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Body size and determinants of laying date variation in the Snow Petrel *Pagodroma nivea*

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We studied several determinants of laying date variation and the relationship between laying date and reproductive success in the Snow Petrel *Pagodroma nivea*. The effects of female body size and condition, year, individual laying period, colony size, mate fidelity, previous reproductive success, and duration of the pre-laying exodus on laying date, were investigated during a 3-year study. The average laying date was 4 December. The laying period was compressed into 10–16 days and was very constant from year to year, both for the population as a whole and for individual females. The laying period of individual females varied from year to year on average by less than one day. Body size explained 24% of the variation in laying dates, with large females laying their egg later than small ones. Laying in large colonies occurred c. 2 days later than in small colonies, mainly because a higher proportion of large females bred in large colonies. There was no effect of mate fidelity, age, body condition and previous reproductive success on laying date, but the duration of the pre-laying exodus was strongly correlated with laying date. Smaller females had shorter pre-laying exodus (c. 17.7 days) than larger ones (c. 20.4 days). During the three years of the study reproductive success either increased, decreased or did not vary with laying date. Although body size is not maintained by selection on laying date alone, the genetic body size component of this species suggests that balancing selection on body size may act through laying date.

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Among birds, intrapopulation variation in the timing of laying has received considerable attention as laying date might influence several life-history traits such as survival of offspring or fecundity (Lack 1968, Perrins 1970, Daan et al. 1989, Rohwer 1992). In seabirds, factors that have been shown to affect laying dates include age or experience (Coulson 1966, Coulson et al. 1969, Fisher 1969, Harris 1973, Davis 1975, Coulson and Horobin 1976, Brooke 1978, Ollason and Dunnet 1978, Gaston 1992, Weimerskirch 1992, Hipfner et al. 1997), change of partner (Coulson 1966, Fisher 1969, Mills 1973, Brooke 1978), outcome of the previous breeding attempt (Rechten 1986), body condition (Weidinger 1996), and feeding conditions during the pre-laying period (Astheimer 1986). Body size is known to influence laying date among passerines (e.g. Murphy 1986), but very few studies have investigated the role of body size on laying date in seabirds (but see Weidinger 1996, León de et al. 1998), and none has found a relationship between these two life-history traits. Relationships between body size and life-history traits at the intraspecific level are relatively difficult to detect among birds because the range of body sizes within species is generally small compared to other taxa (Calder 1984, Schmidt-Nielsen 1984).

The Snow Petrel *Pagodroma nivea* is an abundant Antarctic seabird (Ainley et al. 1984) with a circumpolar distribution (Croxall et al. 1995). A peculiarity of this small fulmarine petrel is its high intrasexual variability in body size; some authors consider that the species can be separated into two subspecies, the large *P. n. major* and the small *P. n. minor*, which are

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sympatric in some localities (Isenmann 1970, Cowan 1981, Jouventin and Viot 1985, Barbraud and Jouventin 1998). Females are smaller than males (Croxall 1982, Barbraud and Jouventin 1998), birds are monogamous and both mate and site fidelity are strong (Brown 1966, Guillotin and Jouventin 1980). Like all Procellariiformes species, the Snow Petrel lays a single egg (Warham 1990). Although many studies have focused on size variation and the breeding biology of this species (reviewed in Warham 1990, Chastel et al. 1993, Barbraud and Jouventin 1998), no study investigating the relationships between body size and other life-history traits has yet been published. The Snow Petrel's large intraspecific size range provides an opportunity to examine the within-species effects of body size on life-history traits.

At Terre Adélie, the variability in body size is significant (Barbraud and Jouventin 1998), and allows the relationship between body size and laying date to be analysed. In this paper, we present data on laying date of Snow Petrels breeding at Terre Adélie in three consecutive years and examine several factors, including female body size, that may explain variability in laying date. We also investigate the relationship between laying date and reproductive success to determine the fitness consequences of laying-date variation.

Materials and methods

The study was conducted at Dumont d'Urville (66°40'S, 140°01'E), Terre Adélie, Antarctica, during the austral summers of 1993/94, 1994/95 and 1995/96. Nests ($n = 121$) were marked and visited daily during the pre-laying and laying periods. Birds were marked with a stainless steel ring and sexed on the basis of their sex-specific call. Males' voices are pitched lower than those of females (Guillotin and Jouventin 1980) when approached on the nest or handled. Measurements taken were bill length, bill depth, tarsus length and wing length for each female (Appendix) and male (see Barbraud and Jouventin 1998 for details). As univariate metrics may be inadequate as measures of overall body size in birds, we used the first component (PC1) of a principal component analysis (Freeman and Jackson 1990). Males ($n = 94$) and females ($n = 121$) were analysed separately. The first component accounted for 74% and 80% of the total variance in males and females respectively, and was highly correlated with all variables (r between 0.77 and 0.92, $P < 0.001$). PC1 scores increased with the size of the birds.

To explain the variability in laying date of the Snow Petrel we studied the effects of year, individual laying period, colony size, body size, body condition, mate change, previous reproductive success and duration of the pre-laying exodus on laying dates. The effects of year, colony size, body size, and their interactions were tested using a General Linear Model (SYSTAT 1997). The effects of colony size on laying dates were tested by categorising all nests into three groups, viz. whether they were part of large colonies (> 20 pairs), small colonies (from 2 to 20 pairs) or isolated. As repeated measurements (over several years) of individual females' laying dates were available we estimated laying periods of individual females, since these periods will give an indication of the amount of laying date variation that can potentially be attributed to fixed female characteristics. Individual laying period was calculated using the deviation from the mean laying date for each individual over the three years (all colonies pooled). Laying dates were normally distributed (one-sample Kolmogorov-Smirnov test, $D_{max} = 0.08$, $P = 0.16$). Repeatability of laying date was also estimated using variance components calculated from mean squares values obtained from one-way ANOVA (Lessels and Boag 1987). Few birds changed partners ($n = 10$), and the effect of partner change on laying date was tested using a one-way ANOVA. The effect of age on laying date could not be investigated as only nine birds were of known age. In the Snow Petrel, after copulation females go to sea to produce the egg (Isenmann 1970). When they return from this pre-laying exodus they lay almost immediately (Isenmann 1970). Thus, the duration of the pre-laying exodus was defined as the difference between laying date and date of departure for the pre-laying exodus. Date of departure for the exodus was determined by daily inspection of nests (Isenmann 1970). Pre-laying exodus duration was determined in 1993/94 and 1995/96 only. As birds were weighed before the pre-laying exodus only in 1993/94 (Appendix), the effect of early body condition on laying date could only be examined for that year. Body mass is correlated with body size in the Snow Petrel (Barbraud and Chastel 1999), thus the body condition of individuals was defined as the residuals of body mass regressed on the factor score for overall body size (Jolicoeur and Mosimann 1960).

Egg size is potentially important as it may be associated with exodus duration (time to acquire resources for the egg) and laying date. Data on egg size were collected in 1995/96 and egg volume was calculated from the formula: volume $(\text{cm}^3) = 0.00051 \times L \times B^2$ (Hoyt 1979), where L is the length and B is the breadth of egg (measured to the nearest 0.01 mm using calliper).

Reproductive success was measured each year of the study. Successful birds were defined as those that fledged a chick and unsuccessful birds as those that failed to hatch their egg or failed to fledge their chick. We used logistic regression to investigate the effect of laying date on reproductive success. We report the likelihood-ratio statistic (LRS) generated by logistic regression analysis to test the hypothesis that regression coefficients differ from zero.

The results are presented as mean ± SD.

Table 1. Timing of laying for Snow Petrels at Dumont d'Urville from 1993/94 to 1995/96.

	1993/94	1994/95	1995/96
Mean (December)	3.8	4.2	3.7
SD (n)	2.7 (46)	2.6 (82)	3.0 (68)
Range	29 Nov– 8 Dec	29 Nov– 11 Dec	27 Nov– 12 Dec
CV (%)	0.79	0.75	0.89

Results

Laying in the Snow Petrel began in the last week of November and its timing varied little from year to year (Table 1). The mean laying date for the three years combined was 4.0 ± 2.7 December ($n = 196$, range 27 November to 12 December), and the coefficient of variation for laying date was low (0.81%; Fig. 1). Constancy in the timing of breeding could have arisen either if the females of the population as a whole laid at the same time each year whilst individual females were not consistently early or late with respect to the population or, alternatively, the population laid at the same time each year and, additionally, individual females were consistently early or late. The between-female variance in laying date was significantly greater ($F_{61,196} = 2.82$, $P < 0.001$) than the within-female variance. The laying period of individual females was very restricted, the average divergence from season to season being 0.92 ± 0.94 days ($n = 61$, range 0 to 4 days). Repeatability of laying date for females was high for the three years combined ($r = 0.66$; $F_{60,111} = 6.55$, $P < 0.001$). Repeatability for 1993/1994, 1994/1995 and 1993/1995 was 0.51 ($F_{60,61} = 3.11$, $P < 0.001$), 0.53 ($F_{60,50} = 3.03$, $P < 0.001$) and 0.93 ($F_{60,50} = 25.32$, $P < 0.001$), respectively.

There was no effect of year on laying date, but we found significant effects of both colony size and body size as independent factors (Table 2). Post hoc Fisher's Pairwise Least Significant Difference (FPLSD) tests indicated that birds nesting in large colonies laid their egg later (mean: 5.1 ± 2.6 December) than birds nesting in small colonies or isolated nests (mean: 3.0 ± 2.5 December; ANOVA: $F_{2,193} = 17.10$, $P < 0.001$). However, the variances in laying date did not differ between large and small colonies or isolated nests (1993/94: $F_{32,14} = 1.45$, $P = 0.23$; 1994/95: $F_{41,41} = 0.95$, $P = 0.56$; 1995/96: $F_{36,32} = 1.49$, $P = 0.13$; overall: $F_{91,105} = 1.05$, $P = 0.41$). Post hoc FPLSD tests also indicated that females nesting in large colonies were larger (mean size: 0.415 ± 0.847, $n = 91$) than females nesting in small colonies or isolated nests (mean size: -0.360 ± 0.986, $n = 105$; ANOVA: $F_{2,193} = 16.20$, $P < 0.001$). None of the interaction terms were significant (Table 2).

There was a significant positive relationship between standardised laying date and female body-size in each year of the study (1993: $r = 0.76$, $n = 46$, $P < 0.001$; 1994: $r = 0.57$, $n = 82$, $P < 0.001$; 1995: $r = 0.31$, $n = 68$, $P = 0.009$; Fig. 2), whereas no significant effect of male body size was detected (multiple regression with female and male body size as explaining factors: female size: $P < 0.001$, male size: $P = 0.34$). In 1993/94, the only year in which this was studied, no significant relationship was found between early body condition and laying date ($r = 0.16$, $n = 26$, $P = 0.44$).

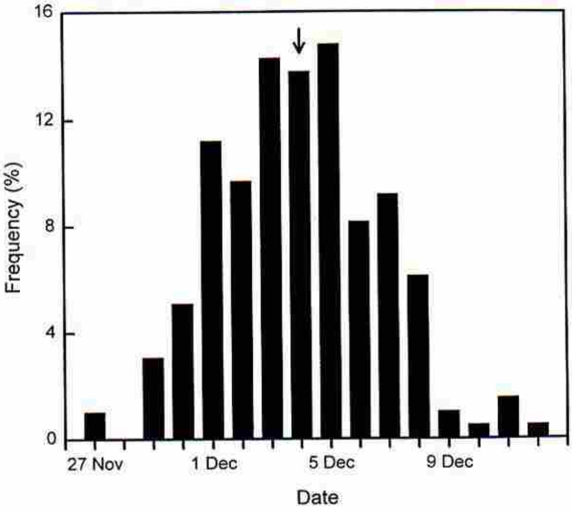

Fig. 1. Frequency (%) of laying dates for female Snow Petrels at Dumont d'Urville for 1993/94, 1994/95 and 1995/96 combined. Arrow indicates mean laying date.

Females that successfully fledged a chick in a particular year did not lay earlier or later in the subsequent year than females that failed to fledge a chick (1994: $t_{61} = 1.11$, $P = 0.27$; 1995: $t_{50} = 1.45$, $P = 0.15$). The variance in laying date for both groups did not differ significantly (1994: $F_{53,8} = 2.13$, $P = 0.13$; 1995: $F_{35,15} = 1.19$, $P = 0.37$). The mean laying date of females that changed partner did not differ from the mean laying date of faithful pairs ($t_{121} = 0.11$, $P = 0.92$). However, there was a slight tendency for the variance in laying date to be greater in the former ($F_{10,125} = 1.77$, $P = 0.07$).

The mean duration of the pre-laying exodus was 18.8 ± 2.9 days ($n = 66$, range 14 to 28 days, $CV = 15.5\%$) and did not differ between the two years ($t = 0.35$, $P = 0.73$). A highly significant correlation was found between the length of the pre-laying exodus and laying date (1993: $r = 0.98$, $n = 27$, $P < 0.001$; 1995: $r = 0.80$, $n = 39$, $P < 0.001$). The duration of the pre-laying exodus was also correlated with female body size (1993: $r = 0.76$, $n = 27$, $P < 0.001$; 1995: $r = 0.34$, $n = 39$, $P = 0.03$). Large females were absent longer than were small females (Fig. 3). For example, the mean exodus duration for females with a negative PC1 score (small) was 17.72 ± 2.36 days ($n = 39$) versus 20.41 ± 2.94 ($n = 27$) for females with a positive PC1 score (large). Departure dates for the exodus were not signifi-

Table 2. Results of GLM tests on the effects of year, colony size and body size on laying date of Snow Petrels at Dumont d'Urville.

Source	d.f.	MS	F	P
Year	2	0.11	0.16	0.853
Coloniality	2	3.36	4.81	0.009
Body size	1	24.54	35.11	<0.001
Coloniality × Body size	2	1.35	1.92	0.149
Year × Coloniality	4	1.44	2.06	0.087
Year × Body size	2	1.48	2.11	0.124
Coloniality × Year × Body size	4	0.84	1.21	0.310
Error	178	0.70		

cantly related to female body size, although there was a tendency for large females to leave sooner than small ones in 1993 ($r = -0.38$, $n = 27$, $P = 0.05$) but not in 1995 ($r = 0.13$, $n = 39$, $P = 0.44$).

The mean egg volume in 1995/96 was 53.27 ± 6.37 cm^3 ($n = 51$, range 43.96–67.97 cm^3). There was a positive relationship between standardised egg volume and standardised female body size (egg volume = $PC1^{0.726}$, $F_{1,49} = 54.52$, $P < 0.001$). This relationship indicates that relative egg size declines with increasing body size. Egg volume varied with laying date in 1995/96 ($r = 0.36$, $n = 51$, $P = 0.01$). Although the absolute exodus duration increased with female body size, the percentage differences between observed and expected exodus durations showed no tendency to increase or decrease with egg size ($r = 0.11$, $n = 50$, $P = 0.47$; Fig. 4).

In 1993/94 birds that successfully fledged their chick laid their egg later (mean laying date 4.93 ± 2.40 December, $n = 14$) than unsuccessful birds (mean 3.31 ± 2.64 December, $n = 32$; LRS = 3.90, df = 1, $P = 0.048$). However, the opposite tendency was observed in 1994/95 (successful 3.90 ± 2.45, $n = 61$; unsuccessful 5.14 ± 2.67, $n = 21$; LRS = 3.75, df = 1, $P = 0.053$), and no tendency was observed in 1995/96 (successful 3.40 ± 1.87, $n = 25$; unsuccessful 3.91 ± 3.44, $n = 43$; LRS = 0.48, df = 1, $P = 0.49$).

Discussion

Overall, female body size explained 24% of the variation in laying date, varying from 58% in 1993 to only 10% in 1995. Weidinger (1996) found no relationship between female body-size traits and laying date in the Cape Petrel *Daption capense* and no study has found an effect of structural body size on laying date among seabirds. Although statistically significant, the difference in laying date between large and small colonies is probably not biologically meaningful. Our results suggest that it probably results from the relationship between body size and colony size.

A remarkable result of this study is the constancy of laying date from year to year, both for the population as a whole and for individual females. The repeatability value of 0.66 for females was higher than any previously published estimate for any other bird known to us (range 0.21–0.657 for significant repeatabilities; Phillips and Furness 1998, Catry et al. 1999). However, our study comprises few years which may have led to high levels of repeatabilities (Catry et al. 1999). Moreover, our repeatability estimates should be corrected for age effects as positive repeatabilities in laying dates can result from low individual age variation during short-term studies on long-lived species (Catry et al. 1999). For example, in a 3-year study, age effects may result in repeatability values ranging from 0.08 to 0.15 (Catry et al. 1999). Repeatability of laying dates tends to be much higher in species where at least one sex exhibits nest fidelity (Phillips and Furness 1998). This is also supported in the Snow Petrel in which nest site is of primary importance for breeding success and hence nest-site fidelity is high (Guillotin and Jouventin 1980, Chastel et al. 1993). As repeatability provides an upper limit to the heritability of the character, our high estimate implies either that the heritability of laying date was high, or that individual birds bred in relatively

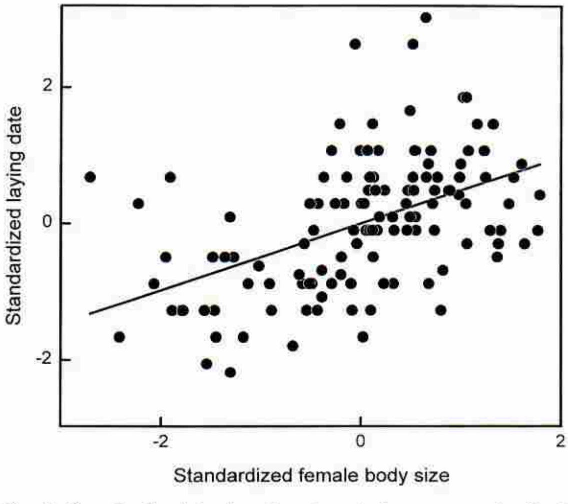

Fig. 2. Standardized laying date in relation to standardized body size for female Snow Petrels at Dumont d'Urville ($r = 0.49$, $n = 121$, $P < 0.001$, $y = 0.49x$). For females that laid more than once during the study period (1993/94 to 1995/96), laying dates were averaged.

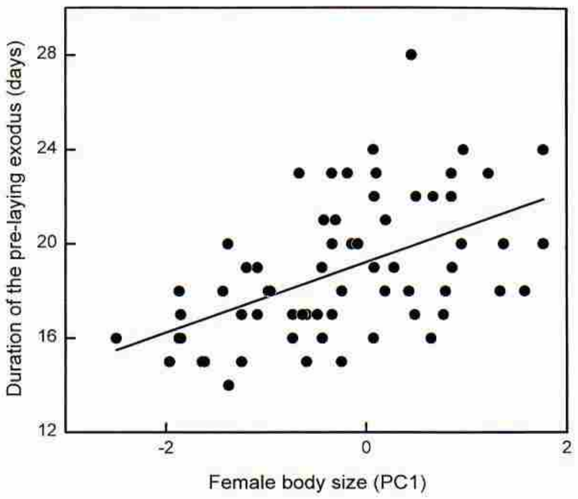

Fig. 3. The length of the pre-laying exodus in relation to female body size for 1993/94 and 1995/96 combined ($r = 0.53$, $n = 66$, $P < 0.001$, $y = 1.5x + 19.23$).

Table 3. Laying periods and laying dates of Snow Petrels at four Antartic localities.

Locality	Laying period (days)	Laying date
Anchorage Island[1]	9	1.6 ± 2.3 December (n = 19)*
Ardery Island[2]	14	28 ± 3.5 November (n = 51)*
Dumont D'Urville[3]	16	4 ± 2.7 December (n = 196)*
Svarthamaren[4]	9	8 December (n = 64)§

[1] Brown (1966). [2] Barbraud unpubl. data. [3] This study. [4] Amundsen (1995). * Mean value; § Median value.

constant conditions from year to year. High inheritance of laying date could be due to the relation between body size and laying date since body size is heritable in the Snow Petrel (c. 60% of the variance in body size is genetically determined, Barbraud 1999). Genes influencing body size may have a pleiotropic effect on laying date. This would cause laying date to evolve directly as a function of body size and would limit the extent to which laying date could be modified independently. Ideally, the genetic correlation between laying date and body size needs to be estimated to test this hypothesis, but at present data are insufficient given the low return rate of fledglings (Chastel et al. 1993). High heritability of laying date may promote adaptability to relatively stable environmental conditions whereas low heritability would probably enable plastic reproductive adjustment in a fluctuating environment (Endler 1986, Hakkarainen et al. 1996). For example, low heritability of laying date was found in Tengmalm's Owls *Aegolius funereus* which breed in environments where food resources are highly variable from year to year (Hakkarainen et al. 1996). By contrast, Snow Petrels breed in an environment where the timing of food abundance is highly predictable from year to year (Warham 1990), although breeding success is highly variable (Chastel et al. 1993). Thus, in such an environment high heritability of laying date could result in the production of phenotypes that optimise fitness.

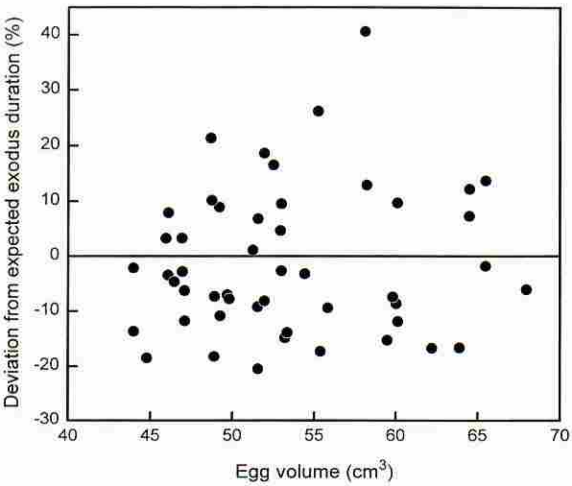

Fig. 4. Difference between observed and predicted exodus duration of female Snow Petrels in relation to the size of their egg for 1993/94 and 1995/96 combined.

The duration of the laying period was particularly compressed in 1993/94 (10 days) and is among the shortest recorded for Procellariiformes (Warham 1990), the shortest being nine days in the Blue Petrel *Halobaena caerulea* (Jouventin et al. 1985). Such constancy of timing is a feature of migrant shearwater and fulmarine species (Warham 1990, Weidinger 1997), but the Snow Petrel shows a particularly high degree of synchrony and constancy (Table 3). Note that a higher proportion of small birds than at Dumont d'Urville breed at Ardery Island (Barbraud and Jouventin 1998) and that only small-sized birds breed at Davis and Svarthamaren, the latter being situated far inland (c. 200 km) in contrast to the coastal colonies mentioned above. Synchronous laying may reduce predation on eggs and chicks. The South Polar Skua *Catharacta maccormicki* is the main predator of Snow Petrels at some breeding sites (Zipan and Norman 1993), but at Terre Adélie South Polar Skuas feed almost exclusively on Adélie Penguins *Pygoscelis adeliae* (Jouventin and Guillotin 1979). Consequently, synchrony as a defence against predation seems unlikely as a general explanation for a compressed laying period and therefore synchrony presumably reflects timing with respect to the short favourable breeding period at these high latitudes (Warham 1990).

Female body condition at arrival on the breeding grounds did not affect laying date in Snow Petrels (see also Barbraud and Chastel 1999). It has been suggested that females with large body reserves may be most prone to lay early, while those with small reserves may postpone laying (MacInnes et al. 1974). Measuring early body condition prior to the pre-laying exodus as we did might have masked any effect of condition on the timing of laying if late body condition influenced the timing of laying.

What mechanism can explain the observed relationship between body size and laying date? One explanation could be that it is adaptive for young and inexperienced individuals to lay late in the season or to defer breeding completely in a given year (Finney and Cooke 1978). This seems unlikely as it would imply a relationship between body size and age, with smaller birds being younger. Minimum age at first breeding is five years in the Snow Petrel (Chastel et al. 1993), when structural growth has ceased. Differences in laying date have also been explained as individual-specific trade-offs between an increasing amount of resources acquired for breeding and decreasing reproductive value with time (Perrins 1970, Reynolds 1972, Drent and Daan 1980, Daan et al. 1989). This hypothesis is partly supported by the observed tendency for a lower reproductive success of late breeders in 1994/95. However, the results obtained during the other two years of the study and the absence of a relationship between body condition (temporal individual quality) and laying date suggest that this hypothesis alone is insufficient to explain the observed variation in laying date. It could be that laying date becomes critical for the reproductive success of a given population only during poor years but there are no data on food availability for the three years of the study.

Another possible explanation for the observed relationship between body size and laying date might be the egg size. If large females produce larger eggs relative to their size than small females they would need more time to produce their egg. However, the relationship between egg size and body size indicates that egg size relative to body size decreases with increasing body size. The timing of breeding in the Snow Petrel may be energy limited as found in several bird species (Perrins 1979, Price 1984, Järvinen and Väisänen 1984, Murphy 1986). The body size/timing of breeding hypothesis in birds suggests that small females, which have lower costs for basal metabolism compared to larger ones (Lasiewski and Dawson 1967, Walsberg 1983), can divert a greater proportion of daily food intake to reproduction and become reproductively active before large females (Downhower 1976). One of the functional interpretations of the pre-laying exodus in Procellariiformes is that it enables the female to get extra food for egg production (Warham 1990). The pre-laying exodus was shorter in small than large females. However, the percentage differences between observed and expected exodus durations were not related to egg size and thus do not support the energy limitation hypothesis.

The relationship between laying date and female body size may result from genetically determined differences in laying date (Koskimies 1957, Findlay and Cooke 1982, Price et al. 1988). Heritability of laying date has been demonstrated for some other species (van Noordwijk et al. 1981, Cooke and Buckley 1987). If laying date was similarly determined in Snow Petrels, the observed relationship at Dumont d'Urville could result from the mixing of birds from colonies having small early-laying individuals with birds from colonies having large late-laying individuals. This is partly supported by emigration/immigration data (Chastel et al. 1993, Barbraud 2000) and by known colonies where birds are small and lay early (see above). At Ardery Island, where one population of large birds and one population of small birds breed (Barbraud and Jouventin 1998), hatching date is not related to body size within each population (Barbraud 2000) which suggests that laying date, as well as incubation, is not related to body size. Moreover, the relatively important genetic diversity found by Jouventin and Viot (1985) at Dumont d'Urville reinforces this hypothesis. Such differences in laying date associated with genotypic differences between females have been found in Lesser Snow Geese *Anser caerulescens caerulescens* (Findlay and Cooke 1982) and Mute Swans *Cygnus olor* (Birkhead et al. 1983). However the year to year difference of only one day in the laying by an individual female may be more related to the condition of her nest than to her genetics. Unfortunately our data provide no evidence to support either the genetic or the ecological hypothesis.

Body size is heritable in the Snow Petrel (Barbraud 1999). If there exists a fitness advantage of early breeding, as found for several other bird species (see Sydeman and Eddy 1995 for a review), and provided laying date is heritable, this would imply selection for small body size in this species at Dumont d'Urville. Early breeding tended to be advantageous only in 1994/95, late breeding was favoured in 1993/94, and no effect of laying date on reproductive success was observed in 1995/96. However, data from other colonies of Snow Petrels at Dumont d'Urville obtained in 1996/97 and 1997/98 indicate that on average birds that successfully raised a chick hatched their egg earlier than those that failed ($t_{73} = 4.21$, $P < 0.001$ and $t_{151} = 10.50$, $P < 0.001$, respectively). Since incubation duration is not related to body size, this suggests that there is directional selection for early breeding and hence towards small body size in some years. This directional selection may be balanced by selection for large body size in other years. Moreover, there is directional selection for large size at Dumont d'Urville through differential survival (males that survived over a 10-year period had a 2.9% longer bill than non-survivors, Barbraud 2000) which may counteract selection for small body size through laying date. Such a scenario would also partly explain how both body size and laying date variations are maintained in this population. Longer time series are needed to measure the magnitude of the selection forces on body size related to laying date and to investigate the heritability of laying date in this long-lived species.

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Appendix. Morphometrics of adult female Snow Petrels for which laying dates were recorded between 1993/94 and 1995/96 at Dumont d'Urville.

Measurement	Mean ± SD (n)	Range	CV (%)
Wing length (mm)	282.5 ± 13.0 (121)	241–307	4.6
Bill length (mm)	21.8 ± 1.5 (121)	17–26	7.1
Bill depth (mm)	9.9 ± 0.7 (121)	8.3–11.3	7.0
Tarsus length (mm)	37.4 ± 1.8 (121)	31.5–41.3	4.8
Body mass (g)[a]	323.7 ± 48.5 (26)	250–440	15.0

[a] 1993/94 only.

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