Size-related life history traits: insights from a study of snow petrels (*Pagodroma nivea*)

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Summary

1. Body size is commonly tied to major life history traits in many animals. The main problem with studies on this topic is that the range of body sizes within species is generally too small to produce enough variation in traits for quantitative analysis. The snow petrel shows considerable differences in body size with structural body size varying by $\approx$ 1·6-fold. This high variability in size provides a good opportunity for examining how life history traits are related to body size intraspecifically.

2. We studied the breeding phenology, foraging parameters and chick growth in relation to body size in two populations of snow petrel in Antarctica. We also investigated the relationship between body size and distance separating colony from the edge of the pack ice using morphometric data from 16 breeding stations.

3. The largest snow petrels laid eggs $\approx$ 2-fold larger and hatched hatchlings $\approx$ 1·9-fold heavier than smallest ones. During the chick rearing period the smallest adults made longer foraging trips ($\approx$ 70 h) and fed their chick less frequently than the largest ones ($\approx$ 40 h). Meal size was positively related to adult body size.

4. Chicks raised by large parents grew more rapidly, reached higher peak mass and asymptotic size than chicks raised by small parents. Chick body size at fledging was correlated to the size of their biological parents. A sample of 20 chicks from parents that differed in body size were swapped. Body size of swapped chicks at fledging was not correlated to their foster parent size. Swapped chicks tended to resemble their biological parents in size but no significant relationship was found.

5. These results provide evidence of intraspecific variability in several ecological variables and life history traits linked to body size. The difference in foraging trip duration between large and small birds was not only because of a lower flight speed or a higher metabolic rate per mass unit of smaller birds and suggests that small birds had lower feeding efficiency or fed on more distant areas. This was reinforced at the population level by a negative correlation obtained between body size and distance between colony and the edge of the pack ice for 16 breeding stations.

6. The results suggest that body size is probably in the main genetically determined but that there is a significant environmental component in fledgling body size.

Key-words: Antarctica, body size, geographical variation, life history traits, phenotypic plasticity.

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Introduction

Individual body size among animals is a central characteristic on which several life history traits may depend. Body size is often closely related to major life history traits such as survival (Beverton & Holt 1959; Boag & Grant 1981; Price & Grant 1984; Promislov & Harvey 1990) and fecundity (Tilley 1968; Petrie 1983; Alisauskas 1987; Marshall 1990). The understanding of the relationships between body size and ecologically important variables is essential to understand the body size variability and its fitness consequences; for example, food availabil-

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ity might influence growth and adult body size, which, in turn, might be related to survival or fecundity (Dobson & Murie 1987; Larsson & Forslund 1991; Madsen & Shine 1993a; Sedinger, Flint & Lindberg 1995; Wikelski, Carrillo & Trillmich 1997). Many studies have investigated the relationships between body size and life history traits at the interspecific level, but analyses that focused on the intraspecific level remain relatively few in birds compared to other organisms, e.g. plants, insects and fish (see Reiss 1989; Roff 1992).

Body size between populations may differ either because of local genetic modifications possibly as a result of adaptation (Grant 1986) or because of a direct phenotypic effect of differing food availability on growth rates (Madsen & Shine 1993a; Sedinger *et al.* 1995). Although genetic and environmental components of body size variation are not mutually exclusive explanations, a distinction between these two is necessary as variation resulting from environmental factors and genetic sources will not have identical evolutionary impacts. As natural selection is the consequence of differences in fitness among individuals in a population, natural selection may operate to change average body size within species provided body size is a heritable trait (Boag & Grant 1981). Recent studies have revealed that intraspecific body size variability may be attributed to environmental variation (Larsson & Forslund 1991; Sedinger *et al.* 1995). Thus, even if body size influences life history traits such as survival or fecundity, phenotypic selection may have no evolutionary consequences when the real target of selection is not the studied characteristic, but an unmeasured, nonheritable characteristic that is correlated with the studied characteristic (Alatalo, Gustafsson, & Lundberg 1990).

The main problem when analysing size-associated ecological traits intraspecifically is to identify a taxon with sufficient range in body sizes to produce enough variation in traits for quantitative analysis (Shine *et al.* 1998). In birds previous interspecific analyses have revealed strong size–life history trait relationships (Saether 1987; Warham 1990) but such intraspecific analyses are scarce, mainly because body size variation in birds is small compared to other taxa.

The snow petrel, *Pagodroma nivea* (Foster), offers a good opportunity for examining intraspecific relationships between body size and ecological traits because intraspecific body size variation is high (Bonaparte 1857). It is a widely distributed species of seabird in Antarctica (Croxall *et al.*, 1995). It breeds around the edge of the Antarctic continent and on nearby islands, but some colonies have also been found on mountain ledges far inland (Mehlum *et al.* 1988). This small fulmarine species shows a high degree of sexual dimorphism in size (Croxall 1982; Barbraud & Jouventin 1998) but also an extensive within-sex variation in size (Prévost 1969; Cowan 1981; Jouventin & Viot 1985), one of the widest among birds. Although several studies have focused on the large size variation of snow petrels (Falla 1937; Prévost 1969; Isenmann 1970; Cowan 1981; Croxall 1982; Jouventin & Viot 1985; Haftorn, Mehlum & Bech 1988; Barbraud & Jouventin 1998), no study investigating the ecological consequences of body size variation in that species has yet been conducted. Such intraspecific variations may represent either phenotypic response to environmental conditions or genetically determined adaptation or a combination of both.

In Antarctica, the snow petrel is a specialist forager and only occurs where there is some degree of sea-ice cover, generally along the edge of the pack ice (Ainley & Jacobs 1981; Ainley, O'Connor & Boekelheide 1984; Veit & Hunt 1991). Snow petrels breeding far from the foraging areas spend more time travelling to and from the foraging zones. Consequently, feeding frequencies of chicks would be lower in colonies situated far from the edge of the pack ice and size at fledging would be lower than within colonies situated close to the edge of the pack ice.

In this study we used a size gradient to examine the relationships between body size and growth and how body size is related to the breeding ecology of individuals using two populations of snow petrel on Ardery Island and Dumont D'Urville. These islands lie near to the Antarctic continent and were chosen because both are home to populations where the greatest body size range (240–570 g, C. Barbraud unpublished data) has been recorded in Antarctica. The main objective of the study reported here is to investigate the ecological consequences of intraspecific variation in body size in a highly size-variable species. As body size is often correlated to the length of breeding events in birds (Saether 1987), we first analysed the relationships between body size and the breeding phenology (laying, hatching, and fledging dates, duration of incubation and chick rearing). Second, we examined how body size is related to the food provisioning strategy and growth in that species using data from the field. A chick swapping experiment was also undertaken to investigate the environmental influence on offspring size. Third, we tested the following hypothesis that the distance between breeding colony and foraging zone (i.e. the pack ice edge) might be related to body size. Using data gathered from the literature and recent data on morphometrics in snow petrels, we examined the relationship between snow petrel body size at different breeding stations in continental Antarctica and distances separating those colonies from the edge of the pack ice.

Materials and methods

NATURAL HISTORY

Snow petrels breed during the short Antarctic summer, when food is most abundant, and have an extremely compressed breeding period (≈ 92 days from egg laying until fledging) compared to other Procellariiformes (Warham 1990). During the breeding season they feed mostly on fish, squid and krill in the leads among the pack-ice and at the base of icebergs (Ridoux & Offredo 1989; Ainley, Ribic & Spear 1993). Birds arrive on the breeding grounds in early November. They stay for about 2 weeks and then leave their nest and stay at sea for about 3 weeks. Laying occurs immediately after this pre-laying exodus. Females lay only one egg without replacement clutch and both parents alternately incubate their egg until hatching and they both feed their chick until fledged (Brown 1966; Prévost 1969). The male is responsible for the first long spell on the egg (incubation shift) while the female is at sea (foraging trip). After hatching the chick is guarded by parents, alternating short spells until it attains homeothermy. Then the chick is left unattended and both parents feed the chick by regular visits until fledging.

STUDY SITES

Snow petrels were studied at Dumont d'Urville (66°40′S, 140°01′E), Terre Adélie, Antarctica during the austral summers 1993/94, 1994/95 and 1995/96, and on Ardery Island (66°20′S, 110°25′E), Windmill Islands, Antarctica in 1995/96. During the summer 1997/98 a chick-swapping experiment was conducted at Dumont d'Urville. Population sizes were 800 pairs on Ardery Island (Barbraud & Baker 1998) and 1050 pairs at Dumont d'Urville in 1996 (T. Micol & P. Jouventin, unpublished data). Study nests ($n = 177$) were individually marked with tags fixed on nearby rocks. Birds (one per pair) were individually marked with dye on Ardery Island. At Dumont d'Urville birds were known from a long-term database (Chastel, Weimerskirch & Jouventin 1993), each bird being banded with a metal band. Individuals were sexed by vocalization, females have higher sound frequency than males (Guillotin & Jouventin 1980).

BODY SIZE

Body size measurements were obtained from adult birds captured while incubating. Because body mass varies greatly with season and year in seabirds (Croxall 1984; Warham 1990), we restricted the analyses to structural measures of size. Measurements taken were wing, bill and tarsus length and bill depth (see Barbraud & Jouventin 1998 for details).

The variation in body size was still revealed when using structural body size (CV = 5·3%, 7·2%, 9·1% and 10·7% for wing length, tarsus length, bill length and bill depth, respectively) instead of body mass (CV = 20·3%). The four measurements of size were combined using principal component analysis to form a single factor (PC1) which was used as a measure of structural body size (Rising & Somers 1989). Birds from Ardery and Dumont d'Urville were grouped for the analysis ($n = 354$). The first principal component accounted for 81% of the total variance and was highly negatively correlated with all variables (mean $r = -0·91$). Thus, PC1 was multiplied by (–1) in order to obtain positive scores for large birds and negative scores for small birds. No age-effect on structural measurements was detected among the same individuals measured in different subsequent years (two-way ANOVA with individuals as a random factor and measurement (first, second, and third) as a fixed factor: wing length $F_{1,121} = 3·45$, $P = 0·26$; bill length $F_{1,90} = 2·99$, $P = 0·35$; bill depth $F_{1,72} = 0·96$, $P = 1·00$; tarsus length $F_{1,12} = 0·13$, $P = 1·00$; after Bonferroni adjustment).

BREEDING PHENOLOGY

Dates of laying, hatching and fledging were obtained in 1993/94, 1994/95 and 1995/96 at Dumont d'Urville by daily inspection of the study nests. As we stayed from 15 December to 1 March on Ardery Island in 1995/96 only hatching dates could be obtained. Incubation period was calculated as hatching date minus laying date, brooding period as the period between hatching and the time at which the chick is first left alone in the nest, and nesting period as fledging date minus hatching date (Warham 1990). Egg measurements were taken on Ardery Island and at Dumont d'Urville during the 1995/96 season. The maximum length and breadth of eggs were measured to the nearest 0·1 mm with a calliper and the volume calculated using the formula (Hoyt 1979): volume = $0·507 \times$ length $\times$ breadth^2. The ratio length/breadth was used as a measure of egg shape (Warham 1990).

DURATION OF INCUBATION SHIFTS, FORAGING TRIPS AND FEEDING FREQUENCY

The incubation period is divided into five to eight incubation shifts and the duration of shifts steadily decreases from about 9 days to about 5 days (Brown 1966; Isenmann 1970). The duration of incubation shifts was studied in 1994/95 and 1995/96 at Dumont d'Urville and in 1995/96 on Ardery Island on all study nests. To determine the duration of incubation shifts, the bird on duty at the first check

was dyed with picric acid and nests were checked twice a day during the incubation and brooding periods. In snow petrels, at egg laying the first shift by the female is very short (about 1 day), and the shifts preceding hatching are also reduced in duration to allow the chick to be fed immediately (Isenmann 1970). These shifts were excluded from the analysis.

The duration of foraging trips during the fledging period was studied simultaneously on 15 nests at Dumont d'Urville and on 15 nests on Ardery Island in 1995/96. To monitor the presence or absence of adult birds in each colony after the chick has been left alone both pair members [60 birds (30 in each site)] were fitted with VHF transmitters (model 2040, ATS, Isanti, Minnesota, USA; 6 g, 55 pulses min^{-1}) glued with Araldite on the central rectrice feathers and protected with an adhesive white tape. Each individual parent was fitted with a transmitter during the brooding period and assigned a different frequency. An automatic recording station, comprising a receiver, a data logger (model R4000 and DCCII D5041, respectively, ATS, Isanti, Minnesota, USA) and a multidirectional antenna were installed in the vicinity of the studied nests in each site. The 15 nests monitored automatically (with two adults fitted) were spread over 100 m at Dumont d'Urville and over 200 m on Ardery Island. The automatic station, powered by 12 V batteries recharged regularly, continuously scanned the different frequencies successively. Each frequency was searched for 10 s, allowing a scan to be made of each frequency every five minutes. In total 33 transmitters were lost during the study, mainly because some birds moulted the feather fitted with the transmitter. At Ardery Island, snow petrel chicks suffered from high predation by south polar skuas [*Catharacta maccormicki* (Saunders)] (Barbraud 1999). Eight chicks whose parents were fitted with transmitters were predated by skuas and parents did not return. The data were downloaded every day during the brooding period and every 3–5 days afterwards using a laptop computer. During the post guard stage, when back from a foraging trip snow petrels usually feed their chick soon after reaching the nest and then rest and sleep on the nest. This stay on the nest is interrupted by infrequent absences during which the birds often toilet in the nearby snow. These absences lasted on average 4.9 ± 2.6 h ($n = 28$, range 0·4–9·5 h). Thus, we have assumed that a foraging trip was longer than 10 h. We tested for significant differences between males and females in the relationship between body size and foraging trip duration using an analysis of covariance (ANCOVA) to test for heterogeneity of slopes between groups. Frequency of feeding was obtained from chicks raised by parents fitted with VHF transmitters during the 1995/96 breeding season

MEAL SIZE

Meal size was estimated from chicks whose parents were fitted with VHF transmitters. To estimate the mass of the meals delivered by the adults 19 chicks were weighed twice a day at Dumont d'Urville at 10.00–11.00 h and 22.00–23.00 h GMT from 23 January until 6 February 1996. The chicks were weighed with a Pesola spring balance accurate to 1 g. To determine meal size from twice daily weighing it was necessary to take into account loss of mass of chicks during their period of fasts as a result of respiration and defecation. As the exact time when the meal was delivered was known we were able to calculate the mass of the chick before being fed and just after being fed. The meal mass was then calculated as the difference between the mass estimated before and after the meal was delivered. As chicks were weighed every 12 h we calculated specific weight losses of 1.65 g h^{-1} (SD = 0·92, $n = 25$) for 0–12 h fasts, 1.44 g h^{-1} (SD = 0·66, $n = 14$) for 12–24 h fasts, 1.39 g h^{-1} (SD = 0·59, $n = 5$) for 24–36 h fasts, and 0.84 g h^{-1} (SD = 0·45, $n = 2$) for longer than 36 h fasts. Although this method is not as accurate as weighing the chick shortly before and after a feeding session, estimates are relatively precise (Lorentsen 1996) and reduce the handling of chicks.

CHICK GROWTH

To study the growth of chicks, chicks from all studied nests on Ardery Island and at Dumont d'Urville were weighed and measured every 3–5 days. For each chick, bill and tarsus lengths were measured to the nearest 0·1 mm with a calliper, and wing length to the nearest 1 mm with a rule. On Ardery Island hatchlings were also weighed just after hatching, when down was dry. At Dumont d'Urville chicks were first weighed at 6 days of age.

Procellariiformes chicks have a typical growth curve with a period of rapid increase to peak mass followed by a period of slow decrease until fledging (Warham 1990). Because standard growth equations (Ricklefs 1973) do not allow estimation of the age attained at peak mass, we modelled the data of each individual using a third degree polynomial equation and calculated the age and mass (P_{max}) at peak mass. The three common growth models (Ricklefs 1973) were fitted to all measurements of each individual for the period of growth to the asymptote, using the least square iterative method from the procedure NLIN (SAS Institute 1987) allowing measurement of the growth parameters. Predation by south polar skuas resulted in some incomplete records for individual chicks for which models could not be fitted. The logistic curve fitted better than the Gompertz curve, as it consistently explained higher proportion of variability and provided estimates of asymptotic size closer to the observed values. The

von Bertalanffy curve was not applicable to any of the individual chicks, mainly because of considerable overestimation of asymptotic values. Hence, all analyses were performed using the logistic equation of the form: size = $A/\{1 + \exp[-K(\text{age}-I)]\}$, where A is the asymptotic size, K is the growth rate and I is the age of maximum growth rate. Parameters K and I determine 'shape' of the curve, whereas parameter A determines its 'scale' (see Ricketts & Prince 1981). We also calculated from the fitted curves the linear growth rate (LGR in g or mm day^{-1}) as the slope of the linear regression over the t_{10-90} period (i.e. the time in days taken to grow from hatching size to 90% of asymptotic size, Ricklefs 1968).

CHICK-SWAPPING EXPERIMENT

During the austral summer 1997/98 a chick-swapping experiment was carried out during the breeding season at Dumont d'Urville. We swapped 20 chicks between breeding pairs of different body sizes just after hatching in nests where both parents were measured. A principal component analysis was performed on the measurements taken on these parents and the first axis retained as a measure of body size (see Body size). Pair body sizes were obtained by adding body sizes of both pair members, and were standardized. Pairs with a positive score were classified as large and those with a negative score classified as small. Because snow petrels mate assortatively by size at Dumont d'Urville (Barbraud & Jouventin 1998) we assumed it was a reliable method to classify pairs into small and large size groups. Chicks from large- and small-sized parents were given to smaller- and larger-sized parents, respectively. Chicks were measured (wing, tarsus and bill lengths and bill depth) and weighed at 40-days-old, just before fledging. Relationships between chick measurements and their biological and foster parent measurements were then examined. We used a group of 30 chicks of known age which remained with their biological parents until 40 days old as a control group.

Resemblance estimates for body size and body mass were obtained by regressing values of offspring on female and male parent body size separately (resemblance = twice the slope) (Falconer 1981). Assortative mating between parents may influence resemblance estimates obtained from offspring–parent regressions (Falconer 1981). Resemblance estimates were thus divided by (1 + correlation between parent body size) to account for assortative mating.

BODY SIZE AND DISTANCES BETWEEN COLONIES AND PACK ICE EDGE

To study the relationship between body size and distance between colony and the edge of the pack ice,

morphometric data from other breeding localities ($n = 10$) were gathered from Croxall (1982), Marchant & Higgins (1990) and Barbraud & Jouventin (1998). Additional data were obtained from six colonies in early 1998 along the Terre Adélie and King George V Land coasts during a seabird survey (Barbraud *et al.* 1999). We retained samples where sexed mature individuals had been measured and where wing length, bill length and tarsus length had been recorded. A principal components analysis was performed on the three measurements and the first component (PC1) was used as a measure of body size. The first principal component accounted for 95% of the total variance.

Longitudinal and latitudinal positions of colonies have been taken from Croxall *et al.* (1995) and using a Global Positioning System (GPS) for those colonies visited in 1998. For each colony, we determined the average latitudinal position (at equal longitude) of the ice edge during the chick-rearing period (January and February) over the last 25 years. Sea-ice extent data were obtained through satellite remote sensing since January 1973. Data were provided by the National Snow and Ice Data Center (University of Colorado, Boulder, Colorado, USA).

STATISTICAL ANALYSIS

Birds from Dumont d'Urville and Ardery Island were grouped to analyse the relationships between body size and other life history traits when no significant differences were detected between both islands. When islands were treated separately, we checked for the normality of the frequency distribution of body size. To avoid the repeated use of the same individual as independent observations, we used averaged values when repeated observations occurred. Statistical analyses were performed using SYSTAT 7·0 (Wilkinson 1997).

Results

BREEDING PHENOLOGY

At Dumont d'Urville there was no significant interannual variation in the average laying date (ANOVA: $F_{2,171} = 0.65$, $P = 0.53$; mean 3.0 ± 2.6 December, $n = 172$, range 28 November– 10 December), the average incubation period ($F_{2,104} = 1.89$, $P = 0.16$; mean 44.5 ± 1.2 days, $n = 105$, range 40–48 days), the average brooding period (Kruskall–Wallis: $H = 5.69$, d.f. = 2, $P = 0.058$; mean 7.8 ± 1.9 days, $n = 102$, range 4–14 days), the average nestling period ($F_{2,100} = 2.56$, $P = 0.08$; mean 46.6 ± 2.0 days, $n = 101$, range 40–52 days) and the length of the breeding cycle ($F_{2,89} = 0.56$, $P = 0.57$; mean 90.7 ± 2.0 days, $n = 90$, range 86–96 days). Thus data from the three years were combined to analyse the relationship

Table 1. Summary of Pearson correlation coefficients between male and female body size and breeding events at Dumont d'Urville (data from 1994/95 and 1995/96)

Breeding event	Male			Female		
	r	n	P	r	n	P
Incubation period	0·247	74	0·204	0·222	74	0·348
Hatching date	0·305	74	0·048	0·568	74	< 0·001
Brooding period	0·250	72	0·204	0·282	72	0·096
Nestling period	0·193	67	0·708	0·008	67	1·00
Fledging date	0·46	66	< 0·001	0·509	66	< 0·001
Breeding cycle	0·293	66	0·102	0·118	66	0·331

between body size and breeding phenology. Significant differences were found in the average hatching date ($F_{1,162} = 272 \cdot 05$, $P < 0 \cdot 001$) and the average brooding period ($F_{1,146} = 4 \cdot 13$, $P = 0 \cdot 04$) between Ardery Island and Dumont d'Urville, thus data were analysed separately.

At Dumont d'Urville no significant correlation was found between male or female body size and the duration of incubation, brooding and nestling period, nor with the duration of the breeding cycle (Table 1). Female and male body size were significantly positively correlated with laying, hatching and fledging date (Table 1), indicating that smaller birds bred earlier than larger birds.

On Ardery Island hatching date was significantly correlated to female body size ($r = 0 \cdot 76$, $n = 50$, $P < 0 \cdot 001$) and to male body size ($r = 0 \cdot 62$, $n = 44$, $P < 0 \cdot 001$). No significant correlation was found between the duration of the brooding period and male or female body size (male: $r = -0 \cdot 01$, $n = 31$, NS; female: $r = 0 \cdot 18$, $n = 35$, NS).

EGG SIZE

In 1995/96 egg volume and egg shape did not differ significantly between Dumont d'Urville and Ardery Island ($F_{1,144} = 3 \cdot 32$, $P = 0 \cdot 07$; $F_{1,144} = 0 \cdot 20$, $P = 0 \cdot 66$, respectively). Egg volume was correlated to female body size ($r = 0 \cdot 71$, $n = 146$, $P < 0 \cdot 001$, $y = 4 \cdot 83 \ x + 52 \cdot 97$), but no significant correlation

was found between egg shape and female body size ($r = 0 \cdot 13$, $n = 146$, NS).

DURATION OF FORAGING TRIPS DURING INCUBATION

There was no significant effect of the locality, but we detected significant effects of the year, the foraging trip, and sex on the duration of foraging trips during incubation (Table 2). No significant effect of body size on foraging trip duration was found (Table 2). Males made shorter foraging trips than females during incubation but, within sexes, large birds made similar foraging trips (in duration) than small birds.

BODY SIZE DEPENDENCE OF PROVISIONING PARAMETERS

Duration of foraging trips

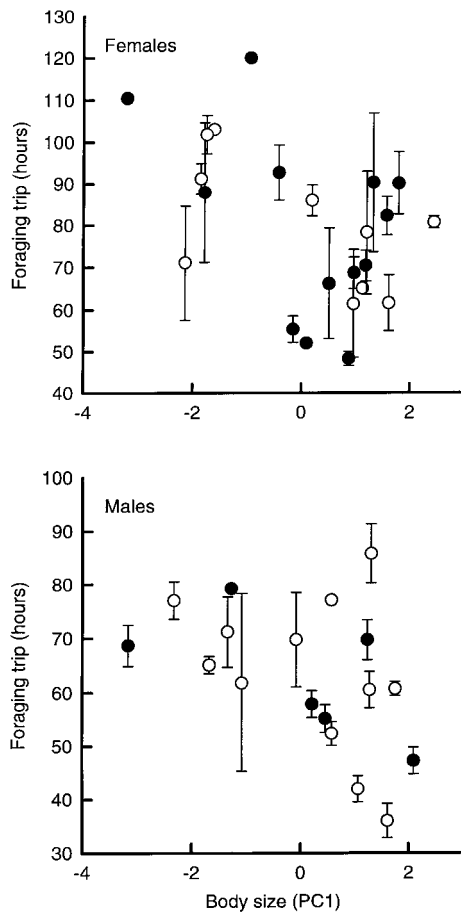Birds fitted with transmitters fledged their chick on average in $48 \cdot 60 \pm 1 \cdot 96$ days ($n = 10$) compared to $48 \cdot 27 \pm 1 \cdot 75$ days ($n = 15$) for birds without transmitters ($F_{1,23} = 0 \cdot 19$, $P = 0 \cdot 67$). In males ($n = 18$) and in females ($n = 24$) there was no effect of the locality (Dumont vs. Ardery) and of the period (brooding vs. after brooding) on the duration of foraging trips (males: locality, $F_{1,109} = 1 \cdot 99$, $P = 0 \cdot 16$; period, $F_{1,109} = 0 \cdot 67$, $P = 0 \cdot 41$; females:

Table 2. Effects of locality (Dumont vs. Ardery), sex, year (1994/95 vs. 1995/96), foraging trip (first, second or third), and body size on the duration of foraging trips during the incubation period

Source of variation	d.f.	Sum of squares	F	P
Locality	1	5·32	3·12	0·078
Sex	1	22·11	12·99	< 0·001
Year	1	11·24	6·60	0·010
Foraging trip	2	178·21	104·70	< 0·001
Body size	1	2·42	1·42	0·233
Error	788	1·70		

locality, $F_{1,110} = 0.20$, $P = 0.65$; period, $F_{1,110} = 0.82$, $P = 0.37$). Thus, data from both periods and localities were grouped for each sex and foraging trip duration was averaged for each individual. Mean duration of foraging trips was 64.42 ± 28.49 h ($n = 113$ trips, range $17.11–175.12$ h) for males and 78.18 ± 38.10 h ($n = 114$ trips, range $18.04–228.13$ h) for females.

Body size was significantly correlated with the average foraging trip duration in males ($r_s = -0.45$, $n = 18$, $P < 0.005$) and in females ($r_s = -0.43$, $n = 23$, $P < 0.025$), indicating that large males and large females made significantly shorter foraging trips than small males and small females, respectively (Fig. 1). The relationships between body size and foraging trip duration were not significantly different between sexes (ANCOVA with body size as a covariate: $F_{1,39} = 0.31$, $P = 0.58$). Females made longer foraging trips than males ($F_{1,40} = 7.76$, $P = 0.008$). As females were smaller than males ($t_{40} = 2.24$, $P = 0.03$), this difference was either a consequence of body size only or a consequence of sex if males had another foraging strategy (different behaviour) than females.

Fig. 1. Relationships between body size (PC1) and foraging trip duration (h) for male and female snow petrels at Dumont d'Urville (○) and Ardery Island (●) in 1995/96. The bars indicate within-individul variation.

Consequently, the number of meals delivered to the chick varied according to the sex of the adult ($F_{1,39} = 6.21$, $P = 0.012$) and according to the size of males and females (chicks reared by large individuals received more meals than chicks reared by small ones). Males delivered on average 0.40 ± 0.10 meal day^{-1} (range $0.28–0.67$) and females 0.33 ± 0.08 meal day^{-1} (range $0.20–0.52$). Overall, chicks with both parents fitted with transmitters received on average one meal every 0.73 ± 0.15 days (range $0.50–1.04$, $n = 14$), i.e. they were fed, on average, every 17.3 ± 3.4 h.

Stays on the colony

There was no influence of the sex of the adult or locality on the duration of the stay on land (sex: $F_{1,70} = 0.47$, $P = 0.50$; locality: $F_{1,70} = 0.002$, $P = 0.96$), but the duration of the stay on land differed between periods ($F_{1,70} = 40.20$, $P < 0.001$). Adults spent on average 23.98 ± 19.66 h ($n = 40$) on the colony during the brooding period and 2.61 ± 3.37 h ($n = 38$) during the fledging period. The body size of adults (males and females) did not influence the duration of the stay on land during the brooding period ($r = -0.04$, $n = 28$, $P = 0.85$) nor after the chick was left alone ($r = 0.14$, $n = 32$, $P = 0.44$).

Meal mass

Estimated meal mass ranged from 14.3 g to 109.8 g (mean 62.4 ± 21.3 g, $n = 58$ meals) at Dumont d'Urville in 1995/96. The size of meals delivered to the chick was related to the body size of the parent ($r_s = 0.55$, $n = 18$ individuals, $P < 0.025$) and to the mass of the chick ($r = 0.31$, $n = 58$ meals, $P = 0.018$), but not to the foraging trip duration ($r = 0.05$, $n = 58$ meals, $P = 0.70$). However, males did not deliver significantly larger meals than females (males: 63.5 ± 20.1 g, $n = 12$ individuals; females: 59.8 ± 24.2 g, $n = 6$ individuals; $F_{1,16} = 0.03$, $P = 0.86$). The average food provisioning rate (frequency of meals × size of meals) was correlated with the body size of adults ($r_s = 0.80$, $n = 16$ individuals, $P < 0.001$; Fig. 2).

VARIATION IN GROWTH PATTERNS

Hatchling body mass was significantly positively correlated to male and female body size on Ardery Island (Table 3), indicating that large birds had heavier hatchlings. Significant differences were found between Dumont d'Urville and Ardery Island in several growth parameters for wing, bill, tarsus and body mass (ANOVA: $P < 0.05$). Thus, both localities were analysed separately. Significant correlations were found between growth parameters for wing
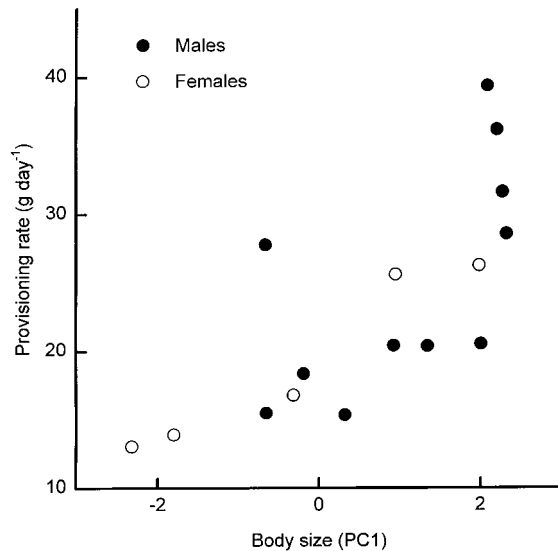
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*Size-related life
history traits in
snow petrels*

Fig. 2. Provisioning rate of the chick (g day^{-1}) in relation to body size of male and female snow petrels at Dumont d'Urville and Ardery Island in 1995/96.

length, bill length, tarsus length, body mass and female size and male size at Dumont d'Urville and on Ardery Island (Table 3). Pearson correlation coefficients indicate that chicks raised by larger individuals reached higher asymptotic values for all measurements. Linear growth rate increased significantly with the size of adults for wing length, tarsus length and body mass on Ardery Island, and for body mass at Dumont d'Urville (Table 3). Chicks raised by large birds reached higher peak mass than those raised by small birds on Ardery Island (Table 3).

CHICK-SWAPPING EXPERIMENT

There was no significant difference in size and mass at 40 days old between controls and swapped chicks

(size: $F_{1,70} = 2.92$, $P = 0.09$; mass: $F_{1,70} = 0.77$, $P = 0.38$). For controls, the size and mass of off-spring was positively related to female size, but not to male size (Table 4). The size and mass of swapped offspring tended to resemble that of their biological female and male parent, respectively (Fig. 3), but the relationships were not significant, perhaps because sample size was small (Table 4). There was no relationship between the size and mass of swapped offspring and the size of their foster parents (Table 4).

DISTANCE FROM COLONY TO ICE EDGE

Negative significant correlations were found between average body size and distances from colony to ice edge for both males and females (Fig. 4). Single-factor analysis of covariance with sex as a factor showed that slopes were similar for male and female snow petrels ($F_{1,29} = 0.46$, $P = 0.50$).

Discussion

Overall, results from our analyses clearly indicated that snow petrels display significant effects of body size on most of the traits that we examined. These effects were found at the individual level but also at the population level. The wide range of variation in body sizes in the snow petrel probably favoured the detection of such allometries, which may be widespread but are difficult to detect in most species of birds because of their limited range of variation in body sizes (CV less than 4% for structural body size).

VARIATION IN EGG SIZE, INCUBATION BEHAVIOUR AND FOOD PROVISIONING

As found in other animal species (e.g. Congdon & Gibbons 1987; Marshall 1990; Larsson & Forslund

Table 3. Pearson correlation coefficients of female and male body size with some chick growth parameters for wing, culmen, tarsus and body mass in snow petrels from Dumont d'Urville and Ardery Island in 1995/96. See text for definition of symbols

		Dumont d'Urville			Ardery Island		
		n	Female	Male	*n*	Female	Male
Wing	*A*	19	0·49*	0·21	29	0·40*	0·47*
	LGR	22	0·28	−0·03	29	0·30	0·43*
Culmen	*A*	19	0·68**	0·38	19	0·44*	0·57**
	LGR	20	−0·09	0·35	26	0·21	0·28
Tarsus	*A*	19	0·86***	0·58**	30	0·63***	0·56***
	LGR	19	0·33	0·26	30	0·34*	0·40*
Mass	*A*	21	0·46*	0·26	28	0·52**	0·51**
	LGR	22	0·44*	0·36*	28	0·53**	0·27
	P_{max}	17	0·40	0·35	22	0·66***	0·51**
Hatchling	–	–	–	–	37	0·67***	0·64***

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$. *A*, asymptotic size. LGR, linear growth rate. P_{max}, mass at peak mass.
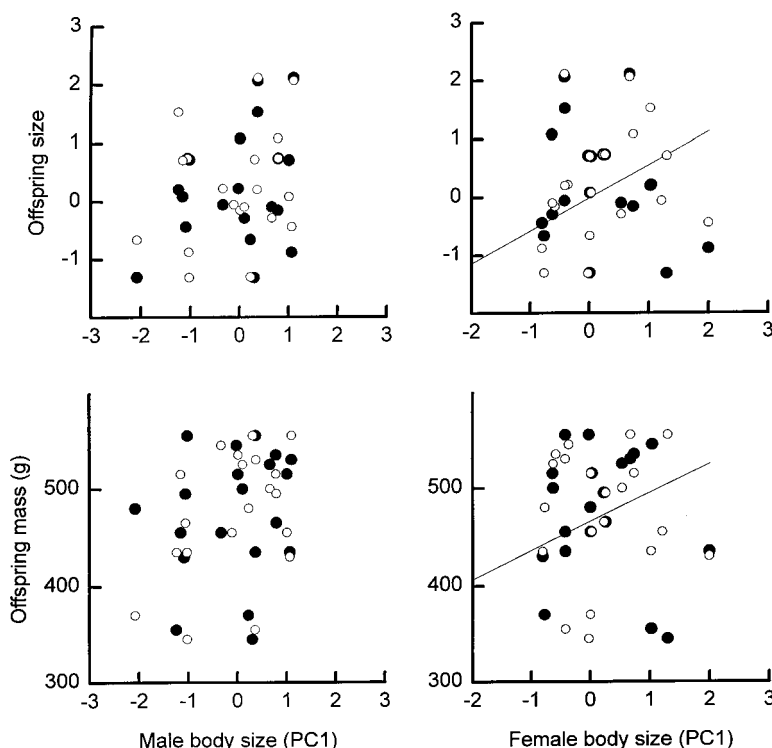
Table 4. Resemblance estimates among offspring body size and body mass and biological and foster parents body size for controls and swapped chicks in 1997/98 at Dumont d'Urville

	Male Resemblance	P	Female Resemblance	P
Offspring size				
Controls	0·083	0·753	1·135	< 0·001
Biological	0·534	0·287	0·923	0·090
Foster	0·610	0·220	0·428	0·454
Offspring mass				
Controls	5·161	0·771	59·243	< 0·001
Biological	59·678	0·063	9·359	0·821
Foster	24·635	0·460	12·952	0·749

1992; see Roff 1992 for a review) egg size was related to female body size in the snow petrel which explained 50% of the variation in egg volume.

During the nesting period the duration of foraging trips is clearly linked to body size, with large-sized birds making shorter trips than smaller-sized ones within each sex, and females making shorter trips than males. To our knowledge the link between adult body size and foraging trip duration has not previously been shown for seabirds. A study on harbour seals (*Phoca vitulina* L.) by Thompson *et al.* (1999) has revealed a relationship between body size and the duration of foraging trips. In that species,

foraging trip duration increases with body size and this relationship may result from variations in the energy constraints acting upon animals of different body sizes. Can the relationship observed in snow petrels be explained by differences in flight efficiency resulting from body size only? Smaller birds have lower wing loading than larger ones and, as aerodynamic theory predicts that flight speed decreases with wing loading (Pennycuick 1989), small snow petrels have a lower flight efficiency than large ones. Consequently, it could take longer for smaller birds to accomplish the same distance during a foraging trip than larger birds. A small snow petrel (250 g)

Fig. 3. Offspring body size and mass in relation to female and male body size. ○ indicate the relationships between swapped offspring and their biological parents. ● indicate the relationships between swapped offspring and their foster parents. Lines indicate the relationship between offspring size ($y = -0.008 + 0.567x$; $r^2 = 0.401$, $n = 30$, $P < 0.001$) and mass ($y = 465.594 + 29.622x$; $r^2 = 0.251$, $n = 30$, $P < 0.001$) and female size for controls.

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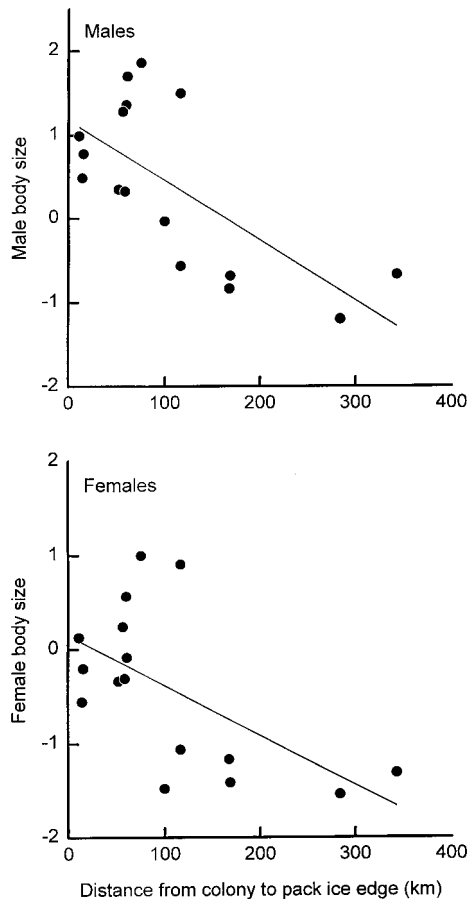*Size-related life
history traits in
snow petrels*

Fig. 4. Male and female body size in relation to distance between colony and the pack ice edge for 16 breeding stations. Males, $r^2 = 0.467$, $P = 0.003$, $y = -0.007x + 1.176$; females, $r^2 = 0.348$, $P = 0.016$, $y = -0.005x + 0.148$.

has an estimated maximum flight speed of $36\,\mathrm{km\,h^{-1}}$ and a large one $(550\,\mathrm{g})$ an estimated maximum flight speed of $42\,\mathrm{km\,h^{-1}}$ (Pennycuick 1989). Assuming large and small birds foraged in the same area, this difference in flight speed (14·3% lower for small birds) is insufficient to account for the observed differences in the length of foraging trips, as small birds spent about 75% more time at sea than large ones (70-h trips vs. 40-h trips). Thus, it is unlikely that the increase in time spent at sea with decreasing body size was only a result of changes in flight speed. Metabolic rate might be involved in the difference in duration of foraging trips between large and small birds. As the rate of energy expenditure per unit mass declines with increasing body size (Peters 1983), one might expect that small birds would use more relative energy than large ones during their foraging trips and, consequently, would need more time to forage for the chick and for themselves. Field metabolic rate per unit mass can be estimated for large and small snow petrels using allometric equations for tubenosed birds (Warham 1996). Estimates are $0.369\,\mathrm{kJ\,day^{-1}\,g^{-1}}$ and

$0.264\,\mathrm{kJ\,day^{-1}\,g^{-1}}$ for small $(250\,\mathrm{g})$ and large $(550\,\mathrm{g})$ birds, respectively. Although small birds have a field metabolic rate per unit mass about 40% higher than large birds, this difference is again insufficient alone to explain the difference in foraging trip duration. Instead, we propose that the increase in time spent at sea with decreasing body size was because of a lower foraging efficiency or because more distant foraging areas were used. This could be achieved through competition for food on the feeding areas, with an advantage for large birds. Other explanations could be differences in food selection between small- and large-sized birds. Small birds may take less accessible prey or may have more difficulties with obtaining the prey as a result of lesser plunging capabilities. Diet differences between large and small snow petrels have not yet been investigated but diving ability has been shown to vary allometrically with body size in alcids, penguins and pinnipeds (Burger 1990; Costa 1991). Lower foraging efficiency with decreasing body size could also explain why females, being smaller than males, made longer foraging trips. In the wandering albatross, females are on average 10% smaller than males and have a lower foraging efficiency during incubation (Weimerskirch 1995). Weimerskirch *et al.* (1997) showed with satellite tracking that the longer duration of short foraging trips in females than in males during chick rearing was the result of females using slightly more distant main feeding areas. Thus, it would be interesting to obtain information on feeding zones relative to sex and body size in the snow petrel. Overall, males tended to make longer incubation shifts, shorter foraging trips and fed their chick more frequently than females. These differences in parental investment between the two sexes suggest that costs incurred by each sex are different.

BODY SIZE-DEPENDENCE OF GROWTH

Chick growth was clearly related to the body size of parents. Most asymptotic values, LGR-values, and peak body mass, were higher for chicks raised by large-sized pairs than by small-sized pairs. Some of these results contrast with what would be expected from wider taxonomic comparisons. In general, large birds grow more slowly than do small birds relative to size (Peters 1983). The snow petrel shows the opposite trend, with large birds growing faster than small birds. Because there is no relationship between the chick-rearing period and the size of adults the more rapid growth rate of the chicks raised by large birds is probably not an adaptation to a shorter period for breeding. The lack of relationship between body size and the duration of the breeding period might reflect the very short favourable period at these high latitudes. Seabirds breeding at high latitudes have short breeding cycles com-

pared to temperate species (Croxall 1984; Warham 1990) and fast growth has probably been selected in these species (Warham 1990). Lorentsen (1996) and Weidinger (1997) found relatively high growth rates in the Antarctic petrel (*Thalassoica antarctica* Gmelin) and in the Cape petrel (*Daption capense* L.), respectively, which breed at high latitudes. As feeding frequency and meal size are positively related to adult body size in the snow petrel, this suggests that the relationship between growth and adult body size is a direct consequence of increased food provisioning with body size. Chicks raised by large parents, receiving larger and more frequent meals would grow more rapidly and reach larger size and mass than those raised by small parents. This implies that food supply may be an important factor determining body size.

In species that provision their young the effect of parental body size on offspring growth has been rarely studied. However, it might have significant effects as the ingestion capacity and prey size are often positively related to body size in many organisms (Peters 1983). de León, Fargallo & Moreno (1998) found that flipper length had a significant effect on meal size in the chinstrap penguin (*Pygoscelis antarctica*), suggesting an advantage of large body size which allows maximization of food carried per visit through foraging efficiency or simply stomach volume. In the sexually dimorphic wandering albatross (*Diomedea exulans* L.) Weimerskirch, Barbraud & Lys (in press) found that male parents bring more food to their offspring than smaller females. This may have important implications for studies on growth rate variation in which the effects of several factors (e.g. egg size, hatch date, parental quality) on growth are disentangled.

DETERMINATION OF BODY SIZE

When we find differences in body size within populations, can they be interpreted as the result of micro-evolutionary changes, or can they be explained by phenotypic plasticity? Results from our chick-swapping experiment make a purely phenotypic determination of body size unlikely. Size and mass of snow petrel chicks were related to the size of biological parents in our control group. Nevertheless the size and mass of swapped chicks were not related to the foster parent size. If size was purely phenotypically determined, swapped chicks would resemble their foster parents in size. Thus, these results suggest that chicks seem partly to inherit the body size of their biological parents. However, this does not imply a purely genetic determination of body size. Otherwise size or mass of swapped chicks would have been significantly related to the size of biological parents, although this tendency was observed. The relationship between foster male bill depth and chick size

and mass together with the relationship between adult size and food provisioning suggest that chick size may be influenced by food availability. Therefore, although body size appears to be partly genetically determined, differences in body size between individuals or populations may result from direct influences of food availability.

Distance and time to reach the feeding areas might influence offspring growth and body size. At Svarthamaren, an inland breeding site situated 200 km from the open sea, Steele (1994) estimated the feeding frequency of snow petrels at once every 19·7 h, although his sample size was low ($n = 3$ nests). This is 2·4 h more than we found on our coastal sites. This slight difference probably reflects the time needed to reach the open sea and the feeding zones. The adult size of snow petrels at Svarthamaren is among the smallest recorded in any colony (Haftorn *et al.* 1988; Marchant & Higgins 1990). Because we found a positive relationship between food provisioning and adult body size, small adult size at Svarthamaren might be partly explained by low feeding frequency as a result of the distance to open sea. This is reinforced by the correlation obtained between body size and distance to the edge of the pack ice for 16 breeding stations. Previous studies have shown that differences in energy supply between populations can account for body size differences (Madsen & Shine 1993b; Wikelski *et al.* 1997). For seabirds in which foraging and breeding areas are commonly spatially disjunct, distances to reach the feeding zones might influence food provisioning and eventually body size. In the black-browed albatross [*Diomedea melanophrys* (Temminck)] Waugh S.M. (unpublished data) found a lower adult body size, a lower feeding frequency and a longer chick-rearing period in a population situated farther from the feeding areas than in a population situated closer to the feeding areas. In the snow petrel our results indicate that the duration of the chick-rearing period does not depend on body size and that body size is related to the distance between colony and foraging area (pack ice edge). Although natal dispersal (Chastel *et al.* 1993; C. Barbraud, unpublished data) would tend to reduce the size variation between colonies in that species, other evolutionary forces may promote this variation.

WHY IS THE VERY LARGE BODY SIZE VARIATION MAINTAINED OVER EVOLUTIONARY TIME SCALES IN THIS SPECIES?

Phenotypic variation may be maintained if selection acts in opposite directions under different environmental conditions (Searcy 1979; Boag & Grant 1981; Endler 1986). Several selection pressures may favour larger or smaller body size at different breed-

ing locations in snow petrels; for example, differential predation by south polar skuas (*Catharacta maccormicki* Saunders) favours small body size at Ardery Island and probably at breeding locations where south polar skuas feed almost exclusively on snow petrels (Barbraud 1999). By contrast differential survival and fecundity promote large body size at Dumont d'Urville (C. Barbraud, unpublished data), and sexual selection in males is suspected to favour large body size at this locality (Barbraud & Jouventin 1998). This, together with natal dispersion and assortative mating by size (Barbraud & Jouventin 1998), could also explain the large body size variation observed at the same breeding colony. Competition among individuals, forcing smaller and maybe less dominant individuals to settle down on remote sites, whereas the larger individuals take the best sites could be another selective force maintaining variation in body size in that species but this has not yet been investigated. Theoretical considerations (West-Eberhard 1989; Moran 1992) and field studies have shown that body size variation (either continuous or discrete) could be maintained over evolutionary time scales. Perhaps one of the most well-known cases of maintenance of body size trait variation is that of Darwin's finches. Beak size is highly variable in *Geospiza conirostris* (Darwin) (CV ≈ 7·2%) and is maintained by the opposing processes of introgression and selection (Grant & Grant 1989). A study on Galapagos marine iguanas (*Amblyrhynchus cristatus* Bell) has shown that body size fluctuates as a result of opposing natural and sexual selection (Wikelski & Trillmich 1997). Among invertebrates, the body size (and horn length) variation in *Onthophagus taurus* (Schreber) is strongly determined by diet quality and plasticity in parental investment and is maintained by alternative reproductive tactics used by large and small males (Moczek & Emlen 1999).

Studies of intraspecific geographical variation in birds generally assume that phenotypic differences are genetic adaptations of populations to local environmental conditions (Gould & Johnston 1972; Zink & Remsen 1986). However, Rhymer (1992) found that body size and growth differences between populations of mallards (*Anas platyrhynchos* L.) are probably caused by environmental factors and do not reflect genetic differences. Other studies also revealed a large environmental component in the geographical variation in avian body size (James 1983; Alatalo & Lundberg 1986; Boag 1987; Larsson & Forslund 1991; Starck, König & Gwinner 1995; Krogstad, Saether & Solberg 1996). Our results also suggested a significant environmental component in the variation in fledgling body size in the snow petrel. It would be interesting to know whether differences in fledgling body size are preserved until adulthood. In that case, the important

intraspecific body size variation in the snow petrel could partly be environmentally determined. Only a common garden experiment, in which hatchlings from different populations grow up under identical conditions, or a reciprocal transplant between coastal and inland sites could distinguish to what degree body size is genetically determined. Such experimental studies conducted on insects or reptiles revealed a considerable sensitivity of body size traits to environmental variations (Shine, Elphick & Harlow 1997; Moczek & Emlen 1999).

This study has shown the importance of examining relationships between body size and life history traits in a bird species showing very large size variation. The very large intraspecific size range provides an opportunity to examine within-species effects of body size on life history traits, and our results indicate that such effects are evident for most of the characteristics examined. One important conclusion may be that it raises the possibility that important life history traits can also be closely correlated with body size in birds, as they are in fish (e.g. Reimchen 1988), reptiles (e.g. Ford & Siegel 1989), mammals (e.g. Clutton-Brock, Guinness & Albon 1983) or invertebrates (e.g. Marshall 1990). If variation in body size is heritable and is linked to major life history traits it may also influence the rate of population change. However, in studies on body-size-related life history traits, determining the relative importance of environmental vs. genetic effects on body size variation is of fundamental importance to understanding the ecological and evolutionary significance of body size variation. Our study reinforces the idea that body size in many organisms seems to be very plastic and may be strongly influenced by environmental variation (Via *et al.* 1995). Environmental effects may even mask microevolutionary responses of structural body size to selection (Larsson *et al.* 1998).

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