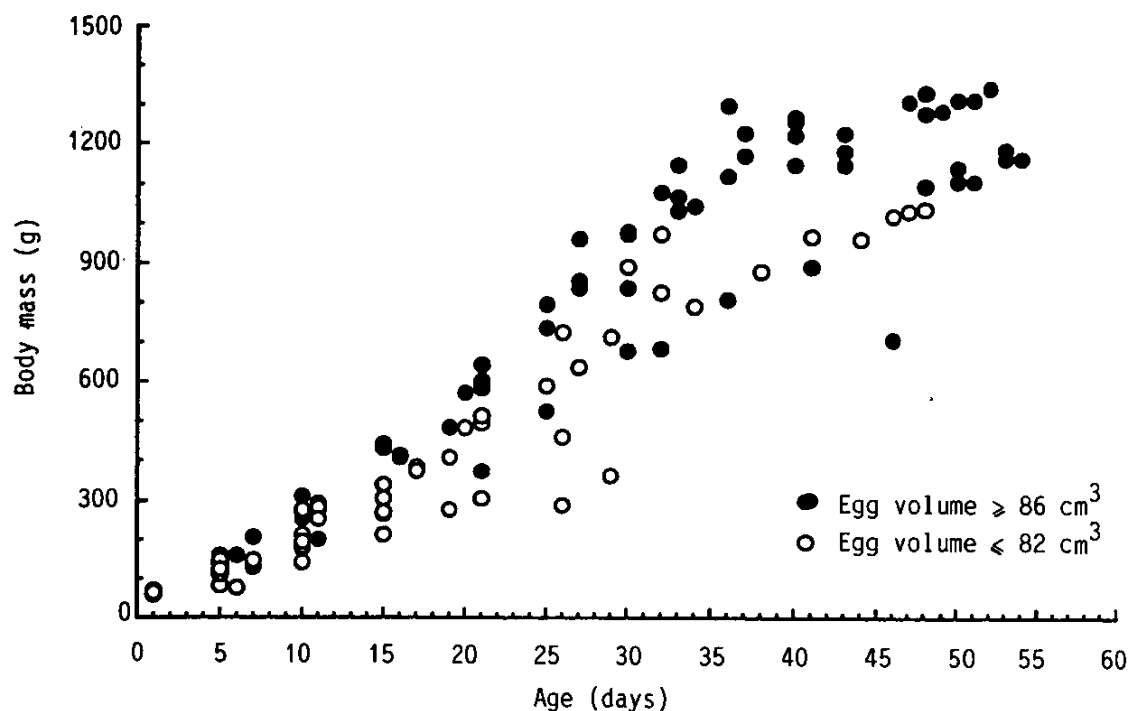


FIGURE 4 — Comparison of growth (increasing body mass, g) of known-age chicks of South Polar Skuas in relation to egg volume

TABLE 2 — Growth rates of chicks (g/day) of South Polar Skuas, Larsemann Hills, east Antarctica

	Age (days)				
	Hatching mass	5 - 10	11 - 20	21 - 30	41 - 50
<b>First chick</b>					
mean	65.1	22.5	26.5	43.9	15.6
s.d.	2.02	4.11	4.11	8.24	10.20
range	63 - 68	17.1 - 29.6	20.9 - 35.0	25.7 - 54.6	7.0 - 26.3
n	10	12	11	10	6
<b>Second chick</b>					
mean	62.7	10.5	19.3	31.5	10.0
s.d.	1.75	6.26	6.72		
range	60.0 - 65.0	0.4 - 18.2	16.0 - 29.3	28.3 - 34.3	
n	6	6	4	2	1



TABLE 3 — Mean increase in condylo-basal length (mm/day) in chicks of South Polar Skuas, Larsemann Hills, east Antarctica

	Age (days)				
	Hatching length	5 - 10	11 - 20	21 - 30	41 - 50
<b>First chick</b>					
mean	52.0	1.42	1.12	1.14	0.43
s.d.	1.34	0.28	0.19	1.14	0.14
range	49.3 - 53.7	0.9 - 1.9	0.9 - 1.3	0.7 - 1.7	0.3 - 0.7
n	10	12	11	11	6
<b>Second chick</b>					
mean	49.9	1.11	1.04	0.7	0.3
s.d.	2.34	0.36	0.35	0.50	
range	46.1 - 52.5	0.6 - 1.6	0.7 - 1.5	0.3 - 1.3	0.1 - 0.6
n	6	5	4	3	2

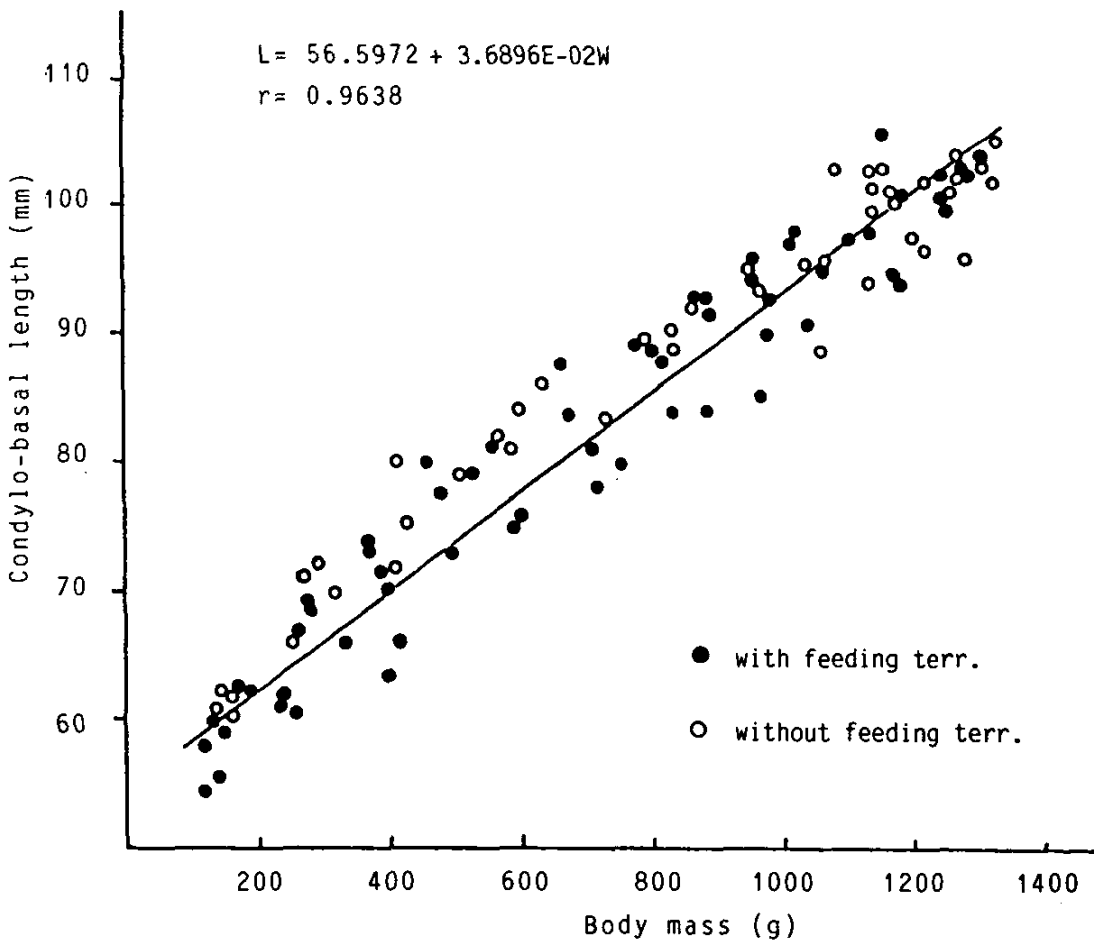


FIGURE 5 — Comparison of body mass (g) and condylo-basal length (mm) in chicks of South Polar Skuas. Details summarised for all chicks (regression line) and shown for those from pairs with or without feeding territories

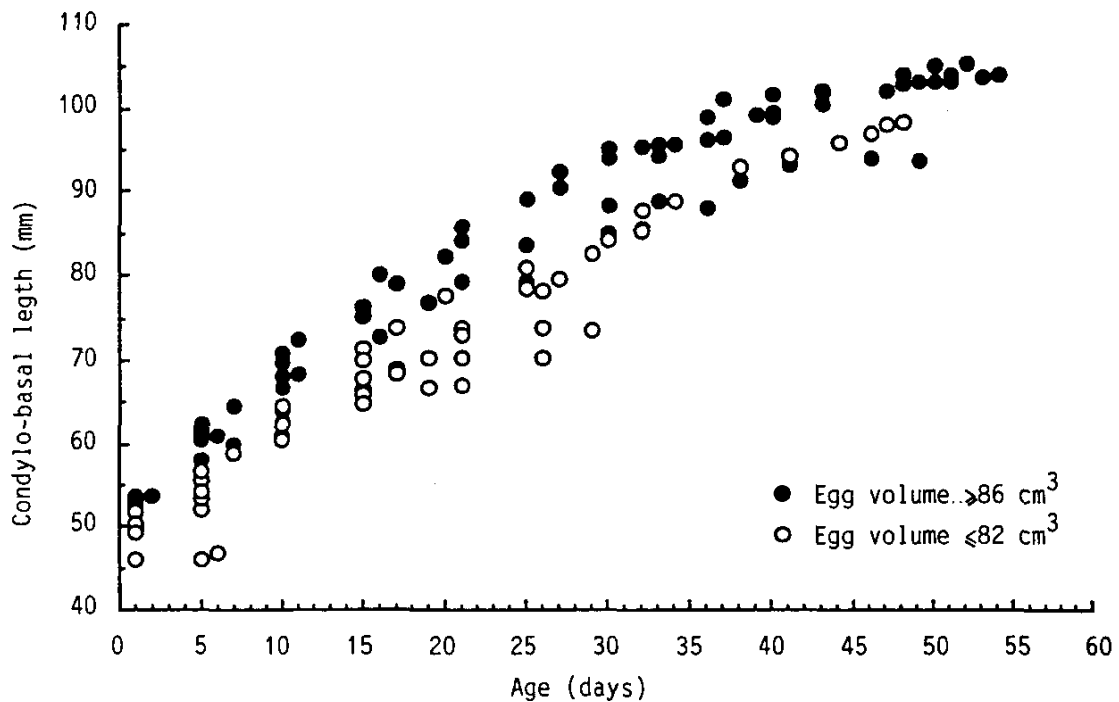


FIGURE 6 — Comparison of growth (increased condyllo-basal length, mm) of known-age chicks of South Polar Skuas in relation to egg volume

86 mL, and those = < 82 mL, suggests a general advantage (increased growth) for those hatching from larger eggs (Figs. 5 and 6). Although all but one of the seven chicks which fledged were hatched from larger eggs, and many chicks from smaller eggs failed to fledge, sample sizes were too small (and losses of eggs or chicks too high) to separate the influence of volume and egg-laying sequence.

### Success and growth in relation to site

Clearly, chick growth and development were also influenced by the ability of adults to provide adequate foods. Some chicks lost weight, failed to develop and died. In this study, only one pair (12) was successful in fledging both chicks (another, pair 7, raised a second chick to 48 days). Growth rates (body mass) for chicks in these clutches are summarised in Figure 7. In both cases, the second chick's growth, although lower, paralleled that of the first chicks, suggesting that food availability did not affect their survival directly or that extended foraging by both parents resulting in inadequate protection. Indeed, at least one adult was present around the nest area at every observation. Pair 7 apparently maintained a feeding territory which included breeding Snow Petrels (82% of food remains collected there were from that species; Wang & Norman 1993) whereas that at site 12 (where refuse from nearby stations comprised 71% of food items examined) had no such territory.

In this study seven pairs (pairs 5 - 9, 11 and 14) had obviously defended feeding territories. If each nest originally held two eggs, then 78.6% (11 eggs) hatched and 28.6% (four chicks) fledged, compared with 75% (eight) and 25% (three) respectively in nests (2 - 4, 10, 12 and 13) without feeding territories. In this small series of samples, nine chicks (75%) from first eggs

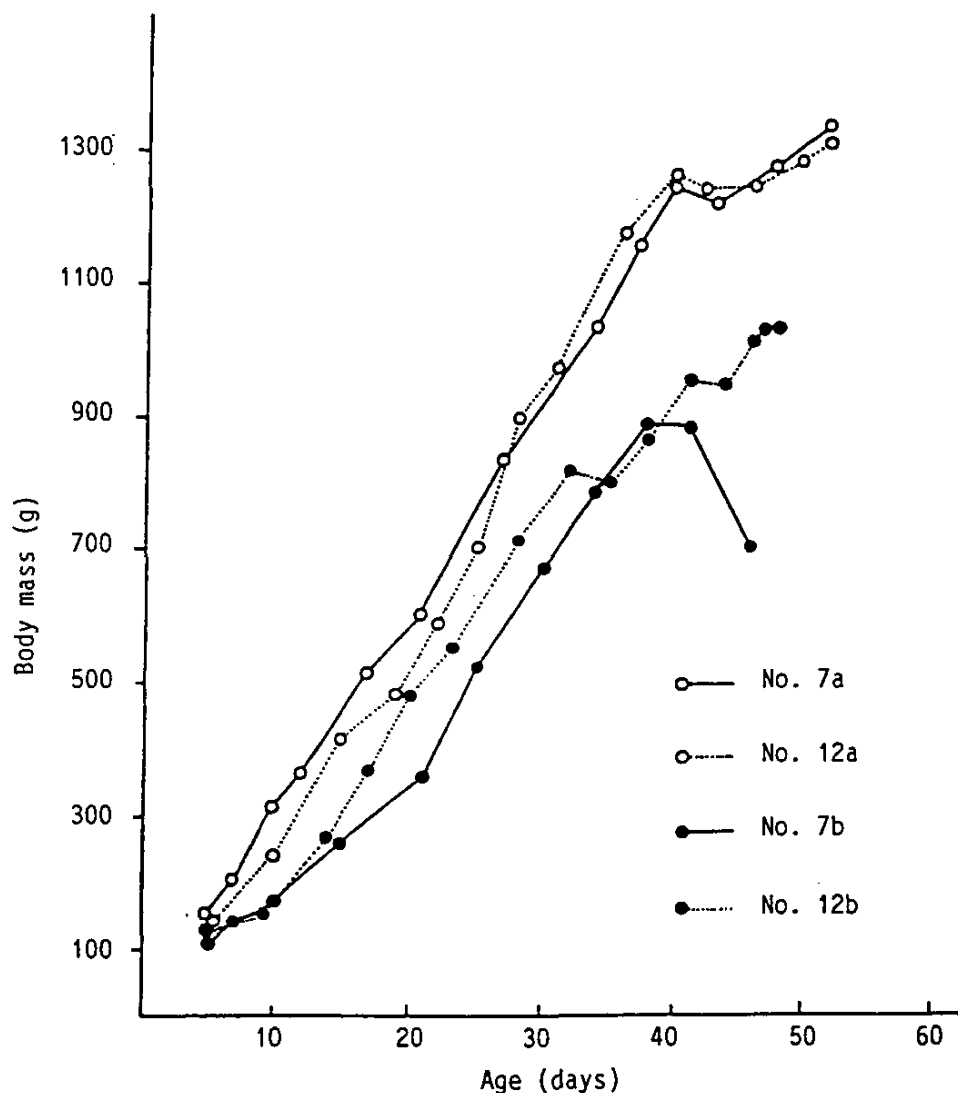


FIGURE 7 — Comparison of growth (body mass, g) of first (a) and second (b) chicks in nests where both chicks were raised to at least 48 days (pairs 7 and 12)

survived for at least 40 days compared with two (33.3 %) chicks from second eggs. At nest sites with feeding territories, foods returned showed a higher incidence of Snow Petrels than at those without territories. Mean daily mass increase (and condylo-basal length) was higher at nests with feeding territories (Table 4).

## DISCUSSION

The timing of breeding of South Polar Skuas, indicated by date of first egg, in the Larsemann Hills is similar to that reported at Magnetic Island, near Davis (Hull *et al.* 1993) and at Cape Crozier (Ainley *et al.* 1978). However, egg-laying dates vary: Hull *et al.* (1993) considered laying to take place from late (25) November to 7 December, whereas further south Ensor (1979) gave a mean date of 20 December at Cape Bird, on Ross Island, Ainley *et al.* (1978) a range from 17 November to 31 December, and Young (1963a) found half had been laid by 4 December. Incubation periods recorded in this study were about 25 or 26 days for each egg, somewhat similar to that found

TABLE 4 — Comparison of daily body mass (g) changes for chicks of South Polar Skuas with or without a feeding territory, Larsemann Hills, east Antarctica

Age (days)	Mean Change ( $\pm$ s.d.)	Nests with feeding territory <sup>a</sup>	Nests without feeding territory <sup>b</sup>
5 - 10	21.6 $\pm$ 2.41	27.6 $\pm$ 2.24	22.5 $\pm$ 1.41
range	17.3 - 26.3	25.2 - 31.7	20.8 - 23.8
n	11	6	5
20 - 30	43.9 $\pm$ 8.24	47.2 $\pm$ 6.57	40.7 $\pm$ 9.06
range	25.7 - 54.0	39.6 - 54.0	25.7 - 49.7
n	10	5	5
40 - 50	15.6 $\pm$ 10.2	21.5	15.1 $\pm$ 10.0
range	5.4 - 30.0	13.0 - 30.0	7.0 - 26.3
n	6	2	3

a = nests 5 - 9, 11, 14

b = nests 2 - 4, 10, 12

elsewhere (see above), and fledging took 53 days, less than the 60 days given by Hull *et al.* (1993) but approximating the 49 - 59 days found by Young (1963a).

The small variations in these parameters may reflect study methods (particularly sampling intervals), variations in ambient temperatures or indeed adult attendance (reflecting food availability). The restricted nature of the breeding period, similar over a wide range, has been related to the limited favourable climatic conditions (Young 1977). However, other seabird species breeding nearby, around Prydz Bay, have similarly restricted (and perhaps more synchronised) breeding periods (e.g. Antarctic Petrels or Southern Fulmars, Norman *et al.* 1992). Such restrictions may well reflect food availability, at about the time of optimum climate, rather than the climate itself; surplus food may lead to earlier fledging (Parmalee 1985) and access to excess foods (refuse) result in a substantial increase in the laying period of skuas (Jouventin & Guillotin 1979).

In this study, in contrast to that of Hemmings (1984), there was a significant size difference between first and second eggs laid by South Polar Skuas. Nevertheless, the minor differences in volume resulted in slight size differences in mean chick hatching mass and size. But these differences were irrelevant by comparison with mass and size differences caused by asynchronous hatching (here 2 - 8 days). The first chick (slightly larger at hatching) had already been fed for some days by the hatch of the second chick, and such differences result in subsequent differential growth and survival of siblings (e.g. Furness 1983, Pietz 1987). Indeed, in the Larsemann Hills first chicks were some 45 g heavier than second chicks as they hatched (cf. Young 1963a, 25 - 30 g); ultimately development of second chicks towards the fledging stage was reduced and unsuccessful (see also Spellerberg 1971, Procter 1975, Parmalee *et al.* 1978).

One consequence of the size differences in sibling chicks is the prevalence of sibling aggression. Previously reported in the South Polar Skua (Young

1963a, Burton 1968, Hemmings 1984), it has been suggested (Procter 1975) that such aggression occurs mainly as result of starvation. In favourable weather conditions, and with abundant foods, parents may adequately care for both chicks, and perhaps supply additional food to the second hatchling, resulting in its improved development (Procter 1975): breeding success may be high and growth of first and second chicks similar (Burton 1968, Hemmings 1984). Maintenance of a feeding territory, and one which supplies an adequate, consistent food supply, would seem to be an advantage in this species, particularly where otherwise food resources and weather may limit foraging.

Reported breeding success in the South Polar Skua varies substantially. Although hatching success was high in this study (at 70%) and similar to that reported by Hull *et al.* (1993), in Ross Sea colonies it may be as low as 20-24%, and egg losses there may exceed 75% (Young 1963a, Spellerberg 1971, Ensor 1979). Later losses may result in relatively few chicks being raised per breeding pair (e.g. 0.34, Wood 1971, cf. 0.5 this study, but 1.3 - 1.5 near Davis, Hull *et al.* 1993). Indeed, Reid (1967) considered that it was rarely possible for adults to provide sufficient food for two chicks; in the Larsemann Hills most losses occurred during chick rearing and only one nest produced chicks which both fledged. At Magnetic Island, though, most losses occurred (as a result of conspecific predation and weather) during incubation and the relatively high success was associated with the abundant food, the low density of breeding skuas and the apparent consequent reduced sibling aggression (Hull *et al.* 1993). Survival is also higher at northern sites (Hemmings 1984), where chick production can reach 1.03 chicks per pair (Peter *et al.* 1991).

In breeding areas elsewhere, South Polar Skuas may maintain both feeding and breeding territories within colonies of Adélie Penguins; those without such access may be forced to feed at sea (Young 1963a) as they do where sympatric with Brown Skuas *C. lonnbergi* (Pietz 1987). Possession of a feeding territory improves chick survival (Trillmich 1978) because in such areas weather may reduce food availability and materially influence breeding success (e.g. Ensor 1979). Decreased food availability may result in decreased attendance at nests, increasing the exposure of chicks to predation (Hamer *et al.* 1991). Skuas nesting in the Larsemann Hills are, however, without immediate access to penguins or other surface-nesting seabird species, the local area often has little open water (as a result, inshore at least, of the persistent pack ice and fast ice in embayments or fjords) and they do not fish locally (or return large quantities of marine foods to nest territories, Wang & Norman 1993). In the Larsemann Hills Snow Petrels are extensively used as a food resource by skua pairs with or without a feeding territory which includes breeding petrels, but food shortages occur, often as a result of bad weather. Given such restrictions, it is perhaps inevitable that alternative foods (human refuse from stations) are used and support (even enhance, Parmalee 1985) the breeding success of pairs with easy access to them. If foods (either from an established feeding territory or from refuse dumps) are readily available to parents, foraging times are reduced, and brooding and defence of eggs and chicks are correspondingly increased, with a consequent improved breeding success (Young 1963b, Trillmich 1978,

Trivelpiece & Volkman 1982, Pietz 1987, Hull *et al.* 1993). Under such conditions, sibling aggression may be reduced (Procter 1975).

In this study we have shown that South Polar Skuas, feeding mainly on Snow Petrels and refuse, lay within the locally optimal climatic conditions (when other potential prey species are also breeding). First-laid eggs, marginally larger than second eggs, hatch first and result in chicks advantaged by weight, food and perhaps appropriately refined experience by the time that the second chicks appear. This advantage is maintained throughout their growth and development, and may result in second chicks being effectively starved or exposed to predation by non-breeding skuas or those from neighbouring territories. We have shown too that, for this study period at least, breeding success in the Larsemann Hills was low in terms of chicks fledged; such success was primarily dependent on the fledging of first chicks from first-laid eggs. Losses occurred throughout the breeding cycle, particularly during chick rearing. Although generally unattributed, eggs and chicks disappeared (presumably as a result of predation); some losses were caused by weather and by associated starvation. Aggressive sibling behaviours may have also predisposed second chicks to such mortality factors (Procter 1975). However, the severity of local conditions (both food availability and climate), and the importance of holding an adequate feeding territory, may be indicated by the failure of some pairs to resume a nesting area from one season to another.

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