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Body Condition and Parental Decisions in the Snow Petrel (*Pagodroma nivea*)

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ABSTRACT.—In Procellariiformes, parents guard the chick for some time after it has attained homeothermy. Such a strategy may have evolved to protect the chick from predation or inclement weather, but it is costly because only one parent can forage at a time. Therefore, the decision to leave the chick seems to be a trade-off between the chick's ability to care for itself, body condition of the parent present at the nest, and ability of the bird out foraging to return to the nest before its mate's body condition has degraded. We studied chick growth and survival together with number of days Snow Petrel (*Pagodroma nivea*) chicks were guarded before being left alone for the first time in relation to the parents body condition and ability to return to the nest in time. Parents in good body condition were more likely to produce a chick that survived the guard stage. They also guarded their chick for a longer period (range 2–8 days, \bar{x} = 4.5) and finally left it alone with a higher body mass than those in poor body condition. However, whether the foraging bird was able to return to the nest in time to relieve its mate was also strongly related to number of days the chick was guarded and its body mass. The chicks' survival from when they were left alone and until day 10 posthatch was positively related both to number of days they were guarded and their body condition (body mass corrected for age).

RESUMEN.—En los Procellariiformes, los padres cuidan del pichón por cierto tiempo después que éste ha alcanzado la homeotermia. Esta estrategia pudo haber evolucionado para proteger a los pichones de la depredación o de las inclemencias del clima, pero es costosa pues sólo uno de los padres puede forrajear en un momento dado. Por tanto, la decisión de

abandonar al pichón parece ser un compromiso entre la habilidad de éste para cuidar de sí mismo, la condición corporal del padre que se encuentra en el nido y la habilidad del ave que se encuentra forrajando para regresar al nido antes que la condición de su pareja se degrade. Estudiamos la relación entre el crecimiento y la supervivencia de pichones y el número de días en que fueron resguardados antes de ser dejados solos por primera vez, la condición corporal de los padres y su habilidad para regresar al nido a tiempo. Los padres en buena condición física tuvieron una mayor probabilidad de producir pichones que sobrevivieran a la etapa de resguardo. Ellos también resguardaron a sus pichones por períodos más prolongados (rango 2–8 días, \bar{x} = 4.5) y finalmente los abandonaron cuando tenían una masa corporal superior que aquellos padres en peor condición corporal. La capacidad del ave que se encontraba forrajando para regresar al nido a tiempo para relevar a su pareja, estuvo estrechamente relacionada con el número de días en que el polluelo fue resguardado y con su masa corporal. La supervivencia de los pichones desde el momento en que fueron dejados solos hasta el décimo día después de la eclosión estuvo relacionada positivamente tanto con el número de días en que fueron resguardados como con su condición corporal (masa corporal corregida por edad).

Seabirds within the order Procellariiformes are well known for their life-history strategy that includes delayed maturity, low annual fecundity, high annual survival rates and slow chick growth (Warham 1990). Their foraging trips may last for several weeks (Harris 1973, Weimerskirch 1995, Weimerskirch and Cherel 1998) and allow parents to search for food over large areas and at long distances from the colony (Weimerskirch 1995, Weimerskirch et al. 1999). Whereas that strategy may alleviate the negative effect of local variability in prey availability, it

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may also be risky because both body mass of the parent guarding the chick and rate of food delivery to the chick will be depleted when foraging trips are long.

In recent years, a number of studies have focused on importance of parental body condition for breeding success in birds (e.g. Chastel et al. 1995a, b; Lorentsen 1996; Erikstad et al. 1997; Barbraud and Chastel 1999). Apparently, parental body condition may outweigh at least some of the negative effect of variation in food availability. Parents in good body condition are more likely to reproduce (Chastel et al. 1995a, b; Barbraud and Chastel 1999) to sustain longer fasting periods (Chaurand and Weimerskirch 1994a, Yorio and Boersma 1994) and to guard their chick for a longer period than those in poor body condition (Tveraa et al. 1998a). Moreover, parents in good body condition provide more food for their chick (Lorentsen 1996, Erikstad et al. 1997).

Among Procellariiformes, parents guard the chick for some days until the chick has attained homeothermy (Warham 1990), and in some species even beyond that stage (Hunter 1984, Tveraa et al. 1998a). That strategy may have evolved to minimize the probability that the chick would be taken by predators, but is costly because only one parent can forage at a time (Warham 1990). Duration of the guard stage is therefore most likely a compromise between the chick's ability to care for itself, body condition of the parent present at the nest, and ability of the foraging parent to return to the nest before the mate is forced to leave to feed.

In the present study, we examine how the body condition of adult Snow Petrels (*Pagodroma nivea*) influences their ability to care for their chick. On the basis of studies on other petrel species (Chaurand and Weimerskirch 1994b; Tveraa et al. 1997, 1998a), we expect that parents in good body condition will guard their chick for a longer period and provide more food for it than those in poorer body condition (Lorentsen 1996). A recent study of Snow Petrel chicks has shown that chicks' ability to maintain homeothermy, at the time when they are left alone, increases with body mass and age (Weathers et al. 2000). We therefore expect chicks' probability of survival over the first few days after the guard stage to be positively related both to number of days it is guarded and their body condition when they are left alone.

Methods.—We studied a Snow Petrel breeding colony of ~500 pairs at Svarthamaren (71°53'S, 5°10'E), Dronning Maud Land, Antarctica, from 8 January to 6 February 1998. The main population of Snow Petrels at Svarthamaren breeds in crevices and holes formed by boulders. Both parents share incubation and feeding of the chick. At Svarthamaren, temperature during daytime is normally <0°C and during the night it may fall well below -30°C, so successful breeding requires that one of the parents be present

at the nest from egg-laying and until the chick has attained homeothermy.

At hatching, we individually marked 78 parents with a steel band and a permanent ink. We measured their body mass (± 0.25 g), wing length (± 0.5 mm), skull length, and bill depth (± 0.05 mm). During daily visits, we recorded whether an adult had newly arrived from the sea, and following that procedure, we also obtained data on chick survival and when the chick was left alone for the first time. We defined "guard stage" as number of days from hatching and until the chick was left alone for the first time. Number of brooding and foraging spells correspond to number of reliefs since hatching. That means that chicks left alone for the first time by the parent present at the nest at hatching were defined as being left alone at spell = 0. Chicks left alone for the first time by the parent that relieved the parent present at the nest at hatching were defined as being left alone at spell = 1, etc.

Individual pair members were not sexed in this study. At Svarthamaren, average sexual dimorphism is 5.5% (T. Tveraa unpubl. data). That means that variation in parental body mass may reflect both variation in structural size and amount of stored energy. In order to remove the effect of structural size and to get an index of amount of stored energy, we have statistically removed the effect of structural size on body mass by regressing the first principal component (PC1) from a principal-component analysis based on wing length, skull length, and bill depth on body mass (Jakob et al. 1996, Sedinger et al. 1997, Green 2001). The PC1 explained 26% of variance in body mass ($n = 78$, $P < 0.001$) of parents present at the nest during hatching. For parents that returned to the nest to the first spell after hatching, that figure was 22% ($n = 50$, $P < 0.001$). Residuals from those regressions were defined as individual's body condition.

Body mass of chicks when they were left unattended was strongly correlated with their age ($r = 0.74$, $n = 50$, $P < 0.001$), and the effect of one of those variables may mask the effect of the other. We therefore defined the chicks' body condition as the residuals from that regression.

One chick died due to a small rockslide, and two chicks disappeared from their nest. Those nests were excluded from all analyses. Throughout all the analyses, we examined residuals in order to evaluate validity of the data. In analysis of number of days the chick was guarded versus parental body-condition, one observation deviated significantly from other observations (Studentized residual = 3.30). Following recommendations by Schlotzhauer and Littell (1991), we removed that observation from the analyses.

Statistical tests were performed using SAS software (SAS Institute 1990). Survival was analyzed using logistic regression models, whereas normally distributed response variables were analyzed using

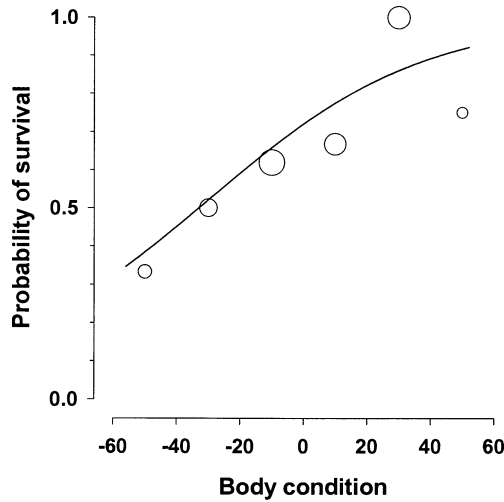


FIG. 1. Probability of Snow Petrel chick survival during the guard stage in relation to the body condition of the parent present at the nest at hatching. Size of the symbols is weighed against sample size, with smallest and largest circles indicating sample sizes of 1 and 22, respectively. (Body condition is the residuals from a regression of body size on body mass.)

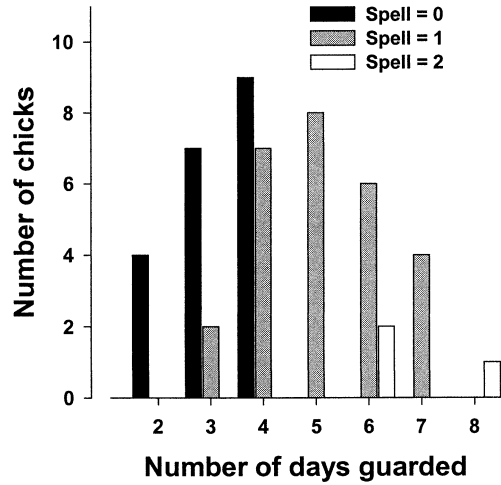


FIG. 2. Number of days Snow Petrel chicks were guarded posthatch before the parents left them alone for the first time (spell 0-2 indicates whether the chick was left unattended by the parent present at the nest at hatching (spell = 0), or at the first (1) or at the second (2) spell posthatch.

linear regression and analyses of covariance. We included the spell at which the chick was left alone for the first time as a factor, whereas parental body condition, chick body mass, body condition and age were included as covariates. All tests are two-tailed and $P < 0.05$ is regarded as statistically significant.

Results.—Only 50 of the 78 chicks survived until they were left alone for the first time. Prospects of the parents producing a chick that survived the guard stage was positively related to body condition of the parent present at the nest at hatching (logistic regression, Wald $\chi^2 = 6.11$, $\Delta df = 1$, $P < 0.05$, Fig. 1).

Chicks were left alone for the first time 2–8 days ($\bar{x} = 4.5$ days, $SD = 1.53$) posthatch. Twenty chicks (40%) were left alone for the first time by the parent present at the nest at hatching, 27 (54%) were left alone for the first time during the first spell after hatching, and 3 (6%) were left alone for the first time second spell after hatching (Fig. 2). Chicks' body mass when left alone ranged from 30.5 to 81.0 grams ($\bar{x} = 54.4$ g, $SD = 13.7$ g).

The number of days the chick was guarded until it was left alone for the first time was positively related to body condition of the parent present at the nest at hatching ($F = 35.0$, $df = 1$ and 45, $P < 0.001$) and number of brooding and foraging spells parents were able to coordinate ($F = 49.6$, $df = 2$ and 45, $P < 0.001$, Fig. 3). For those chicks that were left alone for the first time during the first spell after hatching, that is, by the parent that relieved the individual

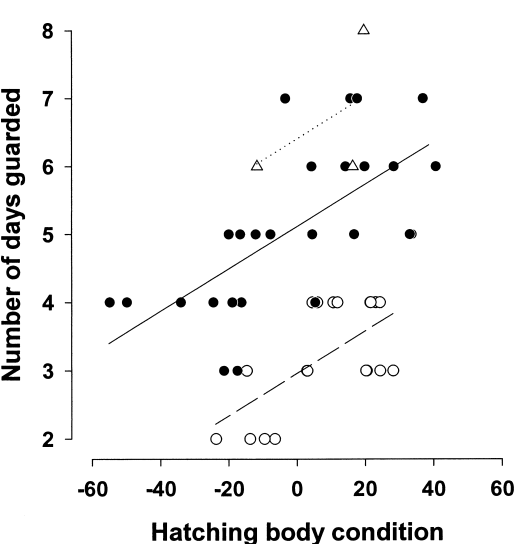


FIG. 3. Number of days the Snow Petrel chicks were guarded in relation to body condition of the parent present on the nest at hatching and whether it was left alone at the hatching (dashed line and open circles), or during the first (solid line and solid circles) or second (dotted line and open triangles) guarding spell posthatch. (Hatching body condition is the residuals from a regression of body size on hatching body mass.)

present at the nest at hatching, we had the opportunity to examine the number of days the parents guarded their chick in relation to their body condition on arrival in the colony. There was a positive relationship between number of days the parents guarded the chick before it was left alone and body condition of the parent ($r = 0.51$, $n = 27$, $P < 0.01$).

Body mass of the chick when left alone was positively related to the body condition of the parent present at the nest at hatching ($F = 33.7$, $df = 1$ and 45 , $P < 0.001$) and number of brooding and foraging spells parents were able to coordinate ($F = 33.1$, $df = 2$ and 45 , $P < 0.001$). However, the positive effect on chick body mass was a function of chick age, and chick body condition (body mass corrected for age) was related to neither the body condition of the parent present at the nest at hatching ($F = 2.0$, $df = 2$ and 45 , $P = 0.16$) nor to number of brooding and foraging spells parents were able to coordinate ($F = 0.7$, $df = 2$ and 45 , $P = 0.49$).

Fourteen (28%, $n = 50$) of the chicks did not survive from when they were left alone until day 10. We tested whether age and body condition of the chick at the end of the guarding period had any influence on its survival until day 10 in a logistic model. The prospect of survival until day 10 was positively related to both their age (logistic regression: Wald $\chi^2 = 7.13$, $\Delta df = 1$, $P < 0.01$) and body condition (Wald $\chi^2 = 4.81$, $\Delta df = 1$, $P < 0.05$). That relationship is given by the logistic equation (E_{\logit}) Probability of survival = $-3.98 + 1.30 \times \text{age} + 0.13 \times \text{chick body condition}$.

Discussion.—We found a large variation in number of days parents guarded their chick, and only 64% of chicks survived the guard stage. A long-term study of the Snow Petrel, spanning over 27 years Chastel et al. (1993), showed that overall breeding success may vary from 21 to 80% and that the most common cause of failure was nest desertion and flooding of the nest. In accordance with that, results from a long-term monitoring program of Antarctic petrels, breeding in the same area, suggest that breeding success was relatively low this season (Tveraa et al. 2000). However, our study suggests that much variation in breeding success can be related to variation in parental body condition. Barbraud and Chastel (1999) have demonstrated that hatching success increases with parental body condition in this species, and a number of studies of other seabird species have also indicated that parental body condition is an important factor regulating breeding success and parental decisions (e.g. Mauck and Grubb 1994; Weimerskirch et al. 1994; Chastel et al. 1995a, b; Lorentsen 1996; Erikstad et al. 1997).

Ability of the foraging bird to return to the nest in time to relieve its mate was also a very important factor regulating number of days the chick was guarded and chick body mass. Because we did not follow the birds prior to hatching, we lack data on their mass change and the duration of their stay at sea. Conse-

quently, we have no measure of their foraging success. However, previous studies have shown that petrels with a high mass-gain return more quickly to the nest (Chaurand and Weimerskirch 1994a; Tveraa et al. 1997, 1998a). Thus, a large proportion of the variation in body condition and reproductive success may be related to stochastic variation in foraging success (Weimerskirch 1995, Tveraa et al. 1997). The significance of body condition for reproductive success is most likely related to ability to buffer short-term environmental instability. For instance, individuals in good body condition will be able to fast longer on the nest, thus allowing the foraging parent to spend more time searching for food (Tveraa et al. 1997).

Probability that the chicks survived until day 10 posthatch was positively related to both number of days they were guarded and their body condition (body mass corrected for age) at the end of the guarding period. In a recent study of the surface nesting Antarctic Petrel (*Thalassoica Antarctica*), Tveraa et al. (1998a) suggested that prolonged guarding of the chick may reduce probability that the chick is preyed upon by South Polar Skuas (*Catharacta macormicki*). However, because Snow Petrel chicks are concealed in crevices, prolonged guarding may not function as an antipredator strategy. In Antarctica, chicks are left alone in a cold and hostile environment and the smallest chick was only 30.5 grams, whereas the largest chick reached 81.0 g before it was left alone. Following recent work by Weathers et al. (2000), chicks' ability to maintain homeothermy increases rapidly until their body mass reach 100 g. Hence, the smallest chicks were probably left alone before they were able to maintain homeothermy.

It is now evident that parental body condition and foraging success are important factors regulating breeding success of Procellariiformes (e.g. Chaurand and Weimerskirch 1994a; Weimerskirch et al. 1994; Chastel et al. 1995a, b; Lorentsen 1996; Tveraa et al. 1998a, b; Barbraud and Chastel 1999). However, to what extent individual variation in breeding success is due to individual variation in quality or to random variation in foraging success is yet poorly understood. There is therefore a need for studies that follow the same individuals over subsequent foraging trips so that effect of individual quality and random variation in breeding success can be disentangled.

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