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Early body condition and hatching success in the snow petrel *Pagodroma nivea*

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Abstract We examined how variations in parental quality affect the reproductive success of a long-lived seabird, the snow petrel (*Pagodroma nivea*). In particular, we focused on how prebreeding body condition (prebreeding body mass adjusted for structural size) influences the hatching success of male and female snow petrel. Condition in females, but not in males, had a significant effect on hatching success. Among breeding pairs, early body condition of pairs was not significantly related to their hatching success. Laying date had a significant effect on hatching success, but this was due to heavy snowfalls during the beginning of the laying period. We suggest that females in poor early condition would not be able to build up sufficient body reserves necessary for successful incubation during the energy-demanding egg formation period. Moreover males, being structurally larger, would have a higher fasting capacity. These results show that the hatching success of the snow petrel is clearly influenced by female condition and suggest that effects of variations in environmental conditions may depend on body condition of individuals. However, the year of the study appeared to be an unusually poor year for reproduction, which may be why female body condition appears to be important.

Introduction

Within individual seabird species, several long-term studies have demonstrated large individual variation in reproductive success (e.g. Ollason and Dunnet 1988; Monaghan et al. 1989; Wooller et al. 1992). Variance in individual reproductive success has two major components. First, variation arises from stochastic environmental effects such as weather (Boersma et al. 1980), oceanographic conditions and marine resources (Croxall 1992; Montevecchi 1993), nest-site quality (Birkhead and Furness 1985) or predation (Penny 1974). Second, variation in reproductive success may be related to individual quality (e.g. Coulson 1968; Chastel et al. 1995; Lorentsen 1996). These two mechanisms are not mutually exclusive and effects of environmental stochasticity on breeding success may depend on the quality of the parents (Saether et al. 1997). In the Antarctic petrel (*Thalassoica antarctica*), high parental quality can reduce the influence of stochastic environmental variation on reproductive success (Saether et al. 1997). The relative effects of these two mechanisms on variation in reproductive success have important consequences for our understanding of the adaptive significance of life-history variation in birds.

Several studies on birds have shown that reproductive success increases with age or experience (see Saether 1990) which, in turn, may be positively correlated to body mass or condition (Newton 1988; Saether 1990; Weimerskirch 1992). Thus, individuals in good condition may be more efficient foragers or feeders than individuals in poorer condition (Reid 1988, but see Weimerskirch 1995).

The snow petrel is a small-sized petrel (250–500 g) endemic to Antarctica and the surrounding Southern Ocean and is circumpolar in distribution (Harrison 1983). The species is a specialist forager and only occurs where there is some degree of sea-ice cover (Griffiths 1983; Ainley et al. 1984). Thus, this highly pagophilic seabird forages over coastal, neritic and pelagic waters during the breeding season (Ainley et al. 1984). Birds visit their breeding grounds a month before laying, which occurs in early December. After laying, both parents incubate the single egg alternately until hatching, males making slightly longer incubation spells (ca. 7 days) than females (ca. 6 days; Brown 1966; Isenmann 1970).

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In the snow petrel (*Pagodroma nivea*) Chastel et al. (1993) have demonstrated the effects of large-scale variation in the marine environment and weather on variation in individual reproductive success. However, no study has evaluated the relationship between individual quality and reproductive success in this species. In this paper we evaluate the importance of individual quality for individual variation in reproductive success of the snow petrel. We examine the variation in early body condition (prebreeding body mass corrected for body size) of adult snow petrel to assess the relationship between early condition and hatching success in both males and females.

Materials and methods

The study was carried out at Pointe Géologie (66°40′S, 140°01′E) in Terre Adélie, Antarctica, during the austral summer 1993/1994. During the prebreeding period (29 October to 20 November), petrels occupied nests and inspections of nests were conducted on 15 November 1993 to measure prebreeding body mass and body size of each individual. Nests occupied by birds were individually marked and birds were tagged with metal bands. Birds were sexed using vocalisation (males have lower pitch than females, Guillotin and Jouventin 1980) and weighed to the nearest 5 g with a 500-g Pesola scale. Nests were checked daily in early December to determine laying dates. Hatching success was determined by inspection of nests a few days after hatching (range: 10–25 January).

We obtained a measure of overall body size of adults from a factor analysis (Rising and Somers 1989) using tarsus length (0.1 mm), bill length (0.1 mm; from feathers to tip of bill), bill height (0.1 mm) and wing length (1 mm; maximum flattened chord). As male and female snow petrel differ greatly in size (Barbraud and Jouventin 1998) they were analysed separately. Factors were extracted by a principal components analysis, and the resulting factor score for each individual (PC1) was assumed to represent overall body size. Body condition of an individual was defined as the residuals obtained when body mass was regressed against the factor score for overall body size (Jolicoeur and Mosimann 1960). Body mass during the prebreeding period was related to the factor scores (body mass = 28.02 PC1 + 389.91, $r = 0.72$, $P < 0.001$ for males, and body mass = 19.95 PC1 + 324.56, $r = 0.73$, $P < 0.001$ for females). As an index of body condition, we used the residuals from this regression of PC1 on body mass. There was no significant correlation between the residuals and PC1 score ($r = -0.01$, $P = 0.95$ for females and $r = -0.004$, $P = 0.98$ for males). To examine the relationship between hatching success and laying date and body condition of males and females we used a logistic regression (with binary response) where the y-variable was success or not success. We started with the full model: hatching success = female body condition + male body condition + laying date. We then skipped the parameters that did not significantly improve the model using the likelihood-ratio test.

Results

Males had significantly higher prebreeding body mass than females (Table 1, ANOVA: $F_{1,91} = 27.73$, $P < 0.001$) and prebreeding condition of males and females did not differ significantly (Table 1, ANOVA: $F_{1,91} = 0.24$, $P = 0.63$). Among breeding pairs, no significant relationship was found between male and female (of the same pair) prebreeding body condition (Pearson correlation: $r = 0.14$, $P = 0.39$, $n = 38$).

Mean laying date was 5.4 ± 2.9 December 1993 ($n = 29$, range: 1–11 December 1993). Laying date was not significantly correlated with female body condition ($r = 0.30$, $n = 29$, $P = 0.11$), but correlated significantly with female body size ($r = 0.51$, $n = 29$, $P = 0.005$). Since body size influences laying date, we corrected the latter by body size (PC1) and examined the relationship between corrected laying date and female body condition. No significant relationship was found between these two variables ($r = 0.13$, $P = 0.51$, $n = 29$). There was a significant effect of laying date on hatching success ($\chi^2 = 22.84$, $df = 1$, $P < 0.001$). Successful females laid their egg later (mean 6.71 ± 2.14 December, $n = 7$) than unsuccessful females (mean 5.05 ± 2.98 December, $n = 22$). Males that successfully hatched their egg tended to be in better prebreeding condition than males that were unsuccessful at the hatching stage (Fig. 1), but the difference was not statistically significant ($\chi^2 = 0.37$, $df = 1$, $P = 0.54$). In females, the same trend was observed and the difference was significant ($\chi^2 = 9.34$, $df = 1$, $P = 0.002$; Fig. 1). Pairs where both male and female were in good body condition tended to hatch their egg more successfully than pairs where male and female were in poor body condition, but the difference was not statistically significant ($\chi^2 = 4.86$, $df = 2$, $P = 0.09$).

In our studied nests few eggs hatched in 1993/1994 ($n = 15$ chicks) and few chicks fledged ($n = 12$ chicks). Thus, we could not compare body condition of individuals that fledged their chick to those that hatched their egg but failed to fledge their chick.

Discussion

The data presented here indicate that laying date had an effect on hatching success in 1993/1994, late-laying females being more successful than early-laying females.

Table 1 Mean (SD) values of body mass and prebreeding condition of male and female snow petrels breeding at Terre Adélie in 1993/1994

	Mean ± SD	*n*	Range
Females			
Body mass (g)	323.6 ± 47.7	42	240–440
Prebreeding body condition	–0.3 ± 32.7	42	–110.0 to 60.6
Males			
Body mass (g)	389.8 ± 66.9	51	265–545
Prebreeding body condition	–1.9 ± 48.3	51	–98.9 to 130.9

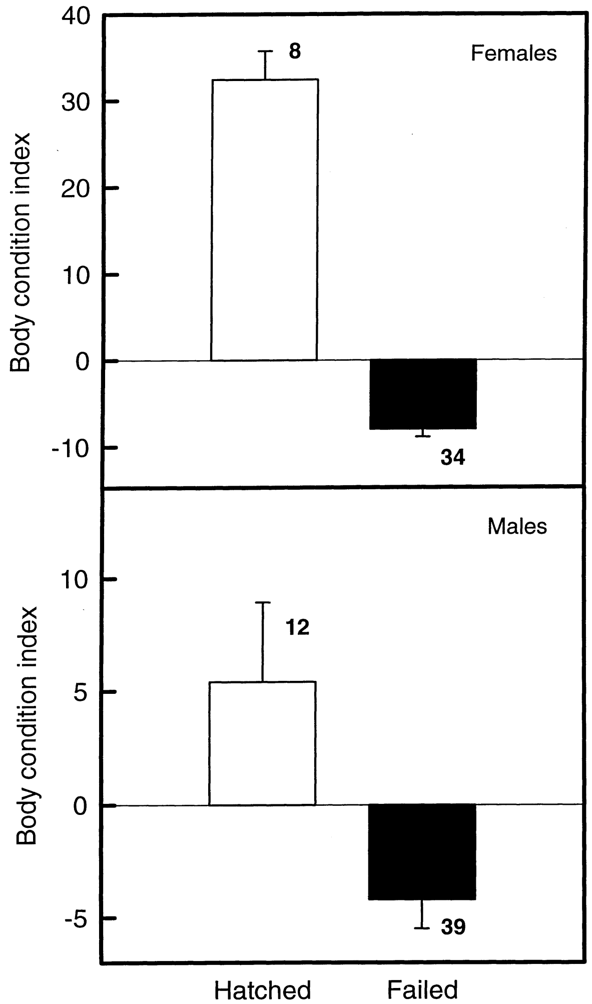

Fig. 1 Average prebreeding body condition of female and male snow petrels relative to hatching success in Terre Adélie in 1993/1994. *Bars* indicate standard errors. *Numbers* indicate sample sizes

However, this effect was mainly due to heavy snow falls that occurred early during the laying period and that caused important nest failure through flooding and ice formation into the nests (C. Barbraud, personal observation).

In this study, variations in prebreeding body condition seem not to have the same implications in males and females. In females, birds exhibiting high condition indices were more likely to hatch their egg. This finding is consistent with the parental-quality hypothesis, which predicts that attributes of the parents influence fecundity. This hypothesis is also supported by studies on other fulmarine petrel species, the Antarctic petrel (Lorentsen 1996; Saether et al. 1997) and the cape pigeon *Daption capense* (Weidinger 1998). Amundsen (1995) found no effect of parental quality on early nestling growth in snow petrels but suggested that egg size, to some extent, reflects parental quality in that species, although his sample sizes were very small. After the prebreeding period female snow petrels leave the nest and stay at sea for ca. 3 weeks (pre-laying exodus) during which the egg is made. After laying, the male incubates the egg for ca. 8 days and is relieved by the female who incubates for ca. 7 days. We suggest that breeding females in poor body condition during the prebreeding period would not be able to build up sufficient body reserves necessary for successful incubation during the energy-demanding egg formation period. Consequently, the females with low condition early in the season would attain more rapidly a threshold mass at which they would abandon incubation. The existence of a threshold mass has been demonstrated for the male blue petrel (*Halobaena caerulea*) by Chaurand and Weimerskirch (1994) and several studies on seabirds have shown that the decline in body mass was the critical factor causing abandonment during incubation (Lorentsen and Røv 1995; Tveraa et al. 1997). Although female snow petrels in poor condition could restore their condition during the first incubation shift carried out by the male, this shift could be too short to attain sufficient body condition necessary for successful incubation.

In contrast to females, body condition had no significant influence on hatching success for males. Male snow petrel also make a pre-laying exodus of ca. 3 weeks. However, as they do not need to produce an egg, males in poor condition during the prebreeding period can restore their condition and attain a sufficient condition to incubate successfully. Thus, condition at the beginning of the first incubation shift is probably more important than prebreeding condition for successful incubation in males, as found in the blue petrel by Chastel et al. (1995). However, the presumed greater ability to restore energy reserves in males than in females in Antarctic petrels and wandering albatrosses (Lorentsen and Røv 1995; Weimerskirch 1995) could partly explain why the influence of body condition on hatching success differed between the sexes in snow petrels.

Our results indicate that the ability of the male to hatch a chick will mainly depend on the female's condition. This finding could also be analysed in terms of an allometric relationship. Larger species have a greater ability to store proportionally more fat reserves than smaller species (Blem 1990). Among petrels, two studies support this hypothesis. In the large wandering albatross (*Diomedea exulans*) (ca. 10 kg) the safety margin, i.e. the difference between the average proportions of mass at relief and at desertion, is nearly 20% (Weimerskirch 1995). In the smaller blue petrel (ca. 200 g) this safety margin is only 3% (Chaurand and Weimerskirch 1994). The snow petrel is one of the most sexually dimorphic species of petrels, males being much larger (nearly 8%) and heavier (20.5%) than females (Barbraud and Jouventin 1998). Structurally larger males may have a greater safety margin than smaller females and thus may be able to endure longer fasting periods during incubation. The duration of incubation shifts seems to be a compromise between the success of the foraging bird and its mate's ability to fast on the nest (Weimerskirch 1995; Tveraa et al. 1997). Thus, if one assumes that males have a greater ability for fasting and restoring body reserves than females, this may partly explain why males' ability to hatch a chick mainly depends on the females' condition. Female body condition may be more important for this species than for many other Procellariiformes as the males are much larger than the females.

The strong effect of early body condition for females may have been related to unusually poor environmental conditions in 1993. Indeed, the hatching success for snow petrels was particularly low in Terre Adélie in 1993 (19.6%, C. Barbraud, personal observation) compared to the average hatching success obtained over a 27-year period (63.3%, range: 37.5–82.7%, Chastel et al. 1993). Thus, good body condition may have been important for snow petrels for reducing the influence of poor environmental conditions on hatching success. Similarly, Saether et al. (1997) found a particularly strong effect of body condition on reproductive success in Antarctic petrels in 1993, which was also marked by poor weather at their study site compared to other more favourable years. Consequently, our results demonstrate that the hatching of the chick in poor years is related to female body condition. Data from more years would be needed to know if female condition is important for reproduction in most years. Ideally, one would have to conduct experimental studies each year to separate the effect of nest quality or egg quality from female body condition if female condition was correlated with these parameters.

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