

## State-dependent parental care in the Antarctic petrel: responses to manipulated chick age during early chick rearing

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Life histories are state-dependent, and an individual's reproductive decisions are determined by its available resources and the needs of its offspring. Here we test how a chick's needs for food and protection influence parental decisions in the Antarctic petrel, *Thalassoica antarctica*, where the parents, due to their long breeding lifespan, are expected to give priority to their own needs before those of the young. We exchanged one-day-old chicks with four-day-old chicks and studied how the parents subsequently provided care to the chick. The duration of the guarding period was adjusted, and parents left older chicks earlier and younger chicks later compared to controls. Three mechanisms were responsible for the adjustments. 1) Parents with an older chick co-ordinated fewer guarding spells whereas parents with a younger chick co-ordinated more guarding spells. 2) At the last guarding spell, i.e. where a parent left the chick alone before the partner returned, less time was spent with older chicks, and more time with younger chicks. 3) Foraging trip duration was shortened by parents given older chicks and prolonged by parents given younger chicks, probably in response to the chick's food demand. Hence, the parents responded quickly to the altered needs of the chick. Parents with high body mass guarded longer and were better able to co-ordinate the guarding spells compared to lighter parents. In conclusion, Antarctic petrels adjust reproductive decisions to their own, their mate's, and their chick's state, and they seem to respond to the chick's needs for both food and protection.

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Life history theory predicts a trade-off between current and future investments in reproduction (Williams 1966). In many species, current investments include care for the offspring after birth (Clutton-Brock 1991), but parental care is only beneficial when it increases the probability of offspring survival without incurring too great a cost for the parents (Clutton-Brock 1991, Roff 2002). Hence, at each point in a breeding attempt the parents should decide how much care they should give to the offspring. The optimal decisions should depend on the parents' physiological state or condition (McNamara

and Houston 1996, Houston and McNamara 1999, Clark and Mangel 2000), such as their body mass, a currency that is linked to an individual's costs of reproduction (Drent and Daan 1980, Erikstad et al. 1998, Wendeln and Becker 1999, Spencer and Bryant 2002, Webb et al. 2002).

To optimise investment in a breeding event, a parent should not only adjust the reproductive decisions according to its own state. Successful reproduction also depends on how the parents respond to the varying needs of the offspring, needs that they are expected to

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respond in order to maximise life-time reproductive success (Winkler 1987, Clutton-Brock 1991). For instance, a parent should respond to the chick's needs for food at a particular point in the breeding attempt. Such responses are common for many birds (Dijkstra et al. 1990), but within seabirds, and particularly within the order Procellariiformes, there have been equivocal results regarding parental regulations to short time variation in the chick's nutritional status (Ricklefs 1987, Hamer and Hill 1994, Bolton 1995a, Weimerskirch et al. 1997, 2001, Hamer et al. 1998, Tveraa et al. 1998b, Granadeiro et al. 2000, Phillips and Croxall 2003). It has been suggested that Procellariiformes have difficulties in adjusting food provisioning to their chick because they experience stochastic variation in foraging success (Ricklefs and Schew 1994). Furthermore, adjustments may be difficult because the chick's needs may change between a parent's two visits to the nest if the chick is fed by the other parent inbetween (Ricklefs 1987), and finally, seabirds are long lived and may have evolved a fixed schedule of parental effort in order to ensure priority to survival rather than fecundity (Sæther et al. 1993).

Chick rearing in Procellariiformes includes a guarding period after hatching (Warham 1990), where both the chick's nutritional needs and its needs for brooding and protection should be considered. During the guarding period the single chick is brooded by one parent at a time until the thermoregulatory ability of the chick has developed (Weathers et al. 2000). Guarding is often continued beyond this point, presumably to reduce the predation risk of the young (Warham 1990). Hence, guarding has benefits, but it is also costly since only one parent can forage at a time. Consequently, the decision to leave the chick unattended is a compromise between chick growth and chick survival. There is large variation in the duration of the guarding period for Procellariiformes (Hunter 1984, Warham 1990), but despite the potential importance of this decision, few studies have investigated the motivation for leaving the chick unattended. However, two studies on petrels breeding under harsh conditions in Antarctica show that parents with high body mass guard the chick longer than lighter parents (Tveraa et al. 1998a, Tveraa and Christensen 2002). Furthermore, Tveraa et al. (1998a) pointed out that the parents' ability to co-ordinate the guarding period is related to how long they guard the chick. A recent modelling study also emphasise the importance of energy reserves for successful guarding of the chick in raptors and owls (Brodin et al. 2003).

In this study we focus on how the chick's needs influence the parents' decisions during the guarding period. We exchanged one-day-old chicks with four-day-old chicks in the Antarctic petrel, *Thalassoica antarctica* (Procellariiformes), and monitored the responses of the parents throughout the guarding period to test if the duration of the guarding period is related to

chick needs. We predicted that the guarding period would be shortened when fostering an older chick and prolonged when fostering a younger chick. This response may take place by: 1) a change in the number of guarding spells, 2) a change in the duration of the last guarding spell, where the chick is left unattended for the first time, and 3) a change in the duration of the foraging trips, which consequently will change the length of the guarding spells prior to the last spell. We expected these responses to be most profound by parents with high body mass.

## Material and methods

### Study site, study species and definitions

The fieldwork was carried out at Svarthamaren (71°53' S, 5°10' E), Dronning Maud Land, continental Antarctica, in January–February 2001. About 200 000 pairs of Antarctic petrels breed at Svarthamaren, which is located about 200 km from the coast (Mehlum et al. 1988). A detailed description of the physical environment is available in Mehlum et al. (1988). The Antarctic petrel is a medium sized petrel, breeding mainly in east Antarctica, and Svarthamaren is the largest known colony (van Franeker et al. 1999). In this colony, the nests are densely located on steep rocky slopes, and the breeding cycle is highly synchronised. Eggs hatch during the second week of January and the chicks are guarded for 7–15 days after hatching. This guarding period consists of alternating spells where one parent forages while the partner protects the chick from predators and harsh weather. Approximately 13% of the chicks are preyed upon by south polar skuas, *Catharacta macrorhynchos* during the first month of the fledging period (Haftorn et al. 1991). The duration of the guarding spells is about five days early in the guarding period, and about two days at the end (Lorentsen and Røv 1995, Tveraa et al. 1998a). Either the male or the female is present at hatching, depending on how the attendance cycle during incubation coincides with hatching (Lorentsen and Røv 1995). We define the spell where hatching occurs as the hatching spell. The subsequent guarding spells are termed spell 1–4. The spell at which the chick is left unattended at the nest for the first time is referred to as the last guarding spell.

### Body mass and parental decisions in the Antarctic petrel

In Antarctic petrels, successful co-ordination of the guarding period is related to the resources of the guarding parent, as light parents may leave the chick alone before the partner returns (Tveraa et al. 1998a). However, successful co-ordination is also related to the

foraging success of the mate, as individuals with high foraging success return earlier to the colony than those with poor foraging success (Tveraa et al. 1997). The foraging parent also seems to adjust its stay at sea according to the parent at the nest, returning sooner to a partner with low body mass (Tveraa et al. 1997, 1998a). Consequently, the best foragers, but also the parents that respond to the state of their partner, are more likely to return in time to assure that the chick is guarded continuously.

### Data collection

On the day after hatching the parent at the nest was caught by hand, individually marked with a steel band, and weighed in a cotton bag using a spring balance ( $\pm 0.5$  g). Wing length was measured with a ruler ( $\pm 0.5$  mm), and skull length and bill depth were measured with a digital calliper ( $\pm 0.005$  mm). The same procedure was followed for the partner when it returned to the nest. Male Antarctic petrels are larger than females (Lorentsen and Røv 1994), and we assumed that the largest bird in a pair was the male (Sandvik 2001). When only one of the birds in a pair was caught ( $N = 6$ ), a discriminant function was used for sex determination (Lorentsen and Røv 1994). To recognise individual birds in a pair at a distance, we used a colour marker to ink parts of the wings red or blue. Chicks were first weighed one day after hatching ( $\pm 0.25$  g when lighter than 300 g, otherwise  $\pm 0.5$  g). The nests were checked daily from a distance, and the adult and the chick were weighed if a changeover had taken place between the parents since our last visit. Additionally, we monitored chick survival for the first week after the chick was left unattended.

### Experimental design

We exchanged one-day-old chicks with four-day-old chicks to generate two experimental groups, so that parents had to foster a chick either three days older or three days younger than their own. For each experimental group we used a specific control group. One-day-old chicks were exchanged with one-day-old chicks to be the control group for parents given an older chick, and four-day-old chicks were exchanged with four-day-old chicks to be the control group for parents given a younger chick. Care was taken to include nests in the experiment such that the hatching date distribution was the same in the experimental groups and their corresponding controls (Table 1), and all comparisons were between the experimental groups and their respective controls. We did not exchange chicks between nests far apart in the study plot or the closest neighbours. A chick exchange was termed successful when the foster parent

continued to guard the new chick. This was the case for all but five chicks, where the parent flew off the nest and did not return in time to prevent predation. These five nests were excluded from the study, leaving 90 nests in each of the four groups except the group fostering younger chicks, which contained 89 nests.

We argue that changing chick-age from the parents point of view, is a more pertinent manipulation in this study than changing chick condition. This is because the chick's ability to care for itself, its food demand, and its assimilatory capacity is then altered permanently and cannot be changed by a few small or large meals. The Antarctic petrel is in fact able to respond to the chick's body condition by altering meal size upon arrival, even without knowledge of the chick's state prior to chick-feeding (Tveraa et al. 1998b). However, it can not be ruled out that the reduced meal size delivered to chicks in good condition come about because chicks in good condition are unable to receive more food (Weimerskirch et al. 1997). On the other hand, a change in foraging trip duration must reflect active regulation by the parent (Weimerskirch et al. 1997). We focus on foraging trips instead of meal size also because during the guarding period food can be given to the chick throughout the whole guarding spell (Ø. Varpe, unpubl.). This requires the chick to be weighed several times a day to get estimates of meal size, which is demanding when working with large samples, and it would cause a high level of disturbance.

### Statistical analysis

Analysis of covariance (Littell et al. 1996) was used to study foraging trip duration and time spent at the nest at the last guarding spell. The experimental design, and the sample sizes available, allowed foraging trip duration to be studied at the first and the second spell. Time spent at the last guarding spell could be analysed when the first, second or third spell ended the guarding period. Survival data were analysed using logistic models with the logit link function and binomial distribution (Allison 1999). All statistical analyses were performed with the SAS software (SAS-Institute-Inc. 1990). Covariates (presented below) were only included in the models if they were significantly related to the dependent variable, and if they contributed significantly to the full model as tested by type III sums of squares. Treatment was included as a factor in all analyses, and all second order interactions were tested, but none were found to be statistically significant. All statistical tests are two-tailed, based on type III sums of squares, and P-values  $< 0.05$  were considered statistically significant. Means are presented with standard errors.

We controlled for the effects of parental body mass because both time at sea and time at the nest are

influenced by the parents' body mass. However, body mass covaries with body size, and we used the first principal component (PC1) from a principal component analysis of wing length, skull length, and bill depth, for each sex separately, as a measure of body size. The PC1 explained 56% of the variation in the morphological characters for males and 46% for females. Inclusion of body size as a covariate in addition to body mass (Garcia-Berthou 2001), did not lead to any different interpretations of the treatment effects. For simplicity, we therefore present results from analyses using body mass only. Similarly, we controlled for the effects of sex, but this did not increase precision, and sex as a factor was omitted. However, adult body mass was standardised to adjust for the size difference between the sexes. The mean body mass was set to zero and the variance to one for each sex and spell, using the Standard procedure (SAS-Institute-Inc. 1990).

The starting points for the guarding spells are dependent on how long into the guarding period the hatching spell lasts. This varies between nests as stochastic processes and possibly different strategies determine how recently prior to hatching the hatching spell started. We observed that the duration of a guarding spell was negatively related to how long after hatching that the spell started. For instance for the second guarding spell, which started between five to eleven days after hatching, the spell was shorter for those parents starting late compared to those starting earlier. Because we were interested in the effects of the manipulation at individual spells, we controlled for the variance in starting point by including original chick age as a covariate.

## Results

### Group characteristics before manipulation

Hatching occurred from 7–17 January. One day after hatching, mean body mass of the chick and of the parents, and the proportions of males at the nest did not differ between the experimental groups and their corresponding controls (Table 1). Also, the experimental

groups and their controls did not differ with respect to hatching date or with respect to when the parents received their new chick (Table 1). Hence, each experimental group had a relevant control. Four-day-old chicks were on average  $36 \pm 3$  g heavier than one-day-old chicks.

### The guarding period

The range of the guarding period was 5–15 days. Parents given older chicks guarded  $1.4 \pm 0.2$  days less, and parents given younger chicks guarded  $1.1 \pm 0.2$  days more than their controls (Fig. 1a). Consequently, the age of the chicks when left unattended also differed between the experimental groups and their controls (Fig. 1b). Furthermore, parents given older chicks left heavier chicks at end of guarding, and parents given younger chicks left lighter chicks, compared to controls (Fig. 1c). The parents also responded to the experiment by using fewer spells if they guarded an older chick, and more spells if they guarded a younger chick (Fisher's exact test: older vs control  $P = 0.001$ ; younger vs control  $P = 0.02$ , Fig. 2).

### Duration of the last guarding spell

We tested whether the age of the chick had any effect on how long the parent was willing to guard during a single spell. This could be studied at the last guarding spell only, as the length of the preceding spells is determined by when the foraging parent returns to the colony. Hence, we tested whether chick age had any effect on the length of the last guarding spell after statistically controlling for original chick age and the body mass of the guarding parent (Table 2). At those nests where the chick was left alone at the first spell, parents given older chicks left the chick  $0.7 \pm 0.3$  days earlier than their control. At only two nests did the parents with a younger chick leave it unattended at the first spell, so this group and its control were not included in this analysis (Fig. 3, Spell 1). At those nests where the chick was left alone at the second spell, parents given older chicks left  $0.6 \pm 0.2$

Table 1. A comparison of experimental groups and their corresponding controls at the start of the experiment.

	Older	Control 1	Younger	Control 2
Mean hatching date (1 = 1 January)	$13.5 \pm 0.2$ (90)	$13.5 \pm 0.2$ (90)	$10.6 \pm 0.2$ (89)	$10.6 \pm 0.2$ (90)
Mean body mass of chick on day one (g)	$77.5 \pm 1.2$ (88)	$78.2 \pm 1.1$ (89)	$75.7 \pm 1.1$ (89)	$75.9 \pm 1.3$ (89)
Mean body mass of parent on day one (g)	$648 \pm 7$ (89)	$657 \pm 8$ (90)	$675 \pm 9$ (87)	$675 \pm 8$ (88)
Proportions of males at the nest on day one (%)	84 (90)	76 (90)	76 (89)	76 (90)
Proportions exchanged at the hatching spell (%)	90 (90)	89 (90)	35 (89)	41 (90)

The four groups refer to parents that received a three day older chick one day post hatching (Older), a chick of the same age on day one (Control 1) or on day four (Control 2), or a three day younger chick on day four (Younger). The chick was received during the hatching spell or during the first guarding spell, where a spell is the period the parent guards the chick while the mate is foraging at sea. Data are presented as means  $\pm 1$  SE, proportions in percentages, and sample sizes in brackets. There are slight sample size differences as some variables could not always be measured.

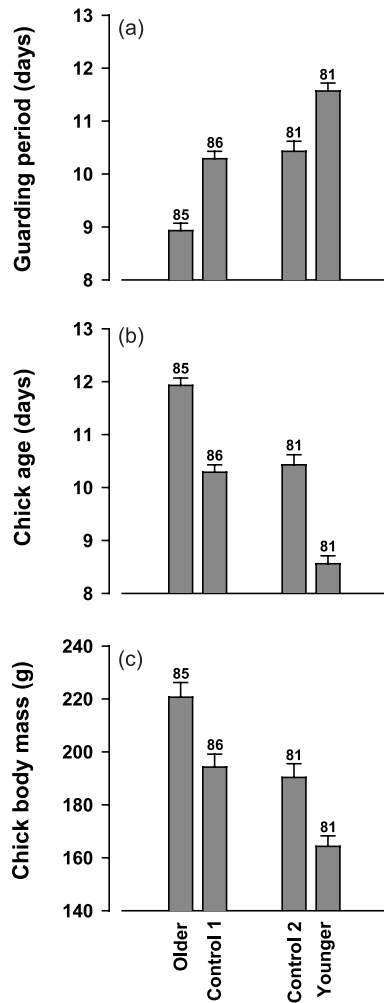


Fig. 1. Measures related to the guarding period of the Antarctic petrel where parents received a three day older chick one day post hatching (Older), a chick of the same age on day one (Control 1) or on day four (Control 2), or a three day younger chick on day four (Younger). (a) The number of days the parents guarded a chick until it was left alone for the first time. (b) The age of the foster chick when left alone. (c) The body mass of the foster chick when left alone. Data are presented as means with 1 SE and sample sizes above the bars.

days earlier than their controls, whereas parents given younger chicks left  $0.4 \pm 0.2$  days later than their controls (Fig. 3, Spell 2). Finally, at those nests where the chick was left alone at the third spell, parents given younger chicks did not differ in guarding time compared to control birds. At only two nests did the parents with an older chick still guard the chick during the third spell, so this group and its control were not included in this analysis (Fig. 3, Spell 3). The duration of the last guarding spell decreased with original chick age, and parents with a high arrival body mass guarded longer than light parents (Table 2).

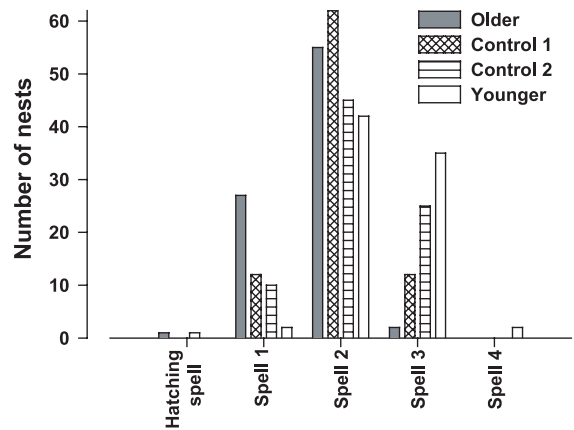


Fig. 2. The distribution of guarding spells where Antarctic petrels left their chick alone for the first time. A spell is the period the parent guards the chick while the mate is foraging at sea. The parents alternate between these two duties until the chick is left unattended. The figure legends refer to parents that received a three day older chick one day post hatching (Older), a chick of the same age on day one (Control 1) or on day four (Control 2), or a three day younger chick on day four (Younger). Data are presented as number of nests per spell and treatment.

Parents that had not seen their foster chick before they arrived from the sea to start the last guarding spell, also adjusted the duration of this spell according to the chick's needs. This result is based on a sub-set of the data, which satisfies the requirement that the foster chick was left unattended at the same spell as the parent first guarded this chick. This applied to the parents which left their chick at the first spell (Fig. 3, Spell 1), and to some of the parents with younger chicks and their control, which left the chick unattended at the second spell (younger vs control:  $3.0 \pm 0.2$  and  $2.4 \pm 0.2$  (days),  $N = 20$  and  $N = 26$ ,  $F = 4.9$ ,  $df = 1,44$ ,  $P < 0.05$ ).

### Time spent at sea

We tested if the experiment had any effect on the number of days spent at sea at each foraging trip, after statistically controlling for original chick age, the body mass of the guarding parent, and the arrival body mass of the foraging parent (Table 3). At the first spell, parents given older chicks spent  $0.4 \pm 0.1$  days less at sea than their control (Fig. 4, Spell 1). Parents with younger chicks and their control were omitted from the analysis at the first spell as only few of the parents in these two groups received their chick at the hatching spell (Table 1) i.e. in time to observe the chick before leaving on the next foraging trip. At the second spell, parents given older chicks did not differ in the amount of time spent at sea compared to their control, but the sample size was limited in the experimental group ( $N = 9$ ). Parents given younger chicks spent  $0.5 \pm 0.2$  days more at sea than their control (Fig. 4, Spell 2). Birds that returned after

Table 2. Tests for the effects of chick age on the time Antarctic petrels guarded their chick at the last guarding spell.

	Original chick age**		Body mass of guarding parent		Treatment	
	F	P	F	P	F	P
Spell 1 Older vs Control 1	8.5	< 0.01		ns*	6.3	0.02
Spell 2 Older vs Control 1	60.0	< 0.001		ns*	16.0	< 0.001
Spell 2 Younger vs Control 2	22.2	< 0.001	9.2	< 0.01	5.5	0.02
Spell 3 Younger vs Control 2		ns*	19.2	< 0.001	0.1	0.74

A spell is the period the parent guards the chick while the mate is foraging at sea. Treatment refers to the four groups where parents received a three day older chick one day post hatching (Older), a chick of the same age on day one (Control 1) or on day four (Control 2), or a three day younger chick on day four (Younger). Original chick age and the arrival body mass of the guarding parent are covariates. Sample sizes are 39, 115, 84, and 60 in the four analyses, respectively. The sign of the covariates are given in the result section and treatment estimates in Fig. 3.

\*Insignificant covariates (ns) were removed and values presented from the refitted model.

\*\*Original chick age range: Spell 1, 2–7 days, spell 2, 5–11 days, and spell 3, 8–13 days.

short stays at sea returned heavier than birds spending more time foraging. Furthermore, birds having a partner with a high body mass on duty at the nest spent more time foraging than if the partner was light. Finally, foraging trip duration was negatively related to original chick age (Table 3).

### Chick survival

From the time of chick exchange until the end of guarding, 94% (N = 357) of the chicks survived, and there was no difference between the experimental groups and their controls (older vs control: 94% and 97%,  $\chi^2 = 0.5$ ,  $df = 1$ ,  $P = 0.47$ ; younger vs control: 92% and 91%,  $\chi^2 = 0.1$ ,  $df = 1$ ,  $P = 0.80$ ). During the first week post guarding, 92% (N = 334) of the chicks survived. The survival probabilities of the chicks post guarding did not differ between the experimental groups and their controls (older vs control: 92% and 95%,  $\chi^2 = 1.0$ ,  $df = 1$ ,  $P = 0.33$ ; younger vs control: 91% and 89%,  $\chi^2 = 0.3$ ,  $df = 1$ ,  $P = 0.60$ ). Because there were no treatment effects, we tested for the effects of chick body mass and chick age at end of guarding across all four groups. The survival probabilities of unattended chicks tended to be positively related to chick body mass ( $\beta = 0.01$ ,  $CI = [0.00, 0.02]$ ), but not to chick age ( $\beta = 0.10$ ,  $CI = [-0.11, 0.30]$ ).

## Discussion

### Regulating the guarding period

As predicted, we observed a change in the overall number of days the parents guarded the chick (Fig. 1a). Parents receiving an older chick guarded 1.4 days less, and parents with a younger chick guarded 1.1 days longer than controls. The observed change in the duration of the guarding period resulted from a

combination of three mechanisms. First, the number of guarding spells was adjusted. Parents with an older chick co-ordinated fewer guarding spells, and if the chick was younger, more guarding spells were used (Fig. 2). This result is in part a consequence of the second mechanism, the endurance of the guarding parent. At the last guarding spell, parents with an older chick departed earlier, while parents with a younger chick extended the time they guarded the chick before they left it alone (Fig. 3). Hence, the willingness to wait for the partner to take over the guarding duty is dependent on the chick's needs for guarding, which consequently changed the probability of how many spells the parents co-ordinated, and how long the guarding period lasted. This behavioural response probably took place during all guarding spells, but could only be studied at the last spell, because the motivation to leave at the previous spells was the arrival of the partner. The time the guarding parent had to wait to assure continuous guarding also changed because the duration of the foraging trips was adjusted in response to the age of the chick; the third mechanism. Parents spent less time at sea if fostering an older chick, and more time at sea if fostering a younger chick (Fig. 4), which may also have contributed to the overall change in the duration of the guarding period.

In the Antarctic petrel the duration of consecutive guarding spells shorten towards the end of the guarding period (Lorentsen and Røv 1995). This is probably a parental response to the chick's demand for food, which increases with age in Procellariiformes (Bolton 1995b, Hamer and Thompson 1997, Weathers et al. 2000), or a response to the chick's ability to assimilate and swallow subsequent large meals, which may improve with age (Bolton 1995b). Hence, the adjustments of foraging trip duration seems to have been a consequence of altered food demands of the chick. We do not know if the food load changed when feeding frequency changed, but for other Procellariiformes an increase in feeding frequency with chick growth has been observed without a reduction in food load, both as a response to increased food

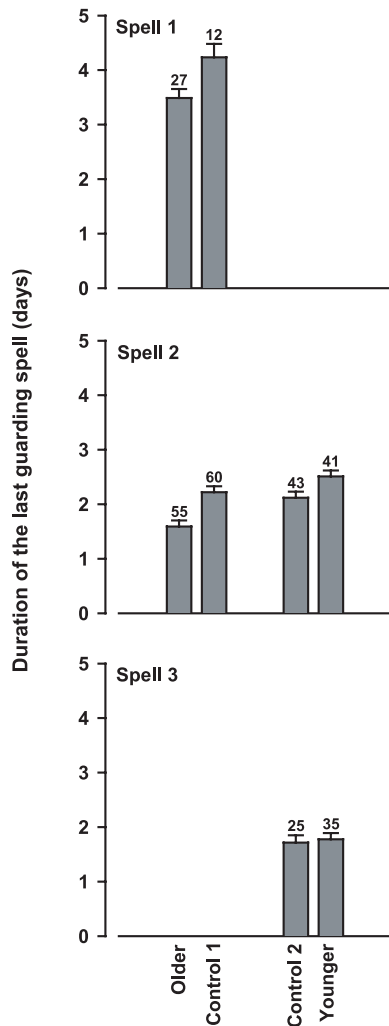


Fig. 3. The number of days Antarctic petrels spent at the nest at the last guarding spell. A spell is the period the parent guards the chick while the mate is foraging at sea. The four groups refer to parents that received a three day older chick one day post hatching (Older), a chick of the same age on day one (Control 1) or on day four (Control 2), or a three day younger chick on day four (Younger). Missing bars are due to a limited sample leaving their chick during that spell (Fig. 2). Data are presented as least square means with 1 SE, based on the models presented in Table 2. Sample sizes are shown above the bars.

demand with chick age (Hamer and Thompson 1997) or to experimentally increased food demand (Takahashi et al. 1999, Granadeiro et al. 2000).

Our observations suggest that the parents quickly adjust both the guarding and the foraging behaviour according to the chick, whose needs for food and protection are altered by the manipulation. This is despite the difficulties that birds with stochastic foraging success and long foraging trips may have in adjusting parental care according to short time variation in chick needs (Ricklefs 1987, Ricklefs and Schew 1994).

### Regulations constrained by body mass

As expected, the parents' response to the chick was related to the parents' body mass. Parents with high body mass at the start of a guarding spell guarded longer than lighter parents. We observed this relationship when we compared parents guarding a younger chick with the control, while it was absent when comparing parents fostering an older chick with the control (Table 2). This suggests that the decision to leave older chicks earlier was motivated by the chick's rather than the parent's needs for food. On the other hand, if the chick was young, the parent guarded until its own energy reserves were depleted as protection rather than food was probably most important for the chick. Therefore, parents with younger chicks may not have compensated for the whole manipulation because guarding is costly and difficult to co-ordinate (Tveraa et al. 1998a, Tveraa and Christensen 2002). Similarly, parents given an older chick did not reduce the guarding time with the full three days, but left relatively old chicks instead (Fig. 1b).

We observed that the parents that had not seen their foster chick before they arrived to the nest also adjusted the duration of the last guarding spell. This immediate response to the chick's needs rules out the possibility that the adjusted duration of the last spell is due to differences between the groups in the fasting ability of the guarding parent, i.e. differences in the amount of food brought from the sea. Rather, the parents' response suggests that, although many seabirds typically desert when approaching a body mass threshold (Chaurand and Weimerskirch 1994, Olsson 1997, Tveraa et al. 1997, Gauthier-Clerc et al. 2001), the decision to leave the chick unattended during the guarding period is not fixed to parental body mass, but depends on the chick's needs. Alternatively, the parents have given more food to an older chick and less to the younger chick (Tveraa et al. 1998b), which may affect the parents own state, and consequently, how long the parent can guard.

Behavioural regulations according to body mass are central also to the foraging bird. We observed that the duration of the foraging trips was negatively related to arrival body mass (Table 3), suggesting that the parents with the highest foraging success returned quickly to the colony (Tveraa et al. 1997). Furthermore, we observed a positive relationship between the duration of the foraging trip of the parent at sea and the body mass of the partner when it started to guard (Table 3). Hence, the parent at sea seemed to adjust when to return according to the guarding abilities of the partner (Tveraa et al. 1998a). Co-ordination by the parents to optimise parental care is rarely suggested for Procellariiformes, but Booth et al. (2000) found that the parents seem to co-ordinate their feeding visits to assure that the chick is fed on a regular basis.

Clearly, the body mass of Procellariiformes is related to how willingly they invest in offspring (Chaurand and

Table 3. Tests for the effects of chick age on the time Antarctic petrels spent at sea at the mate's first and second guarding spell.

	Original chick age**		Body mass of foraging parent		Body mass of guarding parent		Treatment	
	F	P	F	P	F	P	F	P
Spell 1 Older vs Control 1	34.4	< 0.001	29.4	< 0.001		ns*	9.3	< 0.01
Spell 2 Older vs Control 1		ns*		ns*	5.5	0.03	1.1	0.31
Spell 2 Younger vs Control 2	16.2	< 0.001	9.8	< 0.01	5.5	0.02	9.4	< 0.01

A spell is the period the parent guards the chick while the mate is foraging at sea. Treatment refers to the four groups where parents received a three day older chick one day post hatching (Older), a chick of the same age on day one (Control 1) or on day four (Control 2), or a three day younger chick on day four (Younger). Original chick age, arrival body mass of the parent at sea, and arrival body mass of the guarding parent are covariates. Sample sizes are 124, 32, and 103 in the three analyses, respectively. At the first spell Younger and Control 2 were omitted from the analysis as only few nests in these groups received their chick during the hatching spell (Table 1). The sign of the covariates are given in the result section and treatment estimates in Fig. 4.

\*Insignificant covariates (ns) were removed and values presented from the refitted model.

\*\*Original chick age range: Spell 1, 2–7 days and spell 2, 5–10 days.

Weimerskirch 1994, Duriez et al. 2000), a result that also is apparent from several studies on the Antarctic petrel (Sæther et al. 1993, Lorentsen 1996, Tveraa et al. 1997). However, we show that the parents are willing to adjust important decisions during chick rearing not only

according to their own body mass, but also according to the needs of the chick (Tveraa et al. 1998b). This may be adaptive in a variable environment where foraging success, and thereby parental body mass and chick needs, may vary from one spell to the other. Furthermore, this flexibility may be particularly profitable for individuals with high body mass, and such findings may therefore dominate in studies performed in good breeding seasons (Weimerskirch et al. 2001). On the other hand, parents with low body mass may give priority to their own state instead of adjusting behaviour according to the mate or the needs of the chick (Sæther et al. 1993, Erikstad et al. 1998, Tveraa et al. 1998b).

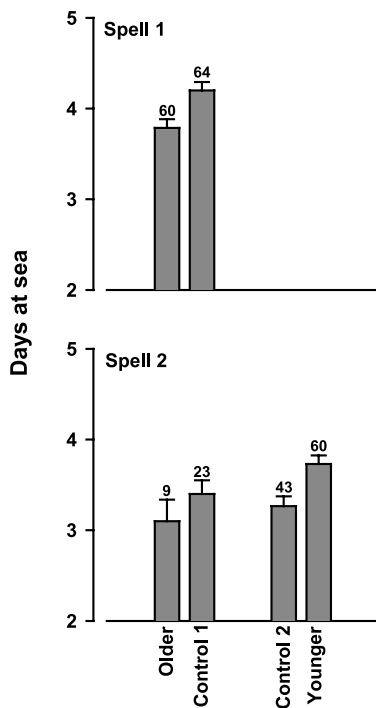


Fig. 4. The number of days Antarctic petrels spent at sea at the mate's first and second guarding spell. A spell is the period the parent guards the chick while the mate is foraging at sea. The four groups refer to parents that received a three day older chick one day post hatching (Older), a chick of the same age on day one (Control 1) or on day four (Control 2), or a three day younger chick on day four (Younger). At the first spell Younger and Control 2 were omitted from the analysis as only few nests in these groups received their chick during the hatching spell (Table 1). Data are presented as least square means with 1 SE, based on the models presented in Table 3. Sample sizes are shown above the bars.

### Consequences for the chick

Even though the parents did not adjust completely for the three days difference in chick age, the chicks' survival did not differ when comparing each experimental group with its control. This may indicate that the compensation was sufficient to avoid differential levels of chick loss. Alternatively, any effects on chick survival may not be found after only one week, or the manipulation may have been too small. However, the survival probabilities tended to be positively related to the chick's body mass at end of guarding, but not to the chick's age. This indicates that the chicks' ability to care for themselves is dependent on their nutritional status rather than their age. For example, well-fed chicks have more stomach oil to spit at attacking skuas (Weidinger 1998). Additionally, well-fed chicks may be more alert and in sum, better able to protect themselves against predators.

### State-dependent parental care

We demonstrate that Antarctic petrels adjust time spent foraging and time spent guarding according to the chick's needs for food and protection. This flexible behaviour is in agreement with general expectations for



parental care (Winkler 1987, Clutton-Brock 1991), but contrary to the lack of such responses observed in several studies on Procellariiformes (Ricklefs 1987, Hamer and Hill 1994, Lorentsen 1996, Duriez et al. 2000). We also demonstrate that reproductive decisions are related to the parents' body mass, which is expected from life history theory, since long-lived species with many reproductive events should not spend undue amounts of resources on current versus future reproduction (Williams 1966, Curio 1988, Lindén and Møller 1989). Parents with low body mass may therefore give priority to their own needs before those of the young, while parents with higher body mass may benefit from adjusting their behaviour to both the state of the mate and the offspring. We propose that adjustments that take place according to many factors simultaneously are commonplace, even for long lived seabirds, and to understand this complexity, these factors must be studied simultaneously. This may be done in well designed field experiments, but dynamic state variable models (Houston and McNamara 1999, Clark and Mangel 2000) may also increase our understanding of the trade-offs that seabirds face during reproduction. Such models may be particularly useful since the birds are faced with decisions that have an uncertain outcome. For instance, continued guarding does not assure that the partner returns in time to relieve the guarding partner, or continued foraging instead of returning to the nest does not necessarily result in more food for the chick. Furthermore, state based models may be useful since the optimal solution to these decisions depends on the parent's own state, the state of the partner, and the state of the offspring.

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