Natural selection on body size traits in a long-lived bird, the snow petrel *Pagodroma nivea*

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Abstract

I consider the possibility of selection favouring large body size in a population of snow petrels (*Pagodroma nivea*), a long-lived seabird species. I measured natural selection on body size traits in a population from 1987 to 1998. There was evidence of selection on body size associated with fecundity and survival. Directional selection on bill length and stabilizing selection on tarsus length associated with reproductive success were detected among males. Selection associated with survival favoured males with longer bills. However, selection was weak in all cases. No evidence of selection acting on female body size traits was detected. Offspring–parents regression suggested that bill length and tarsus length were heritable. Although I was able to identify the targets of selection in this population, I could not demonstrate the ecological implications of both tarsus length and bill length variation. The selection on male, but not on female, body size traits suggests factors such as intrasexual competition for nests and/or mates rather than factors such as feeding efficiency as mechanisms of selection on bill size.

Introduction

Natural selection in wild populations of animals has been documented by several studies (see reviews in Endler, 1986; Price & Boag, 1987). Its measurement is of primary importance as it allows the testing of specific ecological hypotheses and provides a measure of adaptation (Lande & Arnold, 1983; Wikelski & Trillmich, 1997). Among birds, detecting differences in fitness associated with differences in body size traits between individuals is often difficult because of the relatively low variability of morphological characters (≈4%) in this taxa. For example, frequent and intense natural selection has been observed in bird species in which morphological variability is high (e.g. Price & Grant, 1984). Moreover, studies that investigated natural selection on size among birds mainly concern short-lived species (Endler, 1986; Price & Boag, 1987, but see Monaghan & Metcalfe, 1986;

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Davies *et al.*, 1988; Choudhury *et al.*, 1996), as they offer more opportunities to detect selection than long lived species due to a shorter generation time, higher mortality rates, and higher breeding frequencies. However, it is necessary to measure selection in a wide variety of organisms with contrasting life-history traits. For example, the lack of data on important lineages within a major group introduces problems in terms of lack of generality of any patterns that are discerned.

Here I analyse the pattern of selection on a series of body size traits in snow petrels (*Pagodroma nivea*) over an 11-year period. The snow petrel is a long-lived colonial seabird that breeds in Antarctica and nearby islands (Marchant & Higgins, 1990; Chastel *et al.*, 1993). The peculiarities of this petrel species are its high intrasexual morphological variability and a remarkable degree of sexual size dimorphism (Prévost, 1969; Isenmann, 1970; Cowan, 1981; Croxall, 1982; Jouventin & Viot, 1985; Barbraud & Jouventin, 1998). Consequently, it offers a good opportunity to examine selection associated with morphological traits in a long lived species of bird. There are distinct differences between populations of the species in morphological traits. Based on morphological

and electrophoretic data, several authors (Jouventin & Viot, 1985; Barbraud & Jouventin, 1998) considered that the species might be divided into a large and a small subspecies which interbreed at some locations. This makes it likely that intraindividual phenotypic and genetic variation is higher than normally observed among birds and it might be more likely to observe a relation between the phenotype and selection. Within each subspecies sexual size dimorphism is clearly marked, males being larger than females, although the males are relatively larger than females in the larger subspecies than in the smaller subspecies (Barbraud & Jouventin, 1998).

Two previous papers have suggested that in snow petrels large adult birds may have a selective advantage. First we have shown that large individuals were more efficient at foraging at sea than small birds (Barbraud et al., in press). Our data strongly suggested that large individuals had an advantage when competing with small ones on the feeding zones to acquire food. Second, there are some indications that intrasexual selection on male size tends to favour large males through increased reliance on physical combat during nest and/or mate defence (Barbraud & Jouventin, 1998). Thus, we may expect a higher survival and/or fecundity for large individuals compared to small ones. In the present paper, I test this hypothesis by documenting selection on body size traits via adult mortality and adult breeding success, and by providing insight into the strength and the form of selection. I also calculate heritability estimates for the body size traits on which selection was measured. Finally, I consider the possibility that sexual selection reinforces or opposes natural selection.

Materials and methods

Field study

The study was carried out on a snow petrel population at Dumont d'Urville (66°40'S, 140°E) in the Pointe Géologie Archipelago, Terre Adélie, Antarctica. Snow petrels lay a single egg in December without a replacement clutch. In January 1987, 244 individuals were captured in nests while incubating their egg, measured and individually banded with a stainless steel band. All measurements were made by the same person and nests were individually marked with a number painted on rocks. From 1987 to 1998, these study nests were surveyed every year during the incubation and fledging periods, and reproductive success, the number of young raised to independence, was recorded. Breeding pairs in study nests were identified when banded. Nestling were banded just before fledging about 40 days after hatching. Regular searches for banded snow petrels were organized throughout the archipelago during the study period.

Repeated sightings of banded birds through each year indicated that disappearances occurred primarily during the nonbreeding season, thus probably in winter at sea, as only one bird (0.4%) died during summer in the colonies over the study period. Disappearance of adult snow petrels from Dumont d'Urville may result from emigration and mortality. In general adult Procellariiformes return to the same breeding site once they have started to breed (Warham, 1990), and the snow petrel is no exception (Guillotin & Jouventin, 1980). Adult snow petrels are not known to disperse: juveniles born at Dumont d'Urville have dispersed to neighbouring and distant islands (500 m to 1320 km distant), but no breeding adult has yet done so (Chastel et al., 1993; T. Micol and P. Jouventin, unpublished data). Moreover, males are known to be strongly philopatric (Guillotin & Jouventin, 1980) and to defend their nest vigorously (Brown, 1966). I therefore assumed that the disappearance of adults resulted mainly from mortality. Although all offspring were banded during the entire study period, analysis of selection on juveniles was not possible as only 3% of fledglings returned to the study site in subsequent years.

Morphology

Three measures of body size were used in the analyses: wing length, bill length and tarsus length (measurement details in Barbraud & Jouventin, 1998). Body mass was not used as large changes in body mass typically occur in Procellariiformes (Croxall, 1984; Warham, 1990). All measurements were made during the same day in January 1987, thus excluding effects of seasonal variation in dimensions. The average age at first breeding is nearly 10 years (ranging from 5 to 14 years, Chastel et al., 1993) and repeatability of measurements made by the same person on snow petrels in subsequent years is high (Barbraud & Jouventin, 1998). Consequently, studied individuals were probably more than 5 years old and I considered that slight growth and shrinkage were not significant during the study. This was confirmed by the nonsignificant differences in body size traits of individuals measured at 2- to 7-year intervals (bill length: paired t-tests, $t_{164} = 1.62$, $P = 0.11$; tarsus length: $t_{104} = 1.18$, $P = 0.24$; wing length: $t_{164} = 1.18$, $P = 0.24$).

Traits were shown not to deviate from the normal distribution hypothesis within each sex (Kolmogorov–Smirnov one sample tests, P values >0.05), and hence all analyses are based on the untransformed data. Within the sexes, traits were linearly related to each other ($r = 0.43$–0.59, $n = 127$, P values <0.001 for males; $r = 0.52$–0.63, $n = 117$, P values <0.001 for females), as assumed by standard selection analyses (Price & Boag, 1987).

To estimate the heritability of body size traits I measured 21 offspring (wing length, bill length and tarsus length) just before fledging in 1997/98, and their parents during the incubation period in early December 1997. Heritability estimates (h^2) for body size traits were

obtained by regressing values of fully grown offspring (i.e. midoffspring values as offspring were not sexed) on male and female parents separately and midparent values (Falconer, 1981). I detected assortative mating between parents with respect to bill length ($r = 0.64$, $n = 21$, $P = 0.002$) and tarsus length ($r = 0.66$, $n = 21$, $P = 0.0012$), but not with wing length ($r = 0.31$, $n = 21$, $P = 0.18$). As assortative mating between parents may influence heritability estimates obtained from offspring–parent regressions I corrected heritability estimates for bill length for assortative mating using correlation coefficients (Bulmer, 1980). Differences between slopes of regressions were tested for significance by a heterogeneity of slopes model (SAS, 1985).

Natural selection

Data were divided into two components of fitness, survival and breeding success. The snow petrel is a long-lived seabird with a particularly low mortality rate considering its relatively small size, and with a low breeding frequency (Chastel et al., 1993). The breeding history of the 244 individuals over the 1987–98 period indicated that, on average, birds attempted to breed in 69.7% of seasons (SD = 0.192, range 0.11–1.0). However, some snow petrels spent up to 4 years without breeding. Therefore I used the variable 'time not seen', i.e. the number of years since the individual was seen for the last time, as a survival variable. Another approach may be to assume that an individual is considered as dead if not seen during the last 5 years of the study (1994–98), as some individuals may spend four years without breeding. The survival variable then becomes a 0–1 variable and it is then possible to test for significance of selection on wing, bill and tarsus lengths using logistic regression. I started with the full model: survival = wing length + bill length + tarsus length. I then skipped the parameters that did not improve significantly the model using the likelihood-ratio test.

For reproductive data, I estimated fitness as the number of offspring surviving to independence produced by an individual during the study period. Individuals measured in 1987 and then not seen were removed from the analysis to avoid an effect attributable to disturbance caused by the action of taking the measurements.

Analyses of selection on body size were made with wing length, bill length and tarsus length. Coefficients of selection intensity were calculated using the parametric technique developed by Lande & Arnold (1983) which involves calculating the selection differential S, the directional gradient β and the stabilizing selection differential C for estimating stabilizing and disruptive selection. S is the difference between the mean value of the character before and after selection. The directional selection gradient (β) is calculated as the partial regression coefficients of relative fitness regressed on the original three traits combined and standardized (Lande

& Arnold, 1983). R^2 refers to the fit of the model. The stabilizing selection differential C in the absence of directional selection is defined as the change in the variance of a character before and after selection and indicates stabilizing selection when $C < 0$ and disruptive selection when $C > 0$ (Schluter & Smith, 1986). I used methods outlined in Schluter & Smith (1986) to calculate and to test significance of coefficients of selection.

Before calculating directional selection differentials and gradients, all measurements were first standardized to have unit variance (Price & Boag, 1987). Males and females differ in the size of all morphological traits (Barbraud & Jouventin, 1998), and so were analysed separately. Adult birds were sexed by vocalization, calls of males pitched lower than those of females (Guillotin & Jouventin, 1980).

I used the nonparametric cubic spline technique to estimate the fitness function relating relative fitness and survival to male bill length and tarsus length (Schluter, 1988). To estimate confidence limits, standard errors were generated by resampling the original data set with 200 repeated bootstraps (Schluter, 1988). Analyses were performed using a program kindly supplied by D. Schluter.

For significant directional selection differentials, the statistical power of the test was computed using the formula $z(\beta) = \sqrt{(n)} \times S + z(1 - \alpha)$ (Lynch & Walsh, 1998), where n is the sample size, S is the standardized directional selection differential and z gives the proportion of the normal curve that lies beyond a given normal deviate.

Sexual selection

Snow petrels are largely monogamous. Nevertheless, opportunity for sexual selection on morphological traits may be present as not all males acquire a mate and breed during the breeding season following a mate change. I retained males that changed their mate during the study period. I used the number of breeding seasons separating the last breeding event of those males and the first breeding event with a new mate as an index of mating success. Selection differentials were computed and tested as for survival and breeding success data.

Results

Table 1 gives measurements of adult males and females measured in 1987. A multivariate analysis of variance revealed significant sexual dimorphism in the mean phenotype (Wilks' lambda = 0.68, $F_{3,240} = 36.94$, $P < 0.001$). Males were significantly larger than females in all characters (t-tests, $P < 0.001$ in each case). All three morphological measures are strongly correlated with each other (Table 2). Heritability estimates for body traits are summarized in Table 3. Almost all heritabilities were significantly different from zero. Comparisons of

Table 1 Characteristics (mean ± SD) of adult male and female snow petrels measured in 1987 at Dumont d'Urville.

	Males	Females
Wing length (mm)	304.2 ± 9.6 (279–324)	293.0 ± 10.6 (263–316)
Bill length (mm)	25.0 ± 1.6 (21.1–28.9)	23.1 ± 1.4 (19.4–26.6)
Tarsus length (mm)	37.0 ± 1.8 (31.1–41.0)	35.8 ± 2.0 (29.7–39.3)
Sample size	127	117

Table 2 The correlation matrix for morphological measurements in male and female snow petrels measured in 1987 at Dumont d'Urville. All P values <0.001.

	Males			Females		
Character	Wing	Bill	Tarsus	Wing	Bill	Tarsus
Wing	–	0.60	0.39	–	0.64	0.63
Bill		–	0.42		–	0.54
Tarsus			–			–

Table 3 Heritability estimates (h^2) from regressions of offspring on parents for three body size traits in the snow petrel. Sample size is 21, and h^2 values are given ±SE. *P < 0.05, **P < 0.01, ***P < 0.001, the probabilities that h^2 are significantly different from zero.

Offspring	Father	Mother	Midparent
Wing length	0.44 ± 0.32	0.41 ± 0.20*	0.62 ± 0.28*
Bill length	0.78 ± 0.30***	0.91 ± 0.32***	0.84 ± 0.15***
Tarsus length	0.86 ± 0.23**	0.68 ± 0.12***	1.05 ± 0.14***

Table 4 Standardized directional (S) and stabilizing (C) selection differentials associated with reproductive success and survival in adult snow petrels for the period 1987–98. I is the variance in relative fitness, n the sample size, with the proportion surviving in parentheses. *P < 0.05.

	Males		Females	
	S	C	S	C
Reproductive success				
Wing length	0.08	–0.04	–0.03	–0.04
Bill length	0.17*	0.04	0.03	–0.02
Tarsus length	–0.03	–0.08*	0.05	–0.03
I	0.41		0.40	
n	127		117	
Survival				
Wing length	0.07	–0.10	–0.04	–0.04
Bill length	0.17*	0.10	–0.02	0.04
Tarsus length	–0.02	–0.04	–0.02	–0.03
I	0.87		0.83	
n	127 (0.74)		117 (0.79)	

regressions of offspring bill length on values of mothers' and fathers' tarsus lengths showed similar degree of resemblance between offspring and mothers and fathers bill length (ANOVA, $F_{1,38} = 0.22$, $P = 0.64$), and between offspring and mothers and fathers tarsus length ($F_{1,38} = 0.49$, $P = 0.49$).

Although variance in relative fitness for reproductive data was small for males and females (Table 4), there was significant directional selection associated with reproductive success on male bill length ($P = 0.006$; see Fig. 1A). Stabilizing selection acted on male tarsus length ($P = 0.008$; see Fig. 1B) but was weak: the standardized coefficient $C = -0.08$ indicates that variance in tarsus length was reduced by only 8% between 1987 and 1998. Values of the selection gradient β suggest that selection associated with male reproduction was only restricted to bill length (Table 5). The proportion of variance in relative fitness for reproductive data explained by the multiple regression is significant for males ($R^2 = 0.10$, $n = 127$, $P = 0.006$). There was no selection associated with reproductive success on female size traits during the study period (all P values >0.05).

Variance in adult survival was relatively small for males and females (Table 4), suggesting that mortality was low during the period 1987–98. Standardized selec-

tion differentials were significant only for bill length in males ($P = 0.041$; Table 4), indicating that selection favoured males with longer bills. Standardized selection differentials were significant for none of the original three traits in females (Table 4). Logistic regression did not indicate significant selection associated with survival on the morphological traits in both males and females (P values >0.24).

The power of the test for directional selection associated with reproductive success and survival was 0.52 for a two-sided test and 0.60 for a one-sided test.

Among 44 males that changed their mate during the study period, 33 acquired a new mate in the next two following breeding seasons. The directional selection differential for wing, bill and tarsus lengths were –0.09, –0.10 and 0.07, respectively, but none was significant after correction for multiple tests (all P values >0.39). The stabilizing selection differentials were 0.24, –0.09 and 0.08, respectively, for these same traits, and none was found to be significant after correction for multiple tests (all P values >0.07).

Discussion

Despite the relatively low variance in relative fitness associated with reproductive success and survival, there was evidence of natural selection on body size traits in male, but not female, snow petrels over the period 1987–98. Morphological variation in the snow petrels measured in 1987 was relatively low compared to the variability found by several studies at Dumont d'Urville (Isenmann, 1970; Jouventin & Viot, 1985; Barbraud & Jouventin, 1998). Despite this relatively low variability, size in the snow petrel was found to be associated with variation in reproduction. Both directional and
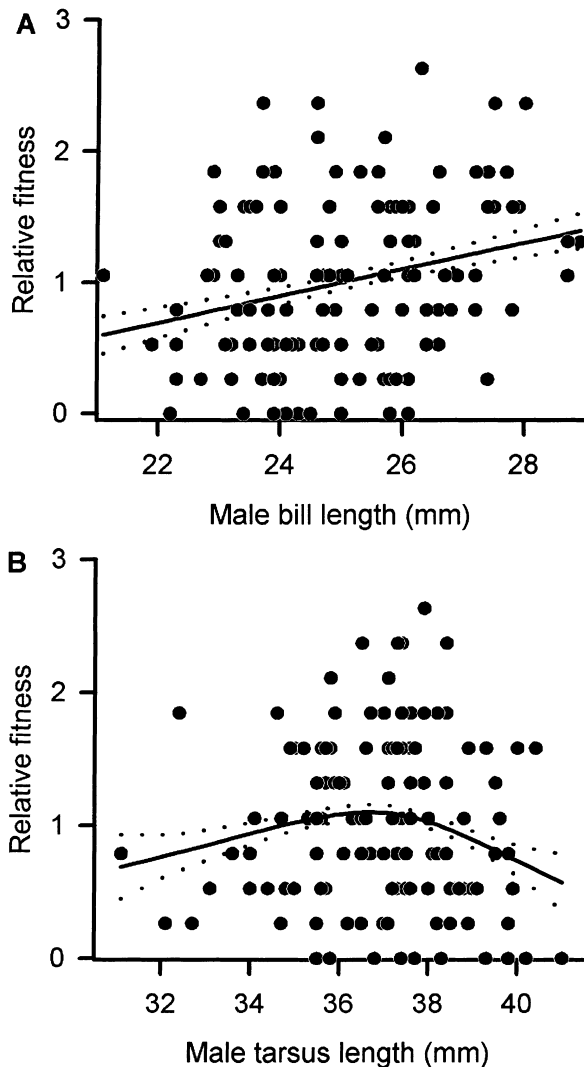
Fig. 1 Fitness functions of two morphological traits in adult male snow petrels calculated using the cubic spline technique (Schluter, 1988). The closed circles indicate raw data values. Relative fitness in relation to (A) bill length and (B) tarsus length. Relative fitness is the number of offspring fledged per male, divided by the mean number of offspring fledged. Data are for the period 1987–98.

Table 5 Selection gradient (β) associated with reproductive success and survival for adult male and female snow petrels for the period 1987–98. *$P < 0.05$.

	Males	Females
Reproductive success		
Wing length	0.01 ± 0.07	−0.13 ± 0.08
Bill length	0.22 ± 0.07*	0.05 ± 0.08
Tarsus length	−0.12 ± 0.06	0.11 ± 0.08
R^2	0.10*	0.03
Survival		
Wing length	−0.02 ± 0.10	−0.06 ± 0.12
Bill length	0.23 ± 0.11*	0.01 ± 0.11
Tarsus length	−0.11 ± 0.09	0.01 ± 0.11
R^2	0.05	0.00

stabilizing selection associated with reproductive success were detected among males. Adult males that produced more young had longer bill than other males, and stabilizing selection acted on tarsus length. These results tend to confirm the hypothesis of a selective advantage for large individuals, but for males only. Selection on male bill length associated with survival was only detected using one method, suggesting that adult males with longer bill than other males had higher survival but that selection was weak. Both estimates of survival (time not seen and dead if not seen during the last 5 years of the study) may not indicate only mortality but also emigration, although adult snow petrels are extremely

philopatric (Chastel *et al.*, 1993) making this hypothesis unlikely.

However, the results suggest weak selection, as indicated by the low selection differential estimates, and relatively low statistical power of the test. Nevertheless, as computed, the low statistical power was more a consequence of low selection differential estimates than a consequence of small sample size. One may argue that the evaluation of the significance of the selection gradients and selection differentials should be improved using Bonferroni correction for multiple testing. First, Bonferroni correction is too conservative as the traits are correlated and even with Bonferroni correction, the level of significance is still below 0.1 which is usually considered marginally significant. Second, as R^2 refers to the fit of the model then a significant overall result and one significant partial regression coefficient can be interpreted as both being significant by Fisher's LSD principle (Miller, 1981). Thus, I conclude that selection is weak but significant.

One may have expected selection on female bill size due to reproductive success or survival through correlated effects of assortative mating by size and differential male reproductive success based on size. Perhaps this was caused by the relatively low correlation coefficient found between male and female size of a pair at Dumont d'Urville (0.58, Barbraud & Jouventin, 1998).

Both subspecies interbreed at the study location and it seems that the study population is a relatively recent admixture of the large and the small subspecies (Barbraud & Jouventin, 1998). This situation probably partly explains the important intraspecific phenotypic variation observed at the study location, which makes it likely that a relation like the one measured in this study between the phenotype and selection would be observed. Although this does not invalidate the present study, it is not clear if this rather special situation generalizes to other long-lived species. The interbreeding of the large and the small subspecies at Dumont d'Urville probably results in heritability estimates higher than usual, and

sample sizes used to estimate heritabilities were small. However, a cross-fostering experiment conducted at the same location indicates that body size is heritable in that species (Barbraud et al., in press).

Since the traits were found to be heritable, the results imply significant potential for evolutionary change. However, these changes will probably be difficult to detect as immigration of nonbreeding birds occurs relatively frequently at Dumont d'Urville (Chastel et al., 1993). The difficulty of finding a response to selection is probably enhanced by (i) the fact that snow petrels are long-lived and populations have overlapping generations, (ii) the relatively low intensity of selection and (iii) the expected response to selection is probably reached slowly and asymptotically as favoured individuals come to dominate the entire age structure (Charlesworth, 1980). The frequency distribution of male body size traits of snow petrels at Dumont d'Urville is left-skewed, indicating a lower proportion of small birds (Barbraud & Jouventin, 1998). This could reflect the differential selection pressure on bill length associated with survival and reproductive success found in this study. Nevertheless, the evidence for directional and stabilizing selection on bill and tarsus length, respectively, and associated performance information suggests that selection at Dumont d'Urville may play a role in reducing the variation observed on this island.

Natural selection operating differentially on males and females with no selection on body size traits on females and with directional (bill length) and stabilizing (tarsus length) selection on males may result in sexual size dimorphism (Darwin, 1871). Interestingly, the sexual size dimorphism in snow petrels is among the greatest in the Procellariiformes (Croxall, 1982; Barbraud & Jouventin, 1998). This pattern of selection also offers an opportunity for sexual selection to operate through female choice for males with long bills. Barbraud & Jouventin (1998) gave results that support the intrasexual selection hypothesis as a factor leading to sexual size dimorphism in that species, but they did not investigate the mechanisms of female choice. Because snow petrels are monogamous and show high mate fidelity, mechanisms of mate choice would probably be difficult to detect. My present results suggest that larger males did not acquire a new mate more rapidly than smaller males. However, the time between the end of one pair-bond and the next breeding may only poorly reflect mating success.

The mechanisms by which selection acted on bill and tarsus length could not be tackled in this study as no observations on the ecological importance of these traits were made. Variation in bill and tarsus length may be related to some combination of foraging abilities (Schluter & Smith, 1986), mating success (Price, 1984) or climate adaptations (James, 1970). Although there is some indication that variation in body size is associated with foraging abilities in the snow petrel, with large

individuals having better foraging abilities than small ones (Barbraud et al., in press), definitive conclusions cannot be drawn. Detailed studies of feeding are necessary to understand the functional and ecological significance of bill and tarsus lengths in snow petrels but are difficult in practice. The fact that selection was found only on male bill size rather suggests that a possible mechanism of selection is intrasexual competition for nest and/or mate. For example, large body and bill size may constitute an advantage during physical combat for nest and/or mate. If a large bill size permits a better foraging ability I would probably have found selection on female bill size. In addition, this also suggests that individuals with a large bill size would be in a better condition. Condition was not measured during the present study but was measured as the residuals of the regression of body mass on body size in 1993 for another purpose. Using these data I found no correlation between bill size and condition in males (Pearson correlation coefficient, $r = 0.03$, $n = 51$, $P = 0.82$) and in females ($r = 0.03$, $n = 42$, $P = 0.86$).

Natural selection on body size traits has been found in several short-lived species of birds (Endler, 1986; Price & Boag, 1987; Smith, 1990; Wiggins, 1991), but very few studies have reported selection on body size traits in long-lived bird species (Monaghan & Metcalfe, 1986; Davies et al., 1988; Choudhury et al., 1996). Long-term data bases on long-lived species of birds are now becoming relatively abundant and should be useful in estimating the occurrence of natural selection on body size traits in these species.

However, my estimates of heritability might have been biased by several factors. First, the estimates of the standardized directional selection gradient may be biased. Indeed, an important assumption of the gradient analysis is that there has been no selection on unmeasured traits that are correlated with the traits measured. Violation of this assumption may lead to biased estimates of β. In the snow petrel, bill depth is highly correlated with the three traits measured in the present study (Barbraud & Jouventin, 1998), and was not measured in 1987. Thus, one can not reject the possibility that selection also acted on bill depth, and estimates of β might be biased. Second, the age structure of the study population was not known when birds were measured and this might have biased the estimates of selection differentials (Endler, 1986). However, inclusion of only breeding birds removed effects of selection on juveniles, immatures and adults prior to breeding. Finally, heritability estimates might have been biased by environmental effects and genotype–environment interactions (Bulmer, 1980; Falconer, 1981), but also by behaviour such as extra-pair fertilization, intraspecific nest parasitism and adoption of alien young (Larsson & Forslund, 1992). Snow petrels are strictly monogamous (Brown, 1966; Isenmann, 1970) and nest site fidelity is high (Chastel et al., 1993); moreover; chicks are nidicolous and adoption of alien

young has never been recorded (Warham, 1990). Thus, the last three factors are probably of minor importance in this species. Environmental effects were not examined in this study; however, between-year differences in fledging bill length and wing length calculated over 6 years are only 2.7% and 3.2%, respectively (Barbraud unpublished data), indicating relatively weak environmental influence on fledging size. Moreover, a cross-fostering experiment conducted on snow petrels shows that a significant part of the parent offspring resemblance in body size is due to genetic factors (Barbraud *et al.*, in press). The nonsignificant heritability value for wing length might be explained by the fact that offspring wing length had not yet reached its asymptotic size when measured, coupled with the larger size of males than females. In Procellariiformes, wing length at fledging is generally less developed than other body dimensions (Warham, 1990). Although genotype–environment interactions may have biased my estimates, I suggest that a substantial proportion of the estimated heritabilities reflects the transmission and segregation of genes with additive effects on body size. This has been shown for many species of birds (Boag & van Noordwijk, 1987). The inability to determine the sex of the offspring measured and the sexual size dimorphism are likely to have lowered the heritability estimates. This is, however, of minor concern since heritability estimates were generally very high.

To conclude, the results show weak directional selection on bill size and weak stabilizing selection on tarsus length in males, but no selection on female body size traits. Determining the extent to which selection acted on male body size may have contributed to the understanding of the present-day pattern of morphological variation in that population with a high proportion of large-sized males. The absence of selection on female bill size may allow us to reject factors linked to feeding efficiency as mechanisms for selection, but rather suggests factors such as intrasexual competition for nest and/or mates.

Acknowledgments

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