

## EGG SIZE AND EARLY NESTLING GROWTH IN THE SNOW PETREL<sup>1</sup>

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**Abstract.** I studied egg size variation, and the influence of egg size on early nestling growth, in Snow Petrels *Pagodroma nivea* breeding at Svarthamaren, Dronning Maud Land, Antarctica (71°53'S, 5°10'E). Egg sizes ranged from 36.4 to 52.1 cm<sup>3</sup>, with a mean of 44.9 cm<sup>3</sup>. Hatching occurred during 16–24 January, with a median hatching date of 20 January. Egg size had a significant effect on the body mass of hatchlings, explaining 30% of the variation in body mass of nestlings hatched within the last 24 hr, and 58% of the body mass variation of nestlings weighed while still slightly wet. An experiment, which included swapping of eggs between nests, together with analyses of non-manipulated nests, revealed an effect of egg size on nestling body masses at ages of two and four days. From the experiment, no effect of maternal quality as expressed by her egg size could be found. At an age of four days, 40% of the nestlings were left alone in the nest by their parents. Nestlings not attended by a parent at this age were significantly lighter than were those with parental company. Parents that had left their young by the time these were four days old may have been poor quality birds, as indicated by the tendency for such birds to have laid smaller eggs than had those still tending their young at the same nestling age.

**Key words:** *Antarctica; breeding synchrony; egg size; hatchling size; nestling growth; Pagodroma nivea; parental quality.*

### INTRODUCTION

Within individual bird species, egg size may vary considerably (Grant 1982, Greig-Smith et al. 1988). This variation has both a genetic (Boag and van Noordwijk 1987, Lessells et al. 1989) and an environmental component (Price et al. 1988). A number of studies have indicated that a benefit is gained by laying large eggs. Firstly, large eggs tend to result in large hatchlings, as has been demonstrated for many species (e.g., Parsons 1970, Nolan and Thompson 1978, Furness 1983, Stokland and Amundsen 1988, Grant 1991, review by Williams 1994). Secondly, nestlings hatching from large eggs tend to grow faster (Schifferli 1973, Williams 1980) and/or to have a higher survival rate (Davis 1975, Howe 1976, Thomas 1983) than small-egg nestlings. Since these general trends have been based primarily on descriptive studies, the apparent effect of egg size could either be due to egg size per se, or to parental quality, the latter being reflected in the size of eggs laid (Amundsen and Stokland 1990, Williams 1994). Several studies have demonstrated egg size to be positively related to maternal age (Wiggins 1990, Croxall et al. 1992, Weimerskirch 1992) or experience (Weimers-

kirch 1990, Thompson and Hale 1991, Sydeman and Emslie 1992), supporting the idea that egg size reflects parental quality. Recently, a few experimental studies aimed at separating effects of egg size per se, and of parental quality, have found an effect of egg size at early nestling ages (Amundsen and Stokland 1990, Reid and Boersma 1990, Magrath 1992). These studies also have demonstrated growth (Amundsen and Stokland 1990, Magrath 1992) and survival (Bolton 1991, but see Meathrel et al. 1993) to be influenced by parental quality (as expressed by the size of eggs laid). Taking the results of these studies together, (1) egg size seems in general to reflect parental quality, and (2) parental quality seems to be a more important determinant of nestling development than is egg size in itself.

The aim of the present study was to analyze the variation in egg size of Snow Petrels *Pagodroma nivea*, and its relationship to nestling growth during the early nestling phase. This was done primarily by analyzing descriptive data, but was also based on a small scale, egg-swapping experiment. Snow Petrels brood and guard their chicks during the first few days after hatching (Mougin 1968, 1975), probably until the chicks have developed a thermoregulatory capacity. Clearly, a trade-off exists between brooding/guarding the chick, and foraging at sea. This is

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particularly pronounced at inland colonies. Here, I present results on the relationship between nestling growth and parental attendance, and also explore potential determinants of the attendance patterns.

## STUDY AREA AND METHODS

The study was carried out at Svarthamaren (71°53'S, 5°10'E), Dronning Maud Land, Antarctica, during 10–24 January 1994. At Svarthamaren, about 500 pairs (Mehlum et al. 1988), or more (own observations), of Snow Petrels breed, mostly underneath boulders, or in crevices. The colony is situated in the Mühlig-Hoffmann mountain range, about 200 km from the continental ice shelf. Snow Petrels breeding at Svarthamaren thus have to fly at least 400 km during each feeding trip (Mehlum et al. 1988).

During 10, 11 and 17 January, I searched for accessible nests within a sub-plot of the Snow Petrel breeding area. I measured the length and breadth of each egg found (to the nearest 0.01 mm, using a digital caliper). Egg volume was calculated from the formula:  $\text{Volume (cm}^3\text{)} = 0.00051 \times \text{Length} \times \text{Breadth}^2$  (Hoyt 1979). Nests with eggs showing signs of hatching (egg shell cracking or punctured) were visited daily, mostly in the evening (20:00–24:00 hours). The hatching date could therefore be recorded, and any nestlings hatched since the previous visit weighed (to the nearest 0.1 g, using a Pesola spring balance). I noted whether the hatchlings were dry, or whether they were slightly wet or scruffy; the latter indicating that they had only hatched within the last few hours. I visited the nests once more when the nestlings were two days old, and, for a smaller sample of nests, also when the nestlings were four days old. The smaller sample at age four days was due to the fact that, as members of the 1993–1994 Norwegian Antarctic Research Expedition, we had to leave Svarthamaren on 24 January.

During the period when I was recording hatching body mass and early nestling growth (18–24 January), I also searched for additional nests to include in the study. Most nests found during this period still had unhatched eggs, and these were measured in the same way as were the eggs in nests found earlier. Some nests, however, did contain hatched chicks at the time of the first visit, with body masses ranging from 32.8 to 79.1 g. The hatching dates of these chicks were estimated from growth data for chicks of known age. These data were primarily used in the analysis

of breeding synchrony. In four nests, however, the nestlings were so small when found (<40 g) that they almost certainly had hatched on that day. These were included in analyses of nestling growth relative to egg size.

In a few cases, nests were not visited on the exact nestling ages (two and four days old), but on the preceding and following days. In such cases I have estimated the body mass on days two and four, respectively, as the mean of the masses when one day younger, and when one day older (i.e., assuming linear growth).

I further carried out a small-scale experiment aimed at separating the effects of egg size per se, and of parental quality, on nestling growth. Based on the first 66 nests found, I divided the nests into three egg size categories. Eggs belonging to the lower 33 percentile were termed "small," those in the 33–67 percentile "middle-sized," and those above the 67 percentile were termed "large." I then swapped large and small eggs between nests. Hatching and subsequent growth were recorded in four nests with small eggs swapped for other small eggs (S/S), four with small eggs substituted with large ones (S/L), five with large eggs swapped for other large eggs (L/L), and four with large eggs swapped for small ones (L/S). Nests with middle-sized eggs, and also some with large or small eggs, were not manipulated.

Statistical tests are two-tailed except when stated otherwise. Means are reported  $\pm$  one standard deviation (SD).

## RESULTS

### EGG SIZE

The mean length of the 113 eggs measured was  $56.5 \pm 2.2$  mm (range 51.0–62.3), and the mean breadth of the eggs was  $39.5 \pm 1.0$  mm (range 36.5–41.8). Egg volume, as calculated from measurements of breadth and length of the eggs (see the Material and Methods section), had a mean of  $44.9 \pm 2.9$  cm<sup>3</sup> (range 36.4–52.1). I found no correlation between the length and breadth of individual eggs ( $r = 0.008$ ,  $n = 113$ , NS).

### TIMING OF HATCHING

Hatching occurred between 16 and 24 January ( $n = 64$ ), with a median hatching date of 20 January. Additionally, five nests contained intact eggs that were either infertile, or hatched later than 24 January. Hatching was highly synchronous: 84% of the eggs hatched during the five-day period 18–22 January. Including only nests with directly observed (not estimated) hatching

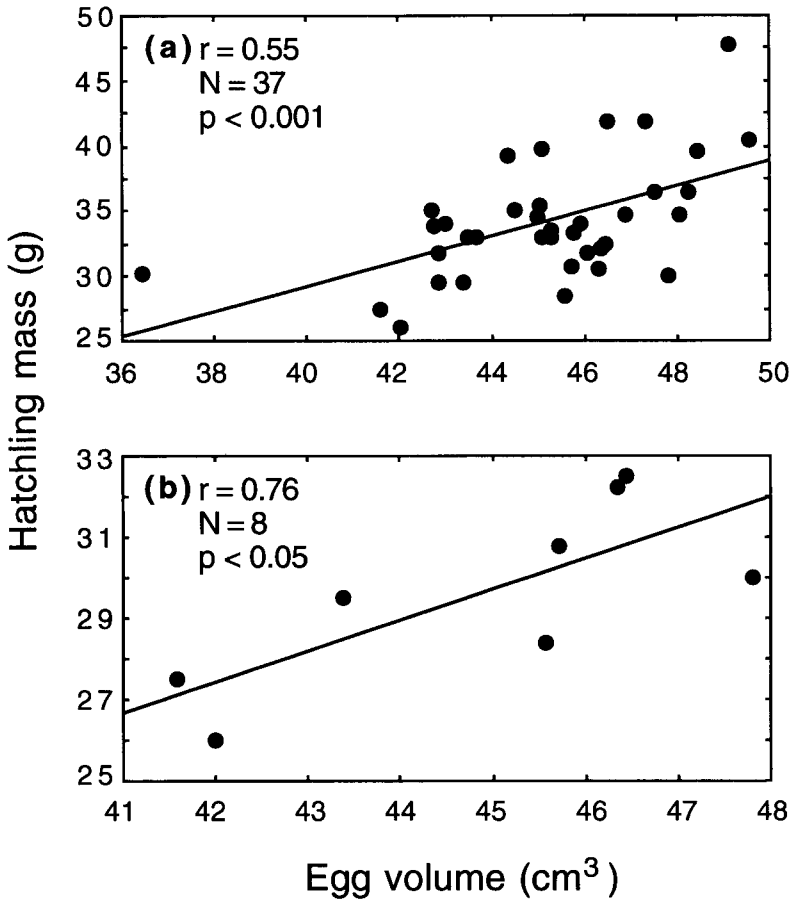


FIGURE 1. Relationship between egg volume and hatchling body mass of Snow Petrels breeding at Svarthamaren, Dronning Maud Land, Antarctica: (a) hatched within the last 24 hr, (b) wet or scruffy, i.e., hatched within the last few hours.

dates, I found no relationship between egg volume and hatching date ( $r = 0.05$ ,  $n = 37$ , NS). Nor did I find any relationship between egg size and the probability of successful hatching ( $t = 0.08$ ,  $df = 98$ , NS).

#### HATCHLING BODY WEIGHT

The mean mass of hatchlings (including only those nestlings known to have been hatched during the last 24 hours) was  $33.9 \pm 4.5$  g ( $n = 41$ ; range 26.0–47.7). When making the same analysis with the data only for the nestlings that were wet or scruffy at weighing time (i.e., hatched within the previous few hours), mean hatchling body mass was  $30.6 \pm 3.0$  g ( $n = 11$ ; range 26.0–37.1).

Hatchling body mass was significantly related to egg volume ( $r = 0.55$ ,  $n = 37$ ,  $P < 0.001$ ; Fig. 1a); i.e., egg volume explained 30% of the variation in hatchling body mass. An analysis of the

data for recently hatched nestlings (wet or scruffy) only, revealed that the variation explained by egg volume increased to 58% ( $r = 0.76$ ,  $n = 8$ ,  $P < 0.05$ ; Fig. 1b).

#### EARLY NESTLING GROWTH

The mean mass of nestlings aged two days was  $47.6 \pm 6.6$  g ( $n = 49$ ). The nestlings showed a mean daily mass increase of  $7.0 \pm 2.8$  g ( $n = 42$ ; Fig. 2) from hatching until two days old. Nestlings aged four days had a mean mass of  $57.7 \pm 13.3$  g ( $n = 33$ ), and had grown by  $5.2 \pm 6.5$  g ( $n = 33$ ; Fig. 2) per day during these two days. Note, however, that the mass development between days two and four proved to be strongly influenced by the presence or absence of the parents (see below).

Including only the data for the nestlings hatched from manipulated eggs (i.e., reared by foster parents), I found a significant influence of egg size

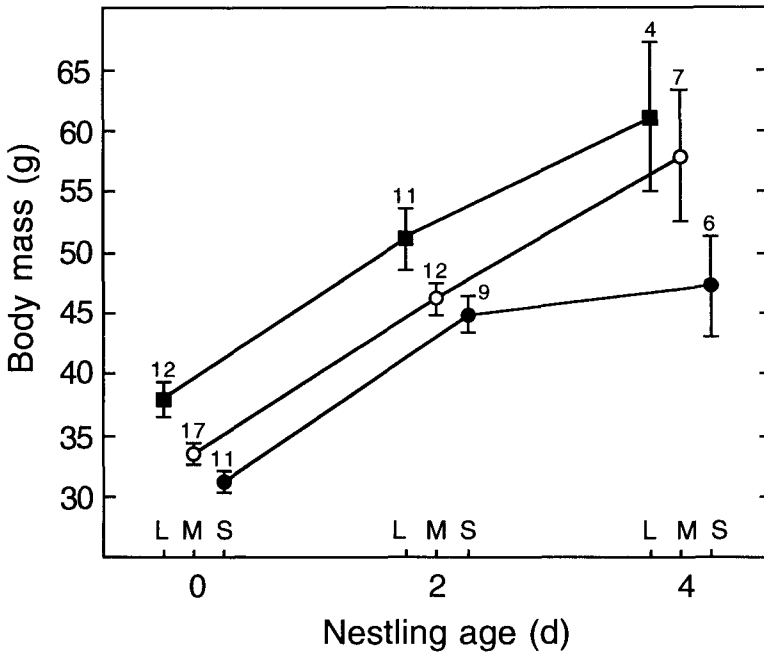


FIGURE 2. Mean nestling body masses ( $\pm 1$  SE) at ages of 0, 2 and 4 days, of nestlings hatching from small (S, filled circles), medium-sized (M, open circles), or large (L, filled squares) eggs. See Methods for definitions. Numbers above error bars indicate sample sizes.

(categories small vs. large) on hatching mass (ANOVA,  $F_{1,13} = 13.86$ ,  $P < 0.01$ ), and on mass when two days old ( $F_{1,13} = 5.94$ ,  $P < 0.05$ ). The original egg size of the foster parents did not influence nestling body mass at any of these stages (data not shown). Too few data were obtained for any analysis to be made of the body mass at day four for manipulated clutches. Since no effect of parental quality (as expressed through maternal egg size) was apparent, an analysis was made to investigate the potential influence of egg size on nestling growth, including the data for both the manipulated and the non-manipulated nests (but only for those with known, not estimated, hatching dates). This analysis revealed a significant effect of egg size on nestling growth during days 2–4 ( $r = 0.59$ ,  $n = 14$ ,  $P < 0.05$ ), and, in consequence, an effect of egg size on the body mass of the nestlings on day 4 ( $r = 0.67$ ,  $n = 14$ ,  $P < 0.01$ ).

#### TERMINATION OF BROODING/GUARDING

At the age of four days, 10 of 25 nestlings (40%) had been left alone by their parents. The body mass on day 4 of the nestlings still attended by a parent (mean  $63.5 \pm 13.5$  g,  $n = 15$ ) was significantly higher than that of the nestlings un-

attended by a parent (mean  $45.2 \pm 6.4$  g,  $n = 10$ ;  $t = 3.98$ ,  $P < 0.001$ ; Fig. 3). The two groups did not differ in regard to the mean volume of the eggs from which they had hatched (attended:  $45.2 \pm 1.6$  cm<sup>3</sup>,  $n = 6$ ; unattended:  $44.3 \pm 1.7$  cm<sup>3</sup>,  $n = 7$ ;  $t = 0.96$ ,  $P = 0.18$ , one-tailed), mean hatchling mass ( $32.6 \pm 3.1$  g,  $n = 13$  vs.  $34.0 \pm 3.2$  g,  $n = 10$ , respectively;  $t = -1.06$ ,  $P = 0.30$ ; Fig. 3), or mean mass at age two days ( $46.3 \pm 6.8$  g,  $n = 15$  vs.  $49.4 \pm 4.3$  g,  $n = 10$ , respectively;  $t = -1.28$ ,  $P = 0.21$ ; Fig. 3). However, the females of attending pairs (day 4) tended to have laid larger eggs than had the females of non-attending pairs ( $45.4 \pm 1.3$  g,  $n = 6$  vs.  $43.8 \pm 1.3$  g,  $n = 7$ ;  $t = 1.57$ ,  $P = 0.07$ , one-tailed). The difference in body mass at age four days seemed to be due to a difference in the mean daily growth rate during the preceding two days. While nestlings still attended by a parent on day four had a mean daily growth rate of  $8.6 \pm 5.3$  g ( $n = 15$ ), those not attended by a parent at the same stage had a mean daily body mass loss of  $2.1 \pm 2.6$  g ( $n = 10$ ), during the 2–4 day period (Fig. 3).

#### DISCUSSION

The eggs of Snow Petrels breeding at Svarthamaren were similar in size to those of birds

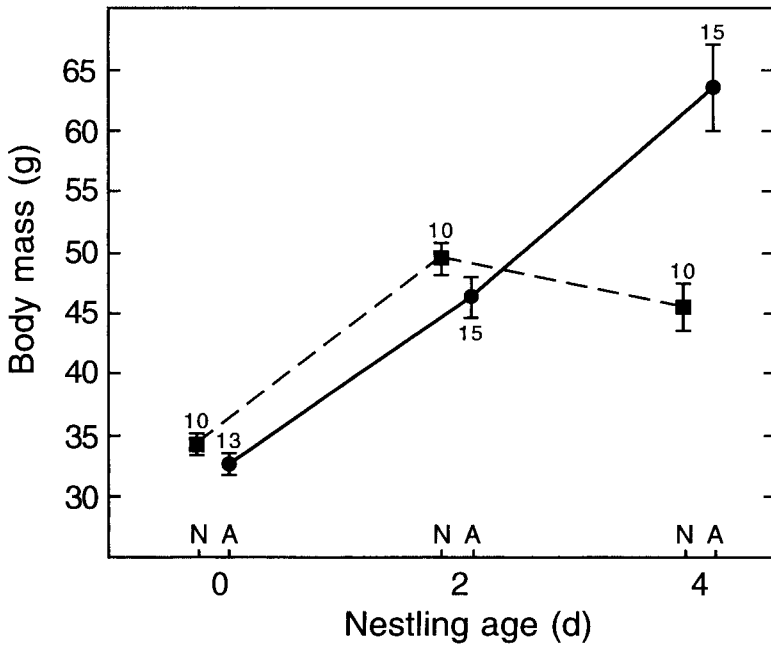


FIGURE 3. Mean nestling body masses ( $\pm 1$  SE) at ages 0, 2 and 4 days, of nestlings attended (A, filled circles) by their parents when four days old, and those not (N, filled squares) attended at the same age. Numbers above error bars indicate sample sizes.

breeding at Davis (Brown 1966), and at Cape Denison (Falla 1937), but were smaller than eggs of birds breeding at Dumont d'Urville (Isenmann 1970). The latter colony is considered to be a pure colony of the larger subspecies *Pagodroma nivea confusa*, whereas the colonies at Davis and Cape Denison, as also that at Svarthamaren, comprise birds of the smaller nominate subspecies *P. n. nivea* (Marchant and Higgins 1990). In fact, the adult size of Snow Petrels at Svarthamaren seems to be among the smallest recorded in any colony (Haftorn et al. 1988, Marchant and Higgins 1990). The mean size of eggs at Svarthamaren in 1994 (this study) was very similar to that of a small sample measured at the same site in 1985 (Mehlum et al. 1986).

Warham (1990, p. 283) has analyzed the general relationship between female body mass and egg size in procellariiform birds. The mean egg size recorded at Svarthamaren was 22% greater than that expected from Warham's (1990) general function, showing that Snow Petrels lay relatively large eggs for their body size.

Hatching of the chicks was highly synchronous, with 84% hatching during a five day period (18–22 January). Synchrony in breeding seems to be a general feature of the Snow Petrel, cf.

Marchant and Higgins (1990, p. 407) who reported laying to be "well synchronized." Breeding synchrony could either be a reflection of the time span available for breeding being restricted, or it could be a means of predator swamping. Concerning the first of these points, the breeding areas probably have to be relatively free of snow for egg-laying to take place, while at the end of the breeding season the young need to become fledged before the sea-ice starts to freeze (the latter resulting in an extraordinarily long flying distance when leaving the nest, as well as a reduction in suitable feeding areas).

I found the mean body mass of recently hatched nestlings to be 30.6 g, and the mean mass of nestlings hatched within the last 24 hr to be 33.9 g. This is about 10 g, or 25%, lower than the hatching body mass recorded at Dumont d'Urville (Mougin 1968, Isenmann 1970), which are the only other data for hatching body mass of this species that I know of. These body mass values, however, are not directly comparable, since the birds at Dumont d'Urville belong to the larger subspecies *confusa* (Marchant and Higgins 1990). The difference in mean hatching body mass for the two colonies (25%) roughly reflects the corresponding difference in egg size (18%).

In the present study, egg volume explained about 30% of the variation in body mass of chicks hatched within the last 24 hr. When the analysis was restricted to nestlings that were still slightly wet or scruffy when found, the value increased to almost 60%. I have no evidence that might indicate how long it takes for a Snow Petrel hatchling to expand its down completely, but I assume that it is a question of only a few hours. Perhaps the average age of these nestlings may be 1–2 hr, whereas the average age of all nestlings hatched within the last 24 hr would be approximately 12 hr. This suggests that nestling mass increases by about three grams during the first 10 hr, or by about eight grams during the first day of life. This is similar to the mass gain observed during the immediately following days. Since the proportion of the variation in body mass explained by egg size decreases rapidly with nestling age, it is evident that the initial growth rate is not related to egg size to any considerable extent.

I found that egg volume had a significant effect on nestling body mass at ages of two and four days, respectively. Probably, this is primarily a reflection of differences in hatchling body mass. It is noteworthy, however, that egg volume significantly influenced the growth rate between days two and four (but not between days zero and two).

In my attempt to separate the effects of egg size per se, and of parental quality (as expressed by the size of eggs laid), I did not find any evidence of an effect of parental quality on growth up to an age of four days. However, this result is not very conclusive, since the sample sizes in my egg swapping experiment were very small.

At an age of four days, nearly half of all the nestlings had been left alone in their nests. This is a relatively young age for termination of brooding and guarding, compared with results from Davis (Brown 1966), Robertskollen (Ryan and Watkins 1989), and Dumont d'Urville (Mougin 1968, 1975). Robertskollen is an inland colony in western Dronning Maud Land (71°27'S, 3°15'W). Like Svarthamaren and Davis, it is inhabited by birds of the smaller subspecies. Chicks at these three colonies would, at equivalent ages, be more vulnerable to chilling than those of the larger subspecies breeding at Dumont d'Urville.

Nestlings found to be alone at the age of four days were significantly lighter than were those that were still attended by a parent. The data

from the present study allow no firm conclusion to be drawn as to whether the low body masses were a consequence of the parents having already left the nest, or their cause, but the former seems more plausible. Those parents that had left their chicks alone at or before a nestling age of four days tended to have laid small eggs themselves, suggesting that these may have been low quality birds. They were thus perhaps less able to withstand long fasting periods, and were forced to leave their young while at an early age, in order to collect food for themselves and for the chick. Despite no observed effect of parental quality on nestling growth, these findings suggest that egg size, to some extent, reflects parental quality in Snow Petrels.

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