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Original article

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Body mass and parental decisions in the Antarctic petrel *Thalassoica antarctica*: how long should the parents guard the chick?

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Abstract In Procellariiformes, the parents guard the chick after it has attained homeothermy. This strategy may reduce the probability that a small chick is taken by predators, but is costly as only one parent can forage at a time. The decision to leave the chick may therefore be a compromise between the chick's vulnerability to predators, the body condition of the parent on the nest and whether the foraging parent returns in time. We studied how the number of days that parents guarded the chick was related to the body mass of the parent at the nest and the time the foraging parent spent at sea in the Antarctic petrel *Thalassoica antarctica*. We also examined how the body mass of the parent on the nest and the duration of the foraging trips influenced the chicks' body condition at the end of the guarding period. When the foraging parent did not return to the nest in time to relieve its mate, the number of days the parent on the nest kept guarding the chick was positively related to its body mass on arrival in the colony. The number of days the foraging parent spent at sea was positively related to the body mass of its mate, but those that returned in time had a shorter stay at sea relative to their mate's body mass than those that did not return before their mate had left. Apparently, both the body mass of the parent at the nest and the ability of the foraging parent to adjust its stay at sea to the mate's body mass is important for the number of days the parents guard the chick and also the chick's body condition at this point. The inability to return to the nest before the mate has left may be the result of needing a minimum amount of time at sea to find food, or because some parents having low foraging success and therefore prolong their stay at sea.

Key words Antarctica · Body mass · Body condition · Regulation of foraging trips · Costs of chick guarding · Antarctic petrel

Introduction

Seabirds within the order Procellariiformes have evolved an extreme life history strategy. Their delayed maturity, long lifespan, low annual reproductive output, and slow chick growth (review in Warham 1990) are presumably related to the patchy and sparse distribution of their prey species (Ashmole 1971). During the incubation period, the incubation and foraging spells may last for several weeks (e.g. Harris 1973; Weimerskirch 1995), and the interval at which the parents feed their single chick may exceed 1 week (e.g. Warham 1956; Richdale 1963). Such long spells offer the opportunity to forage at long distances from the colony (Weimerskirch et al. 1993; Weimerskirch 1995) and increase the probability of finding food. However, during long foraging trips the body mass of the bird on the nest will become depleted, increasing the probability that the nest will be deserted (Chaurand and Weimerskirch 1994a; Yorio and Boersma 1994; Tveraa et al. 1997), an important factor causing breeding failure in Procellariiformes (review in Johnstone and Davis 1990).

Among Procellariiformes, one of the parents guards the chick even after it has attained homeothermy (e.g. Hunter 1984). Such a strategy has presumably evolved in

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order to minimise the probability that the chick is taken by predators, but is costly as only one parent can forage at a time (review in Warham 1990). The decision to leave the chick is therefore influenced by the body condition of the parent on the nest and whether the foraging bird returns in time, i.e. before the body condition of the mate on the nest has deteriorated (Chaurand and Weimerskirch 1994a; Tveraa et al. 1997).

Chaurand and Weimerskirch (1994a) proposed that the time available for foraging during the incubation period is limited by the fasting ability of the mate on the nest. Parents with high foraging success can quickly reach the body condition which is needed for the next spell on the nest. On the other hand, individuals that have low foraging success must prolong their stay at sea in order to reach a proper body condition for their next spell. However, prolonging the time at sea will increase the risk of nest desertion by the mate on the nest. The foraging bird may therefore have to return to the colony with a low body condition in order to prevent nest desertion by the mate. Accordingly, Tveraa et al. (1997) suggested that if the stay at sea is short relative to the mate's body condition and ability to fast on the nest, then the duration of the foraging trip may be regulated by the parent's own foraging success. On the other hand, if the stay at sea is long relative to the mate's body condition and ability to fast on the nest, then the foraging parent may adjust its stay at sea according to the body condition of the mate. Similarly, the duration of the guarding period may be related to the parent's ability to adjust its stay at sea according to its foraging success and its mate's body condition. However, the probability of breeding failure due to "desertion" of the chick should be negatively related to the size of the chick. At a certain point, parents may therefore lose their interest in guarding their chick.

In the present study, we examine how the number of days Antarctic petrels guard their chicks is related to the body condition of the parent on the nest and the ability of the foraging bird to return before the body condition of its mate has become depleted. In turn, we also examine how this may influence the chick's body condition at the end of the guarding period. A previous study of incubating Antarctic petrels in the same colony has shown that parents adjust their stay at sea to both their own foraging success and their mate's body condition (Tveraa et al. 1997). Accordingly, we expect that parents in good body condition can sustain a longer period at the nest than those in poor body condition, but that the ability of the foraging parent to adjust its stay at sea to the mate's body condition is also important for the duration of the guarding period. Furthermore, if parents with a high foraging success spend less time at sea than those with a low foraging success in the guarding period, we expect parents with the shortest stay at sea to be in better body condition on arrival in the colony and have chicks in better body condition at the end of the guarding period than those that stay longer at sea.

Methods

This study was carried out at a colony of approximately 250,000 pairs of breeding Antarctic petrels (Røv et al. 1994) at Svarthamaren, Dronning Maud Land, Antarctica from 27 December 1996 to 26 January 1997. All study parents had left their chick unattended when the study ended.

The Antarctic petrel breeds on the ground in scree slopes. Both parents incubate the egg and brood the chick. The duration of the incubation and brooding spells decrease from 12–23 days after laying to 1–4 days at the end of the guard period (Lorentsen and Røv 1995). Most chicks are left unattended by the parents at day 11 post-hatch (Bech et al. 1988), but obviously they attain homeothermy earlier. For instance, S.-H. Lorentsen (unpublished data) found that 6-day-old chicks were homeothermic for a period of 2 h. Approximately 100 pairs of south polar skuas, *Catharacta maccormicki*, breed at Svarthamaren, and their main diet is Antarctic petrel eggs and chicks. There are no observations of south polar skuas preying on adult petrels at the nest, but approximately 13% of the chicks at Svarthamaren are eaten by south polar skuas (Haftorn et al. 1991).

We recorded the hatching date of 216 eggs. On 158 (73.1%) of these nests, the male was present at hatching and on 58 (26.9%), the female. The nests were visited daily, and new birds that arrived from the sea were individually marked with a steel ring, their body mass measured, and their arrival date recorded. We also measured their skull length (±0.05 mm), bill depth (±0.05 mm), and wing length (±0.5 mm) to determine the sex and the size of the birds (see below). All reliefs at the nest during the study period were recorded and the body mass of the bird that arrived from sea was measured. Following this schedule, we also obtained data on the duration of the parent's stay at sea between their spells at the nest and the age and body mass of the chick when it was left alone for the first time. Ninety chicks were followed for 3 days after they were left unattended in order to measure their survival. We did not attempt to estimate the body mass of the parents at the time they left the colony. Such a measurement requires daily measures of the body mass of both the parent and the chick and is likely to cause much disturbance to the birds.

We defined the guarding period as the number of days post-hatch before the chick was left alone for the first time. This includes both the brooding period when the parent covers the chick and also the period when the chick has attained homeothermy and sits beside the parent (see also Hunter 1984).

The number of days the chick was guarded did not differ among those chicks which hatched with the male (10.4 ± 0.14 days, $n = 134$) or the female (10.4 ± 0.19 days, $n = 47$) on the nest ($t = 0.21$, $df = 179$, $P = 0.84$). Due to the small sample available where the females were present at hatching, we present only data with the males on the nest at hatching. This means that the female was present during the first spell, the male during the second, and the female during the third spell post-hatch.

The sex of the bird was determined according to the discriminant function presented by Lorentsen and Røv (1994) which is based on skull length, bill depth, and wing length.

To control for body size, we regressed body mass on the first principal component (PC1) from a principal component analysis based on the morphological characters. Body size (PC1) explained 9% ($n = 151$, $P < 0.001$) of the variance in body mass of the females that arrived in the colony for the first spell after hatching, 6% ($n = 134$, $P < 0.01$) of the variance in the male's body mass when they arrived for the second spell, and 15% ($n = 53$, $P < 0.01$) of the variance in the female's body mass when they arrived for the third spell. However, using body condition (body mass corrected for body size) and body mass in the analyses gave similar results and conclusions. For simplicity, we therefore present analyses and results for body mass only.

To control for the effect of chick age on body mass at the end of the guarding period, we regressed chick body mass on age. Age explained 25% ($n = 134$, $P < 0.001$) of the variance in chick body mass at the time when then chick was left alone. The residual from this regression was defined as the chick's body condition.

We analysed time spent at sea using analyses of covariance with hatching date, body mass at arrival in the colony, and mate's body mass as covariates. Whether or not the parent at sea returned in time to relieve its mate was entered as a factor. A similar procedure was used to analyse chick body condition. Hatching date and interactions were insignificant and hence removed from the analyses.

All statistical tests are two-tailed and performed using SAS software (SAS 1990), and $P < 0.05$ is considered as statistically significant. Means ± 1 SE are given.

Results

The total number of days the parents guarded their chick varied from 7 to 15 with a median of 10. Twenty-two chicks (16.4%) were left unattended during the first spell after hatching (female present), 85 (63.4%) during the second spell (male present) and 27 (20.3%) during the third spell (female present). Chicks left unattended during the first spell after hatching were on average left unattended earlier (9.0 ± 0.31 days) than those that were left during the second (10.2 ± 0.11 days) and third spell (12.1 ± 0.30 days; $F = 40.8$, $df = 2{,}131$, $P < 0.001$, Fig. 1).

During the first spell, the time spent at sea by the foraging parent was negatively related to its body mass on arrival in the colony ($F = 16.43$, $df = 1{,}122$, $P < 0.001$, Fig. 2A). There was no difference in the time spent at sea between those parents that returned in time to relieve their mate and those that did not ($F = 1.03$, $df = 1{,}122$, $P = 0.31$). During the second spell, the time spent at sea by the foraging parent was, however, not related to its body mass on arrival in the colony ($F = 0.10$, $df = 1{,}47$, $P = 0.75$, Fig. 2B), but parents that returned in time to relieve their mate spent less time at sea than those that did not ($F = 6.44$, $df = 1{,}47$, $P = 0.02$).

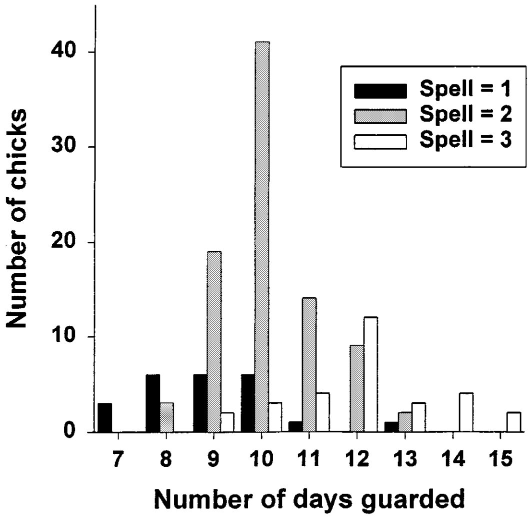

Fig. 1 The number of days Antarctic petrel chicks were guarded post-hatch before the parents left them alone for the first time (*Spell 1–3* indicates whether the chick was left unattended during the first, second or third guarding spell after hatching, respectively)

In those cases where the foraging parent did not return in time to relieve its mate, the number of days the parent at the nest guarded their chick before it was left unattended was positively related to the parent's body mass on arrival at the colony (chick left during first spell: $r = 0.59$, $n = 22$, $P < 0.01$; second spell: $r = 0.48$, $n = 85$, $P < 0.001$; third spell: $r = 0.46$, $n = 25$, $P = 0.02$, Fig. 3). This suggests that foraging individuals that have a mate with a high body mass can spend more time at sea without the risk that their mates will leave the chick.

We controlled for the effect of own arrival body mass on the time spent foraging during the first spell (using the residuals from the regression between time spent at

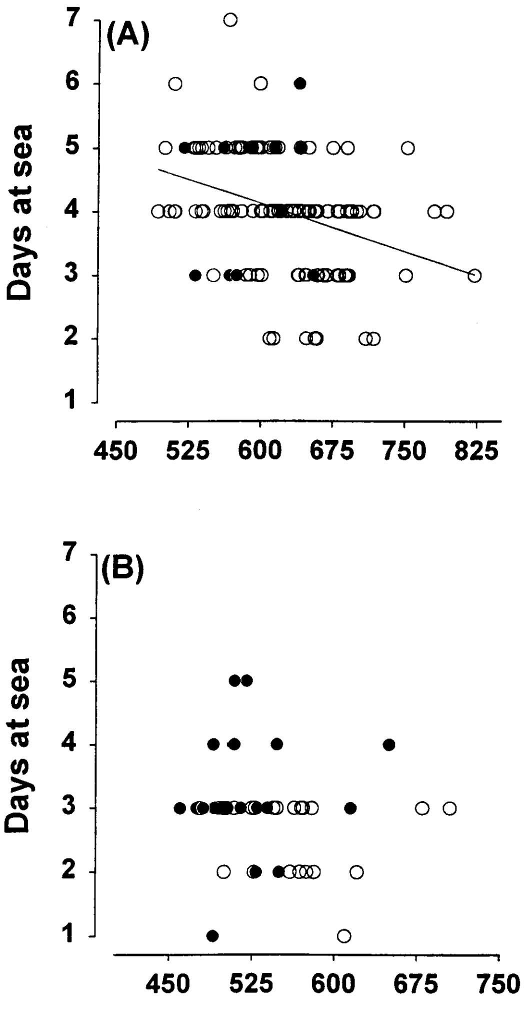

Fig. 2 The number of days that Antarctic petrel parents spent at sea in relation to their body mass on arrival in the colony during the first spell (male at sea) (**A**) and second spell (female at sea) (**B**) after hatching. *Open circles* represent those parents which returned in time to relieve their brooding mate while *closed circles* represent those who did not return in time

sea and the first-spell arrival body mass, i.e. the residuals from Fig. 2A) and then examined how the time spent at sea was related to the body mass of the mate on the nest. A foraging parent that returned in time spent less time at sea relative to its mate's body mass than one that did not return before the parent on the nest left the chick ($F = 13.02$, $df = 1{,}122$, $P < 0.001$). Moreover, this analysis shows that the time spent at sea was positively related to the body mass of the mate at the nest both for those that returned in time and those which did not ($F = 39.27$, $df = 1{,}122$, $P < 0.001$, Fig. 4A). For the second spell, there was no relationship between the time spent at sea and the arrival body mass of the foraging bird, so we simply related the time spent at sea to the body mass of the mate. This analysis revealed that during the second spell also the stay at sea among parents that returned in time was shorter, relative to the body mass of their mates, than that of those that did not ($F = 7.84$, $df = 1{,}47$, $P < 0.01$). Moreover, the time spent at sea by the foraging birds was positively related to the body mass of their mates ($F = 23.59$, $df = 1{,}47$, $P < 0.001$, Fig. 4B).

We examined how the duration of the foraging trips, the body mass of the parent on the nest, and the parent's ability to return in time to relieve its mate influenced the

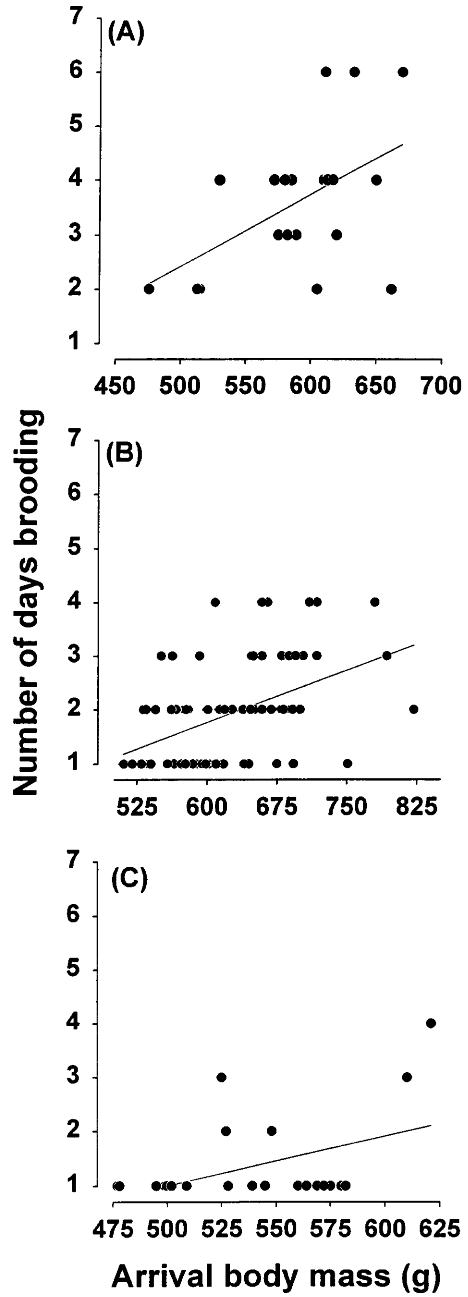

Fig. 3 The number of days Antarctic petrel parents sustained brooding of their chick in relation to their body mass on arrival at the colony during the first (female at nest) (**A**), second (male at nest) (**B**) and third (female at nest) (**C**) spell after hatching

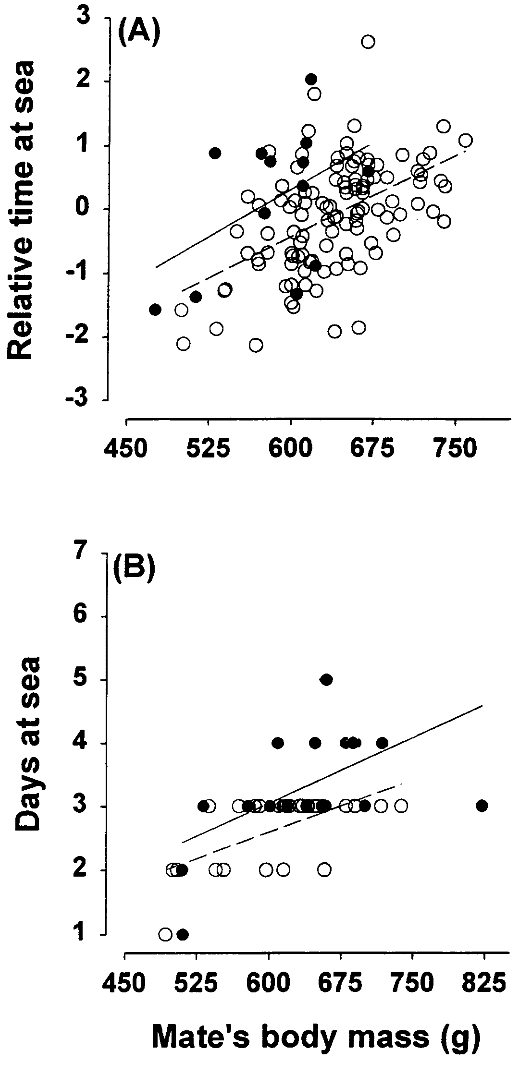

Fig. 4 The number of days spent at sea by foraging Antarctic petrel parents in relation to the body mass of their mate of those that returned in time to relieve their brooding mate (*open circles* and *dashed line*) and those that did not (*closed circles* and *solid line*) during the first (**A**) and the second (**B**) spell. Because the time spent at sea during the first spell was negatively related to the arrival body mass of the foraging parent (see Fig. 2A), we removed this effect using the residuals from Fig. 2A. Regression lines are from simple regressions

chick's body condition at the end of the guarding period. For the first spell, there was a positive effect of the body mass of the parent on the nest on the body condition of the chick at the end of the guarding period ($F = 13.31$, $df = 1{,}121$, $P < 0.001$). Moreover, parents that had a short stay at sea had chicks in better body condition than those that had a longer stay at sea ($F = 24.90$, $df = 1{,}121$, $P < 0.001$). Whether the foraging parent returned to the nest in time to relieve its mate or not did not significantly influence the chick's body condition after controlling for the effect of the body mass of the parent on the nest and the duration of the foraging trip, although there was a trend (least-square means of chicks body condition; 3.78 ± 3.70 vs –13.4 ± 11.8, $F = 1.89$, $df = 1{,}121$, $P = 0.17$). During the second spell, there was also a positive effect of the body mass of the parent on the nest on the chick's body condition at the end of the guarding period ($F = 10.53$, $df = 1{,}46$, $P < 0.01$). There was no effect of the duration of the foraging trip on the chick's body condition ($F = 0.99$, $df = 1{,}46$, $P = 0.33$). However, parents that returned in time to relieve their mate had chicks in better body condition than those that did not (least-square means; 26.2 ± 7.5 vs –16.8 ± 8.1, $F = 14.00$, $df = 1{,}46$, $P < 0.001$).

Only 8 of the 90 chicks that we followed for 3 days after they were left unattended died. There was a tendency for chicks that were left early to have a lower survival probability than those that were left later (died; 9.4 ± 0.4 days, $n = 8$, survived; 10.1 ± 0.2, $n = 82$), but this relationship was not significant (logistic regression: Wald-$\chi^2_1 = 1.86$, $P = 0.17$). For chick body condition, there was no such trend (died; 8.4 ± 9.7, $n = 8$, survived; –0.81 ± 4.8, $n = 82$; logistic regression: Wald-$\chi^2_1 = 0.41$, $P = 0.52$).

Discussion

The results from this study can be summarised as follows. (1) The parents left their chick unattended for the first time during spells 1–3 when the chick was 7–15 days old (Fig. 1). The age at which the chick was left unattended for the first time was positively related to the number of spells during which it was guarded. (2) During the first spell, the stay at sea was negatively related to the body mass of the foraging bird on arrival in the colony (Fig. 2), suggesting that unsuccessful foragers spent most time at sea. However, no such relationship was evident during the second spell. (3) When the foraging bird did not return in time to relieve its mate, the number of days the parent at the nest remained there was positively related to its initial body mass on arrival at the colony (Fig. 3). (4) Those individuals that did not return in time to relieve their mates stayed longer at sea relative to their mates' body mass than those that returned in time. Moreover, the time the foraging parent spent at sea was positively related to the body mass of its mate both for those that returned before their mate had left the chick and those who did not, but some parents returned only just too late to relieve their mate. This suggests that the stay at sea is also regulated by the mate's body mass and that all parents are able to assess this (Fig. 4). (5) Parents that had the shortest stay at sea and were able to return in time to relieve their mate had chicks in better body condition at the end of the guarding period.

As also shown for incubating Antarctic petrels (Tveraa et al. 1997) and blue petrels, *Halobaena caerulea*, (Chaurand and Weimerskirch 1994a), there was a negative relationship between the time spent foraging and the body mass on arrival in the colony. This may suggest that parents with a high foraging success had the shortest stay at sea (cf. Tveraa et al. 1997). However, such a relationship was only evident on arrival after the first spell (Fig. 3). Three factors may explain this difference among spells. First, we only measured the parents' body mass at their time of arrival in the colony, not their mass gain during the stay at sea which may more accurately indicate the parent's foraging success. However, a previous study of the Antarctic petrel at Svarthamaren has shown that there is a close relationship between the duration of the stay at sea, the mass gain during the trip and the body condition at arrival in the colony (Tveraa et al. 1997). Second, the feeding of the chick may have confounded such a relationship, as older chicks may receive 80–250 g food (Haftorn et al. 1991; Lorentsen 1996) and parents in good body condition deliver larger meals to their chick than those in poor body condition (Lorentsen 1996; Tveraa et al., in press). Third, as argued by Tveraa et al. (1997), parents should regulate the length of foraging trips to their own foraging success when the probability that their mate will desert the nest is low. However, as the probability that the mate at the nest will desert increases, the foraging parent should to a larger extent use the body mass of its mate as a factor regulating the length of the foraging trips. At present, we cannot separate these two latter explanations.

This study suggests that the number of days the parents guard the chick is regulated by the body mass of the parent on the nest. During the first spell after hatching, light parents left their chick unattended after only 2 days whereas heavy parents waited 6 days at the nest before they went to the sea. During the second and third spells, light parents left their chick after only 1 day whereas heavy parents waited for 4 days at the nest before they went to the sea (Fig. 3). Apparently, the decision to leave the chick is taken according to a lower threshold in body mass, as shown for incubating birds (Chaurand and Weimerskirch 1994a; Tveraa et al. 1997). Thresholds in body mass also regulate the amount of food delivered to the chick after the guarding period is over (Chaurand and Weimerskirch 1994b; Weimerskirch et al. 1994), suggesting that thresholds in body mass are an important clue when monitoring the costs of current reproduction (e.g. Drent and Daan 1980; Weimerskirch 1995; Naulleau and Bonnet 1996). During the third spell, a higher proportion of the parents left their chick after only 1 day at the nest than during the first and second spell (Fisher's exact test: $P < 0.01$; see Fig. 3). This may suggest that there is an upper limit above which the benefits of tending the chick are too small compared to the costs involved. At Svarthamaren, the only predator on the chicks is the south polar skua, and older chicks may be more difficult for the skuas to catch than younger ones. This suggestion may be supported by the finding that the chicks that died after they were left alone tended to be left at an earlier age than those that survived. However, only 8 of 90 chicks that we observed for 3 days after they were left unattended died.

During the first spell, parents that did not return in time to relieve their incubating mates did not spend more time at sea than those that returned in time. However, relative to the body mass of their mate on the nest, the time spent at sea was longer among those parents that did not return in time than among those that did (Fig. 4). Similarly, parents that did not return in time to relieve their mate during the second spell spent longer time at sea relative to the body mass of their mates than those that returned in time (Fig. 4). These results suggest that all the parents adjust their stay at sea according to the body mass of their mate (see also Tveraa et al. 1997) and emphasise its importance for successful co-ordination of the spells. However, if the body mass of the mate is too low, they are apparently unable to return in time. This is probably because a minimum amount of food is needed for the next spell at the nest (Prince et al. 1981; Johnstone and Davis 1990; Chaurand and Weimerskirch 1994a; Weimerskirch 1995). Parents with a low foraging success may also have to prolong their stay at sea in an attempt to find the amount of food needed for the next spell on the nest (Chaurand and Weimerskirch 1994a; Weimerskirch 1995; Tveraa et al. 1997).

We compared the body condition of the chicks at the end of the guarding period of parents that left their chick alone during the first spell with those that left it on later spells. The body condition of the chick was positively related to the body mass of the parent on the nest during the spell and negatively related to the duration of the stay at sea by the foraging bird. Similarly, when comparing the body condition of chicks that were left alone on the second spell with those that were left on the third spell, we found that the chick's body condition was positively related to the body mass of the parent present on the nest. Moreover, chicks that were left on the second spell were in poorer body condition than those that were left during the third spell. This finding supports the idea that the duration of the stay at sea is related to the foraging success of the birds at sea. Co-ordination of the spells may be important for chick survival even after the guarding period, as a previous study of the Antarctic petrel in the same colony has shown that chicks that are heavy at the end of the guarding period have higher prospects of surviving to the end of the chick-rearing period than light ones (Sæther et al. 1997).

In conclusion, both the body mass of the parent on the nest and the ability of the foraging parent to adjust its stay at sea according to the mate's body mass may be important for how long the chick is guarded and its body condition at this stage. This study suggests that the Antarctic petrels adjust their foraging trips to both their own foraging success and their mates' body mass (see also Tveraa et al. 1997). Moreover, parents that did not return to the nest before their mate had left also tried to adjust their stay at sea according to their mates' body mass but returned just too late. This suggests that all parents are able to assess their mate's body mass, but that some parents are not able to adjust their stay at sea accordingly. This inability of some parents to return in time may be related to the fact that a minimum amount of time is required to find sufficient food for the next spell on the nest. Another explanation is that some parents have a lower foraging success than those that return in time and therefore prolong their stay at sea. As the foraging parents adjust their stay at sea according to their mates' body mass, the foraging success and body mass of the foraging birds may, in turn, constrain the time available for foraging by the other mate (see also Tveraa et al. 1997). Similarly, an undernourished chick may also constrain the time the parents have available for foraging later in the breeding season (see Ricklefs 1987). However, the Antarctic petrel's ability to adjust the duration of each stay at sea according to own foraging success and the fasting ability of the mate may be highly profitable in a variable environment where both foraging success and body mass, and hence their fasting ability, vary among spells.

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