

Incubation routine, body mass regulation and egg neglect in the Blue Petrel *Halobaena caerulea*

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The incubation routine and mass changes of male and female Blue Petrel *Halobaena caerulea* were studied at the Kerguelen Islands to investigate factors influencing the durations of incubation stints and foraging trips at sea and the factors determining nest desertion and return to the nest.

The body mass at the start of an incubation shift and also when the bird was relieved varied throughout the incubation period, whereas the mass when birds deserted the nest was stable. Birds deserted the nest when their mass decreased to threshold, independent of the duration of the fast. Temporary egg neglect was observed in successful as well as in unsuccessful breeding attempts, but it increased the risk of breeding failure. The net and daily mass gained at sea during the second part of the incubation period were higher than during the first part, suggesting an increase in food availability. During the first part, the mass gained at sea and time spent foraging were inversely related to the mass of the bird before it left the burrow, whereas a similar relationship did not occur thereafter.

The results suggest the occurrence of a fixed mass threshold when birds decide to leave the nest if not relieved by their partner. The mass when a bird left its nest influenced the time spent foraging or mass gained when food was scarce. Although decision rules to leave the nest or return from the sea are related to body condition, the possibility of neglecting the eggs temporarily enables Blue Petrels to regulate the trade-off between risks of breeding failure and risks of an increase in adult mortality. A model for behavioural decision to stop incubating or stop feeding, based on a variable set point, is proposed.

Reproduction often reduces opportunities of foraging so that reproductive individuals may incur a cost that could reduce future survival (Williams 1966). An individual could take the optimal decision to maximize its own fitness (Sibly & McCleery 1985). In birds undergoing important changes in body mass through the breeding season, body mass could be an important factor in behavioural decisions for changing activities during the reproductive period (MacNamara & Houston 1986). In this context, the status of body reserves is claimed to be an important factor influencing the decision to reproduce or not (Drent & Daan 1980).

Many pelagic seabirds undergo large variations in their body mass during the incubating period when the male and female alternate on the nest (Fisher 1967, Prince *et al.* 1981). Incubation in pelagic seabirds represents a simple situation where the short term interest of reproduction, i.e. warming the egg on land, directly competes with the necessity to restore body reserves at sea. Incubating and foraging are clearly separated, both in time and space, because pelagic seabirds incubate for long incubation shifts and forage from their nest. As pelagic seabirds are generally long-lived (Lack 1968), it is particularly important to minimize the risk of

adult mortality in the course of reproduction (Williams 1966). This suggests that body mass should be closely regulated. The role of body mass in the behavioural decision during incubation is suggested in Procellariiformes by the frequent occurrence of spontaneous egg desertions after long fasting shifts (Boersma & Wheelwright 1979, Jouventin *et al.* 1985). Although the decision to desert the egg could be based on the actual level of reserves of the fasting bird, alternative hypotheses are possible. For example, birds could desert their egg after having fasted for a maximum time or after having lost a maximum amount of mass. The only precise study on the subject (Johnstone & Davis 1990) indicates that the Great-winged Petrel *Pterodroma macroptera* deserts its egg early in the fasting shifts and at a higher mass than when normally relieved.

Similarly, when at sea, the level of body reserves could be important in the decision to return to land. For example, Mougin (1989) suggests that adults return when they reach a defined mass threshold whatever the time spent foraging, but other studies suggest the prevailing importance of trip duration (Davis 1988, Johnstone & Davis 1990). The respective roles of time and body mass in the decision to stop foraging, therefore, are unclear. Moreover, it is possible that the duration of foraging trips is influenced by the fasting

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Table 1. Mean (\pm s.d.) duration of incubation shifts, mass at start and end of the shift, mass at desertion and proportion of shifts with desertions in Blue Petrels (sample sizes in parentheses)

Shift	Sex ¹	Duration (days)	Mass at start of shift (g)	Mass when relieved (g)	Mass at desertion (g)	% of desertions
First	F	1.4 \pm 1.2 (21)	—	182.5 \pm 10.0 (13)	165.8 \pm 6.6 (5)	28% (28)
Second	M	12.0 \pm 1.6 (15)	226.5 \pm 15.0 (21)	181.6 \pm 12.9 (16)	164.7 \pm 8.9 (10)	38% (26)
Third	F	10.4 \pm 1.1 (5)	210.1 \pm 10.5 (26)	171.0 \pm 13.0 (3)	163.4 \pm 9.4 (12)	80% (15)
Fourth	M	8.3 \pm 2.1 (6)	209.1 \pm 11.2 (13)	170.1 \pm 10.4 (12)	165.8 \pm 6.9 (14)	54% (26)
Fifth	F	9.1 \pm 1.6 (13)	210.4 \pm 11.7 (25)	175.2 \pm 6.0 (9)	164.3 \pm 6.1 (4)	31% (13)
Sixth	M	8.2 \pm 0.8 (5)	226.4 \pm 15.1 (13)	—	—	—

¹ F = female, M = male.

capacity of the partner at the beginning of the shift: a small fasting capacity may favour a short foraging trip to minimize the risk of egg desertion.

The aim of this study was to investigate the role of adult mass on the behavioural decisions during the incubation routine of a small burrowing petrel, the Blue Petrel *Halo-baena caerulea*. Three questions are addressed: (1) What is the role of adult mass in the process of egg desertion? (2) Is the duration of the foraging dependent on the fat reserve of the partner at the beginning of the shift? (3) Does the duration of the foraging trip depend on the mass of the adult? The answers to these three questions are discussed in the light of a model suggesting the crucial importance of body mass regulation in the incubation routine of the Blue Petrel.

METHODS

The study was carried out on Mayes Island, in the Morbihan Gulf, Kerguelen Islands (southwestern Indian Ocean, 49°S, 70°E) between 27 October and 25 December 1988, during the incubation period of Blue Petrels (Weimerskirch *et al.* 1989). Fifty burrows were each fitted before the onset of the breeding season with a door over the incubating chamber that allowed regular observations during the incubation. The burrows were checked daily during daytime (changeover on the egg always took place at night) throughout the incu-

Table 2. Mean (\pm s.d.) duration, mass gain and daily mass gain of shifts at sea in Blue Petrels

Stay at sea	Sex ¹	n	Duration (days)	Mass gain (g)	Daily mass gain (g/day)
First	F	15	11.4 \pm 1.8	28.8 \pm 6.5	2.7 \pm 0.9
Second	M	13	13.6 \pm 2.1	34.4 \pm 11.6	2.7 \pm 1.1
Third	F	9	12.2 \pm 1.2	54.1 \pm 13.8	4.4 \pm 1.1
Fourth	M	12	10.8 \pm 1.1	63.0 \pm 9.3	5.9 \pm 1.0

¹ F = female, M = male.

bation period except for three periods when the observers were absent (1–4 November, 15–20 November and 12–16 December). To minimize the handling of the birds and reduce disturbance, fine sticks were placed at the entrance of the burrow: the arrival or departure of a bird was revealed by the disturbance of this indicator. During incubation, birds were weighed with a spring balance accurate to 1 g at arrival, 5 days later (incubation bouts last an average of 8 days) and every second day thereafter until departure. The birds were sexed by cloacal examination (Serventy 1956) and by voice (Bretagnolle 1990). Averages are given \pm 1 s.d. (in parentheses).

RESULTS

Incubation schedule

Incubating male and female Blue Petrels alternated incubating the egg with shifts lasting usually 8–12 days, except for a short, first shift by the female after she had laid the egg (Table 1). Incubating birds lost mass as a result of complete fasting on land. The rate of mass loss averaged 5.1 (\pm 0.65) g/day (range 3.75–6.43 g/day, n = 42) or 2.37 (\pm 0.32)% of the initial body mass per day (range 1.62–2.81%, n = 42). Because of this small variability, the total mass lost was closely related to the time spent fasting (r_{40} = 0.88, P < 0.001). The rate of mass loss was similar between male and female (respectively, 5.01 [\pm 0.69] g/day, n = 25 and 5.20 [\pm 0.59] g/day, n = 17, t_{40} = 0.93, n.s.) and increased slightly but significantly as the season progressed (r_{40} = 0.36, P < 0.02). The average masses of birds at the start of a shift and when relieved by the partner varied significantly between shifts (males $F_{2,44}$ = 7.1, P < 0.002; females $F_{2,60}$ = 30.2, P < 0.001 and males $F_{1,26}$ = 6.4, P < 0.01; females $F_{2,22}$ = 2.9, respectively, n.s.; Table 1). Thus the mass at the start of a shift and when the bird was relieved was, on average, lower between the second and fourth shifts by the males (t_{32} = 3.4, P < 0.001 and t_{26} = 2.4, P < 0.02, respectively; Table 1). Individual males were lighter when they started the fourth shift than when they started the

Table 3. The relationship between the mass of Blue Petrels leaving their burrow after an incubation shift and the duration of the foraging trip, the mass when the bird returns to the nest and mass gain at sea during the two parts of the incubation period. Values are correlation coefficients (r)

	Part of incubation period	Duration of the stay at sea	Mass when return from the sea	Mass gain at sea
Mass when bird leaves burrow	First $n = 29$	-0.41 $P < 0.03$	0.73 $P < 0.001$	-0.49 $P < 0.01$
Mass when bird leaves burrow	Second $n = 21$	-0.21 n.s.	0.47 $P < 0.03$	-0.26 n.s.

second shift (Wilcoxon signed rank test [Siegel & Castellan 1988], $n = 8$, $T+ = 38$, $P < 0.005$).

Egg desertions

When incubating adults were relieved by their mates, they usually returned to sea during the same night. However, adults returned to sea before being relieved by their partner in 46% ($n = 98$) of the observed changeovers. Temporary periods of egg neglect occurred in 94% of the burrows studied in the colony. The proportion of temporary egg desertion varied significantly during incubation ($\chi^2_3 = 11.8$, $P < 0.01$), being maximal in the middle of the incubation and minimal at the beginning and end (Table 1). An average of 1.58 (± 0.93) periods of egg neglect (range 1–5) was observed in 36 burrows studied over the entire incubation period. There was significantly less temporary egg neglect in burrows where the chick hatched than in unsuccessful burrows (respectively, 1.17 [± 1.03], range 0–5, $n = 12$ and 1.75 [± 0.68],

range 1–3, $n = 24$, $t_{34} = 2.9$, $P < 0.05$). The duration of each period of egg neglect was similar in the successful and unsuccessful burrows (respectively, 2.75 [± 1.54] days, range 1–5, $n = 12$ and 3.06 [± 1.70], range 1–6, $n = 35$; $F_{1,45} = 0.31$, n.s.). The total duration of temporary egg neglect in burrows which produced a hatched chick was 4.1 (± 4.0) days (range 1–13, $n = 8$).

Individuals deserted the egg after a variable amount of time spent incubating, ranging from 1 to 14 days. This fasting time till desertion had no influence on the adult mass at desertion ($r_{22} = -0.09$, n.s.) but was related to the initial mass of the adults ($r_{22} = 0.90$, $P < 0.001$; Fig. 1). This suggests that adults deserted their egg when they reached a mass threshold independent of the duration of the fasting shift. Indeed, for the same individual, the mass at desertion was significantly lower than the mass when relieved (Wilcoxon signed rank test, $T+ = 114$, $n = 15$, $P < 0.001$). The mass at desertion tended to be the same in individual birds

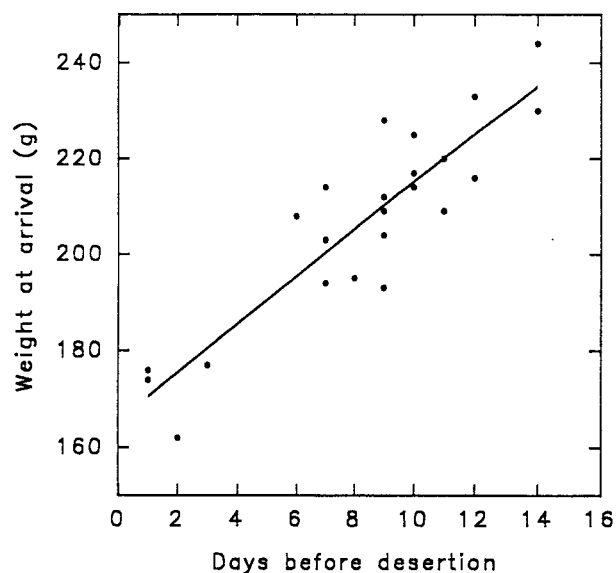


Figure 1. Relationship between the mass at the start of an incubation shift and the duration of the shift before desertion in the Blue Petrel ($y = 4.9x + 165.6$, $n = 23$).

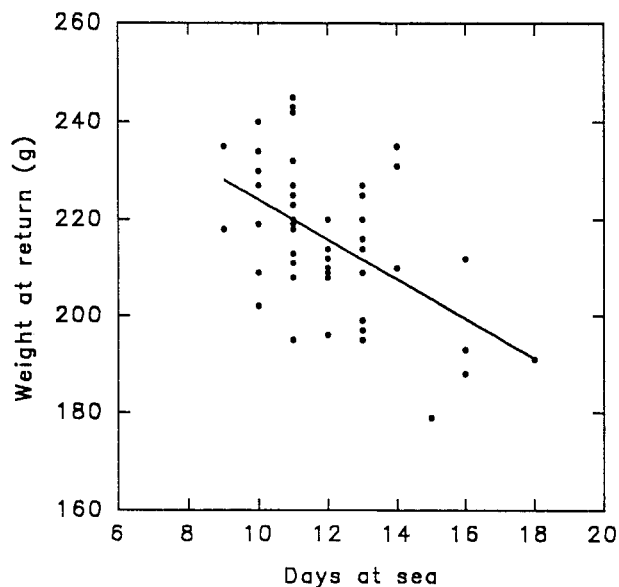


Figure 2. Relationship between the duration of a foraging trip and the mass of the Blue Petrels when they return to the nest ($y = -0.065x + 26.1$, $n = 50$).

Table 4. The relationship between the mass at the end of an incubation shift and the time spent at sea in Blue Petrels. Values shown are correlation coefficients (r). n.s. = not significant

	First stay (female)	Second stay (male)	Third stay (female)	Fourth stay (male)	All combined
r	-0.60	-0.67	0.48	-0.10	-0.52
n	15	14	9	12	50
P	<0.02	<0.01	n.s.	n.s.	<0.001

for which the mass was recorded for two different shifts ($r_4 = 0.95$, $P < 0.05$). Mass at desertion did not change significantly through the incubating period (males $F_{1,22} = 0.1$, females $F_{2,18} = 0.2$, both n.s.; Table 1). There was no significant difference in the mass at desertion between males and females (165.3 [± 7.6] g, $n = 21$ and 164.1 [± 7.9] g, $n = 24$, $t_{43} = 0.2$, n.s.).

Return from the sea

Adults increased in mass during their foraging trips at sea at a rate ranging from 1.0 to 7.3 g per day (average 3.80 [± 1.67] g/day, $n = 50$). For each sex, the average daily mass gain was lower during the first part of the incubation period than during the second part (males $t_{23} = 7.3$, females $t_{22} = 3.9$, both $P < 0.001$; Table 2). For all foraging trips combined, this rate increased significantly with the average date of the trip ($r_{48} = 0.72$, $P < 0.01$).

The mass when birds left the nest to return to sea was inversely related to the time spent foraging and mass gained at sea, but only during the first part of the incubation period (Table 3). Similarly, the duration of the foraging trip was inversely related to the body mass at the return to the nest only during the first part of the incubation period (Fig. 2, Table 4). The amount of mass lost during the fast or the duration of the fasting shift was not related to the foraging parameters (Table 5).

Although the decision to return to the nest depends only

Table 5. The relationship between the duration and mass loss during the fast and the duration and mass gain during the stay at sea in Blue Petrels. Values shown are correlation coefficients (r)

	Duration of stay at sea	Mass on return from the sea	Mass gain at sea
Duration of shift $n = 50$	-0.30 n.s.	0.00 n.s.	-0.16 n.s.
Total mass loss $n = 50$	-0.36 n.s.	-0.05 n.s.	0.09 n.s.

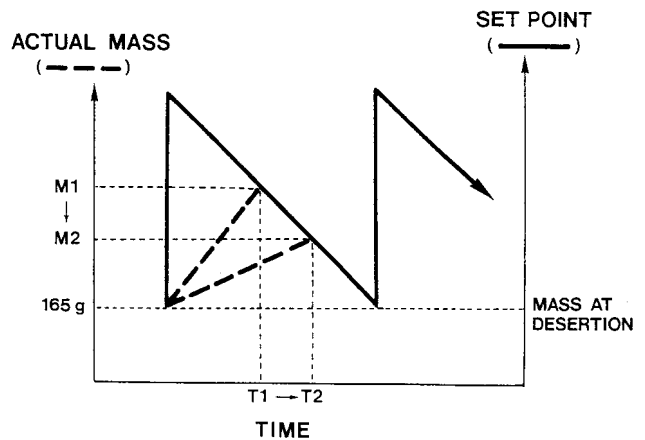


Figure 3. Model showing the change over time in a set point for the decision of the Blue Petrel to feed (go to sea) or to stop feeding (return to the nest). The actual mass (dotted lines) of the bird can increase more or less rapidly according to the success of foraging. If the success is good, the actual mass (m_1) reaches the set point at a high value and the bird returns to the nest after a short period at sea (t_1). If the foraging success is not good, the bird forages for a longer time and reaches the set point at a lower mass (m_2) after a longer period at sea (t_2). Although the mass is lower, the bird returns to the nest to relieve its partner in order to reduce the risk of egg desertion.

on the foraging adult, it is possible that some information exchanged during the changeover (e.g. vocalization displays) could influence indirectly this decision according to the mass of the partner, which has been shown to be a measure of its fasting capacity. There was, however, no significant influence of adult mass on the duration of the foraging trip of its mate ($r_{21} = 0.09$, n.s.) nor on the total mass gained ($r_{21} = -0.14$, n.s.).

DISCUSSION

Although it is known that some bird species change behaviour or even desert their eggs when energy reserves fall to a critical low level (e.g. Aldrich & Ravelling 1983, Sibly & McCleery 1985), our results demonstrate the existence of a precise mass threshold when Blue Petrel temporarily desert their eggs. This mass threshold is the same throughout the incubation period and is similar for males and females. It is similar for the same individual, and the variance of the average mass threshold is probably the result of the variability in size of birds as the mass of the same individual recorded twice tends to be the same. The mass on desertion is very close to the mass of Blue Petrels when they return from a short trip to feed their chick (Chaurand & Weimerskirch 1994), suggesting that when they are rearing the chick they work at a minimum mass, possibly to reduce flight energy costs for a period of high energy demand (Norberg 1981).

The results of Johnstone & Davis (1990) contrast with our results and those of other authors (Skutch 1962, Sibly & McCleery 1985, Jones 1987, Mougin 1989). They showed that Great-winged Petrels deserted their eggs early in the fasting shifts and at a higher mass than when normally relieved, suggesting that the duration of the foraging trip, at least for the females, was predicted by the time elapsed since laying. Although this factor could have some influence, their results also could be the result of the very high sensitiveness to handling of gadfly petrels compared to other seabirds. The desertions at the beginning of the incubation fast also could be the result of inexperienced birds.

Temporary egg desertion appears to be common in the Blue Petrel. The decision to desert the egg appears to be controlled by the mass of the adult bird and not by the time spent incubating or by the amount of body reserves used. Desertion increases the incubating time and may also reduce reproductive success. In the Fork-tailed Storm Petrel *Oceanodroma furcata*, the hatching success decreased with the amount of egg neglect (Boersma & Wheelwright 1979), and our study indicates that pairs of Blue Petrels that were eventually unsuccessful deserted their eggs more frequently than successful ones. The extent of egg desertion depends on the ability of birds to restore their reserves at sea. During the first part of the incubation period, i.e. the first two stays at sea, males and females probably had more difficulties in finding food than during the next stay at sea, as the daily mass gain was much lower at this time. This could have resulted from an increase in food availability as the season progressed. Zooplankton volumes increase at this time of the year in the sub-Antarctic (Foxton 1956). When food was less available, some birds returned at low masses despite long foraging trips. These birds that had more difficulty gaining weight when food was less abundant could have been inexperienced, as has been shown for the Antarctic Fulmar *Fulmarus glacialis* (Weimerskirch 1990). The average masses reached at the end of the third and fourth shifts by the female and the male Blue Petrel were only 8 and 5 g higher, respectively, than the average mass at desertion. These small differences coincided with the higher rates of desertions in mid-incubation. When food was more abundant at the end of the incubation period, there was no longer a relationship between foraging time and mass at return from the sea, suggesting that at this stage the constraints were no longer important and that birds could restore their body reserves easily. With the ability of eggs to resist chilling, temporary egg desertion enables the birds to regulate the inability of pairs to alternate efficiently on the egg, especially when food is scarce.

When fasting, Blue Petrels clearly use a decision rule according to which stopping incubating occurs when energy reserves fall below a given point. The presence of a stable set point, with a small variance, for the decision to leave the nest contrasts with the absence of such clear threshold value for the decision to return to the nest, as the individual mass when the birds returned from the sea varied from one shift to the next. However, although individual birds did not try

to return to the same mass from the end of one foraging trip to the next, the significant relationship between the mass at departure and the mass at return to the nest throughout the incubation period indicates that birds try to regain a mass in relation to the mass at departure. Since the decision to return to the nest may be viewed as precisely the opposite of the decision to leave the egg ("stop feeding" against "feeding"), we can expect that it is related symmetrically to a high but changing set point that triggers the change in behaviour. The study of Sherry *et al.* (1980) on the domestic hen demonstrated that mass change during incubation was genetically programmed by a linearly decreasing set point. Can the decision of the Blue Petrel to return to the nest when at sea be modelled simply in relation to a high but steadily decreasing set point? This is illustrated in Figure 3. The duration of foraging trips or of incubation shifts appears much less variable than that of other species of Procellariiformes such as albatrosses, gadfly petrels or storm petrels (see Jouventin *et al.* 1985, Weimerskirch *et al.* 1986), suggesting that Blue Petrels spend a less variable period at sea than do other species. If birds can reach the set point rapidly, i.e. they have good foraging success, they return to land after a short stay at sea. If the foraging success is poor, they cannot afford to spend a prolonged period at sea, which would increase the risk of nest desertion by their partner, and they return to land at a lower mass because the set point has become lower (Fig. 3). Such a model can explain the rather unexpected negative relationship between trip duration and bird mass at the end of the trip: when bird mass increases slowly as a result of low foraging efficiency, the set point is reached after a long time and consequently has a low value. The absence of a significant demonstration of this relationship during the second part of incubation may be due to the small variability in trip duration at this time. The significant inverse relationship between the mass of the bird when it leaves the nest for the sea and the duration of the trip at sea or the mass gain (Table 3) is also a logical consequence of this model; the set point can be attained more rapidly if the mass is high. Thus, the decision to desert the egg or to return from the sea can be understood as a consequence of the regulation of adult mass with regard to a changing set point.

This study was supported by "Terres Australes et Antarctiques Françaises" and is part of the programme directed by P. Jouventin. We thank J. Lallemand for helpful comments.

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Submitted 7 August 1993; revision accepted 6 September 1993