State-dependent decisions in long-term fasting king penguins, *Aptenodytes patagonicus*, during courtship and incubation

MICHEL GAUTHIER-CLERC, YVON LE MAHO, JEAN-PAUL GENDNER, JOEL DURANT & YVES HANDRICH
Centre d’Ecologie et Physiologie Energetiques—CNRS, Strasbourg

(Received 16 October 2000; initial acceptance 14 December 2000; final acceptance 2 June 2001; MS. number: 6727)

Using an automatic identification and weighing system, we investigated changes in adult body mass in relation to reproductive behaviour during courtship and incubation in free-living king penguins. Despite stressful nutritional conditions and variability of fast length, the majority of pairs incubated successfully by accumulating large body reserves before fasting, which provided flexibility in fasting strategies. Our data indicate a low body mass during fasting below which males either delayed or stopped breeding: (1) at 12 kg, the male interrupted courtship to replenish his body reserves at sea before re-engaging in courtship; and (2) when body mass dropped to 9 kg during incubation, the male deserted the egg. The behavioural decision to go to sea was not controlled by the time spent fasting, but by the amount of body reserves. In deserting males, the depletion of body reserves during incubation before relief by the females was due to a lower stored energy (−2 kg) at the onset of courtship compared with successful males. Unsuccessful males weighed only 12 kg when they started to court, and consequently had no safety margin that allowed them to wait for a delayed female. The unusual depletion of body reserves of male breeders caused only 3% of incubation attempts to fail. Compared with successful pairs, their female partners gained less body mass at sea (−40 g/day) and made a slightly longer foraging trip (+5 days). We suggest that the deserting males had risked breeding with the lowest fasting safety margin possible, rather than breeding later that year. However, the low body mass at desertion did not affect the penguins’ survival or their feeding capacity, and therefore did not compromise another breeding attempt during the next season.

According to life history theory, animals are faced with trade-offs in the allocation of limited energy reserves to different functions (Williams 1966; Stearns 1992). During the breeding season, the allocation of resources is a trade-off between adult survival, reproduction and the amount of energy going into current and future production of offspring (Stearns 1992).

For long-lived birds, life history theory predicts that adults behave as prudent parents and limit their risk of increased mortality during reproduction (Drent & Daan 1980; Stearns 1992; Weimerskirch 1999) because the optimization of lifetime reproductive success in these species depends primarily on adult survival rather than on seasonal fecundity (Williams 1966; Clutton-Brock 1991). On the other hand, the allocation of resources to survival and to reproduction may depend on the animal’s physiological state, such as body reserves (Drent & Daan 1980; McNamara & Houston 1996). Furthermore, behavioural decisions during breeding probably depend on the attainment of threshold body reserve levels (Weimerskirch 1999). Hence, a bird may use body reserves as a signal to adjust its reproductive effort, and to decide to desert the egg or to return to the nest when foraging (Chaurand & Weimerskirch 1994; Olsson 1997; Ancel et al. 1998).

Like most pelagic seabirds, king penguins have a high rate of adult survival (90–95% between seasons) and relatively low reproductive success and lay only a single egg (Stonehouse 1960; Barrat 1976; Weimerskirch et al. 1992). During courtship and incubation, adults undergo large variations in body reserves. During these periods, they feed on myctophid fish mainly at the polar front, up to 400 km south of the breeding islands in Crozet Archipelago (Jouventin et al. 1994; Bost et al. 1997). Thus, they have to alternate periods of fasting while incubating with several weeks foraging to rebuild body reserves (Stonehouse 1960; Barrat 1976). However, in king penguins foraging trip durations are particularly variable (Weimerskirch et al. 1992), depending mainly on marine resources that undergo large and unpredictable interannual changes in localization and availability (Bost...
et al. 1997). Consequently, the return of the nonincubating partner can be delayed. Both body reserves and the length of a mate’s absence are factors that an adult must assess in its risk-taking behaviour when deciding whether to initiate, continue with or abandon incubation (Olsson 1997). Previous behavioural and physiological studies on captive fasting penguins have shown that they are stimulated to feed below a body mass threshold, the critical body mass (king penguin: Groscolas et al. 2000; emperor penguin, Aptenodytes forsteri: Le Maho et al. 1988; Robin et al. 1998). This critical body mass corresponds to a physiological change, that is, a transition from lipids to proteins as the main energy fuel, which anticipates a total depletion of fat stores (Cherel et al. 1988; Le Maho et al. 1988; Groscolas 1990).

We investigated the role of individual body mass variations and fasting durations on the decisions of free-living breeding king penguins to desert during courtship and incubation. Our main objective was to answer the following questions. (1) In free-living penguins, are the behavioural decisions to stop breeding to refeed at sea controlled by the time spent fasting or do they operate below the critical body mass threshold? (2) Are the ecological causes of these breeding desertions a prolonged fast caused by a longer courtship or a delay in the partner’s return from its foraging trip at sea, or a depletion of body reserves caused by a lower energy store acquired before fasting or a more rapid use of body reserves during the fast? (3) Do adults desert their egg at a level of body reserves that affects their future return to the breeding colony?

**METHODS**

**Study Species**

After the moult, breeding king penguins forage for 2–3 weeks before returning to their colony for courtship and pair formation. The female lays her single egg and partners relieve each other during incubation, which lasts on average 54 days (Handrich 1989). The female undertakes the first incubation shift (shift 1), which lasts for a few hours up to 2 days after laying, and the third shift (shift 3). The male does shifts 2 and 4. Hatching usually occurs at the beginning of shift 5 (female) and in a few cases at the end of shift 4 (Barrat 1976). The incubating adult fasts for several weeks and never leaves the egg during this period. At the same time, the nonincubating partner feeds on myctophid fish and accumulates body reserves, mainly fat (Cherel et al. 1994).

**Data Collection**

We carried out the study in a colony of 25 000 pairs (Weimerskirch et al. 1992) at Possession Island (46°25’S, 51°45’E), Crozet Archipelago. A breeding area with ca. 200 pairs situated at the periphery of the colony was enclosed at the end of 1990 with 1-m-high wire-netting double fences. Here a measuring system was installed, which automatically weighed and identified breeding king penguins when they crossed a weighbridge at the single opening of the enclosure (Gendner et al. 1992; see Le Maho et al. 1993 for a complete description). The study was approved by the Ethical Committee of the Institut Français pour la Recherche et la Technologie Polaires.

Individual identification was based on the permanent implantation of a miniature transponder tag (TIRIS; length 30 mm, diameter 3 mm, mass 0.8 g). From December 1990, 644 breeding birds were implanted. To minimize disturbance when we implanted the transponder, we caught adults by hand on the beach just before they left for the sea, after being relieved during incubation or brooding. Within 2–3 min of capturing them, we anaesthetized the birds for 5–10 min by inhalation of halothane and oxygen to reduce handling stress. The transponder was implanted by injection (with an applicator provided by Texas Instruments) under the skin of the middle of the back such that it was horizontal when the bird was standing. Bill length was measured as an index of body size since it appears to be a more reliable index than flipper or foot length (Barrat 1976).

The birds were double banded with metal flipper rings to permit visual identification with binoculars. The bands, made of stainless metal, weighed 23 g and were 13 mm wide by 5.5 cm long (manufactured by Lambourne, Solihull, U.K.). Flipper banding has been known to affect king penguin survival, mostly during the winter after banding, and may induce a delay in the arrival date to the colony for courting (Froget et al. 1998). However, there is no evidence of an effect when food is plentiful during the summer (Froget et al. 1998). Banded birds engaging in reproduction do not differ in their breeding cycle during the incubation and brooding periods compared with unbanded birds (M. Gauthier-Clerc & Y. Le Maho, unpublished data). In our study, the successful and deserting birds that we compared were all banded and did not differ significantly in their arrival dates (see Results); we therefore considered the banding effect to be similar in the two groups.

The birds were left to awaken from the anaesthesia in a recovery enclosure at the edge of the colony. Halothane’s short recovery time (5–15 min) allowed the birds to return to the field on their own, without being disturbed by any human presence. Usually, they proceeded with their current activities. In the summer of 1994, we recaptured the birds to replace their flipper rings with others engraved with larger numbers (11 instead of 6 mm high). No ring loss was detected (Froget et al. 1998). The automatic identification system started in January 1991 and weights were collected from April 1991 onwards. The system enabled identification at a distance of up to 0.7 m from the detector which was located at the weighbridge. The birds were identified and weighed each time they passed the weighbridge during courtship and at the beginning and end of each foraging trip. The first transponder implant did not work on five of the 644 implanted individuals. They were then caught again and implanted with a second transponder. The automatic data acquisition was complemented with visual observations. On most days throughout the summer, we
checked the breeding area and beaches with a telescope and binoculars to identify flipper-banded birds and to determine their breeding status, that is courtship, incubation, or nonbreeding. We used courtship or egg exchange to identify the breeding partner if marked, and the location of their territory. We determined the sex of the birds according to the stage of the incubation cycle and confirmed it by listening to display songs. A total of 298 females and 275 males were determined.

In this study, body mass was based only on automatic weighing. Weighing data of incubating penguins were recorded during four successive summers (1992–1995). In April 1995, the enclosure was opened and the majority of penguins then ignored the weighbridge. However, we collected some additional data on male desertion during the summer of 1996.

Data Analysis

We deduced the timing of the breeding cycle from a combination of automatic data and visual observations using custom-made software (J. Lage, C.E.P.E.-C.N.R.S.). Individual weights, that is, weighbridge crossing events, were analysed with another custom-made software (J. P. Gendner, C.E.P.E.-C.N.R.S.). This interactive software allows one to select on a plot of the weighing signal the largest steady state section and accordingly to calculate the body weight. For several reasons, such as wind, simultaneous crossing of several birds or power cut of the equipment, 30% of the weight curves were not retained or were not available. We calibrated the weighbridge regularly (every 2 months) with a 5-kg standard mass. Accuracy of measurements was between ± 30 and ± 100 g, that is, 1% of king penguin body mass, depending on the waddling gait of the birds and wind velocity. As we did not catch birds before laying, there were no weight data corresponding to the courtship period or to the first two incubation shifts for those individuals not yet equipped with a transmitter. Given the size of the colony, new breeders in the enclosed area were not necessarily newly recruited breeders.

Breeding Failures During Incubation

Overall, 21% of 424 breeding pairs in the study area failed during incubation (all 4 years pooled). However, this percentage varied from 12 to 34% between years (Table 1). Incubation failure in the absence of the mate can be due to fights with neighbours, predation, or body reserve depletion of the incubating adult (Barrat 1976). To separate desertions caused by body reserve depletion from other causes of breeding failure, we classified failed birds according to fast length and body mass. Figure 1 shows that the failed males are segregated into two distinct groups: males that stopped incubating within 12 days of fasting with a body mass >11 kg (group 1), and males that stopped after 20 days or more of fasting with a body mass <10 kg (group 2). Based on previous studies on egg desertion in king penguins (Olsson 1997; Groscolas et al. 2000) or in other species (Handrich et al. 1993; Robin et al. 1998), we consider that the males of group 2 had failed because their body reserves were depleted and we therefore focused on this group, which represented 13% of all cases of incubation failure (3% of breeding pairs). Two body mass measurements are not shown in Fig. 1 because they were not accurate enough to be used.

We compared the timing of the breeding cycle and the corresponding variations in body mass between successful and deserting birds during the same summer to avoid

Table 1. Number of adults implanted with transponders per year, pairs observed, pairs unsuccessful in incubation and males deserting their egg

<table>
<thead>
<tr>
<th>Summer</th>
<th>Number implanted</th>
<th>Pairs observed</th>
<th>Unsuccessful</th>
<th>Egg desertion</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990–1991</td>
<td>125</td>
<td>54</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>1991–1992</td>
<td>323</td>
<td>136</td>
<td>31</td>
<td>0</td>
</tr>
<tr>
<td>1992–1993</td>
<td>144</td>
<td>124</td>
<td>15</td>
<td>1</td>
</tr>
<tr>
<td>1993–1994</td>
<td>31</td>
<td>80</td>
<td>27</td>
<td>10</td>
</tr>
<tr>
<td>1994–1995</td>
<td>21</td>
<td>30</td>
<td>6</td>
<td>0</td>
</tr>
</tbody>
</table>

One male deserting its egg in 1996 is included in the analysis but is not shown in the table.
the influence of food availability variation in different years. Sometimes data were missing and therefore sample sizes vary between analyses. All tests were two tailed. Results are presented as means ± SE.

RESULTS

Body Mass at Desertion

Throughout the study only 12 desertions of males were due to body reserve depletion. They deserted the egg at the end of incubation shift 2 at a body mass of 9.18 ± 0.18 kg (N=10). (The body mass measurements of two of the males were not accurate enough to be used.) Males relieved at shift 2 weighed significantly more (9.87 ± 0.06 kg, N=207) than deserting males (two-sample t test: t_{215}=2.50, P=0.006). The mass at desertion was positively related to the structural size of males (Pearson correlation: r_{xy}=0.68, P=0.03; Fig. 2).

For eight of the 10 males, the body mass at desertion was their lowest measured during the study, regardless of season (Table 2). The other two birds had reached a body mass lower than at desertion at least once in the past: one individual at the end of the moult and the other at the end of shift 2.

Deserting versus Successful Males

Male desertions were not due to inexperience as none were newly recruited breeders and all had successfully incubated at least once during previous years. Since food availability is variable between years in the sub-Antarctic, we compared successful and unsuccessful males breeding in the 1993–1994 summer, for which we have the largest sample size of deserting males. Arrival dates of deserting and successful males were similar (median arrival date 17 December 1993 for both deserting males (N=10, range 22 November–12 January) and successful males (N=48, range 23 November–6 January); Mann–Whitney U test: U=223, NS). Deserting males started to incubate 11 days later than successful males (median egg-laying dates: deserting males: 7 January 1994 (N=10, range 25 December–22 January); successful males: 27 December 1993 (N=58, range 30 November–27 January); Mann–Whitney U test: U=429, P<0.02). Six males interrupted their courtship when their body mass reached 12.36 ± 0.22 kg (range 11.80–12.85) and left the colony to replenish their body reserves. After this foraging trip they engaged in courtship and started to incubate. Three of them finally deserted their egg because of the depletion of their body reserves. This break during courtship explains the difference in laying dates between deserting and successful birds. For males taking a break, we analysed data during the second courtship period prior to laying.

Visual observation of birds during courtship indicated that there were no significant differences in the duration of the different phases of the prelaying period between deserting males and males relieved by their partner (Table 3). The duration of temporary pair bonds before the final pair had formed also did not differ between deserting (3 ± 1.0 days, N=8, range 0–8) and relieved males (2 ± 0.5 days, N=43, range 0–11; Mann–Whitney U test: U=124, NS). Their mates showed the same duration of temporary bonds (deserting: 1 ± 0.7 days, N=8, range 0–4; relieved: 1 ± 0.3 days, N=47, range 0–6).

We compared automatically collected data for individual body mass and duration of sojourn in the breeding area for the different phases of courtship and incubation between deserting and successful pairs (Table 4). We used a logistic regression to estimate the factors that may influence egg desertion by males. The dependent variable, egg desertion or relief, is discrete: it is equal to 0 if the male deserts the egg and 1 if the male is relieved. In the most parsimonious models including only one independent variable, the coefficients of the variable and the model chi-square statistic were significant for: (1) the male’s body mass at arrival in the breeding area (logit coefficient estimate=2.093, P=0.019, likelihood ratio=14.61, χ_{1}^2 for model fit P<0.001, correct predictions=83%); (2) the male’s body mass at departure to sea (logit coefficient estimate=2.793, P=0.008, likelihood ratio=13.93, χ_{1}^2 for model fit P<0.001, correct predictions=79%); and (3) for the female’s foraging trip duration (logit coefficient estimate=−0.973, P=0.004; likelihood ratio=25.27, χ_{1}^2 for model fit P<0.001; correct predictions=87%). The probability of egg desertion was not related to the duration of the male’s fast, the length of incubation shift 2, the female’s body mass at departure to sea or the female’s body mass at return to the colony. In all models tested, the coefficients of these four variables were never significant. Male body masses at arrival in the breeding area and at departure to sea were not independent and consequently were not tested simultaneously in the same model. Nonsignificant variables were not included in the following analysis. We tested the model with two independent variables: male body mass at arrival in the breeding area and female foraging trip duration. This model was slightly superior according to the likelihood ratio test and the percentage of correct predictions (likelihood ratio=21.48, χ_{2}^2 for overall model fit P<0.001, correct predictions=92%). Thus, the logistic
regression shows that egg desertion by the male is associated with its body mass at the beginning of the fast and the trip duration of the partner. The durations of the different phases of courtship and incubation were similar for successful and deserting pairs (Table 4, Fig. 3): from arrival in the breeding area for courting to their departure to sea after laying (28 days in males and 9 days in females); from their first mating in the breeding area to their departure (26 days in males and 8 days in females); and for length of incubation shift 2 (by the male, 18 days). The rate of daily mass loss was similar for deserting and relieved males at 200 g/day during courtship and 90 g/day during mating and incubation. However, all body masses of deserting males were lower than those of relieved males (Table 4): at the beginning of courtship −2.2 kg, at mating −1.5 kg, and at departure to sea −1.0 kg. Females that did not succeed in relieving their males foraged for 23 days compared to 18 days for successful pairs (Table 4). The females of deserting males gained on average less body mass/day at sea than females relieving their mate (0.16 versus 0.20 kg/day; Mann–Whitney U test: U=31, P<0.05; Table 4). All deserting males were able to incubate more than 18 days (Table 4). Thus, they would have been successful if their partner had made a foraging trip equivalent to the mean 18-day trip duration of the females in the population.

Four successful males started courtship when their body mass was <12.5 kg, the body mass at which others went back to sea. The duration of the foraging trip of their females was shorter than for pairs where males deserted (16.4 versus 22.8 days; Mann–Whitney U test: U=0, P<0.01).

For one deserting male (no. 153701) we obtained body mass data in 3 years (Fig. 4). This male, who incubated successfully in 1993 and 1994, deserted in summer 1996 when his body mass before laying was 1 kg lower than in the 2 previous years. The foraging trip of his partner was not longer than in the previous year.

**Survival and Restoration of Body Reserves after Desertion**

Eleven of the 12 deserting males were later seen in the colony; the other male may have died at sea.

We compared the body condition after desertion of the seven deserting males in summer 1993–1994 with 28 relieved males from the same incubating season. Deserting males departed to sea with a body mass significantly lower than that of relieved ones, foraged 3 days longer but returned to the colony with a similar body mass as successful males (Table 5). The foraging capacity

---

**Table 2. Body masses measured throughout the study of males that deserted, including summer and winter data**

<table>
<thead>
<tr>
<th>Bird number</th>
<th>Years</th>
<th>Body mass (kg)</th>
<th>Range (kg) excluding desertion mass</th>
<th>Body mass (kg) at desertion</th>
</tr>
</thead>
<tbody>
<tr>
<td>166016</td>
<td>1</td>
<td>12.45±0.48</td>
<td>14.77–11.00</td>
<td>9.08</td>
</tr>
<tr>
<td>165931</td>
<td>4</td>
<td>13.35±0.21</td>
<td>16.41–10.07</td>
<td>9.42</td>
</tr>
<tr>
<td>165965</td>
<td>2</td>
<td>13.16±0.23</td>
<td>15.93–11.11</td>
<td>9.96</td>
</tr>
<tr>
<td>165945</td>
<td>2</td>
<td>11.87±0.19</td>
<td>14.45–8.78*</td>
<td>9.02</td>
</tr>
<tr>
<td>030046</td>
<td>4</td>
<td>13.13±0.23</td>
<td>16.76–8.27†</td>
<td>9.44</td>
</tr>
<tr>
<td>153701</td>
<td>5</td>
<td>13.14±0.15</td>
<td>16.61–8.95</td>
<td>8.32</td>
</tr>
<tr>
<td>154781</td>
<td>3</td>
<td>13.85±0.21</td>
<td>16.75–10.21</td>
<td>9.79</td>
</tr>
<tr>
<td>154788</td>
<td>2</td>
<td>11.34±0.16</td>
<td>15.51–8.68</td>
<td>8.35</td>
</tr>
<tr>
<td>153822</td>
<td>5</td>
<td>12.45±0.11</td>
<td>14.58–9.93</td>
<td>8.76</td>
</tr>
<tr>
<td>133250</td>
<td>3</td>
<td>12.29±0.21</td>
<td>14.30–9.93</td>
<td>9.69</td>
</tr>
</tbody>
</table>

The number of years the individual frequented the breeding site is shown. Means are given±SE, with N in parentheses.

*End of moult.
†Relieved at the end of incubation shift 2.

**Table 3. Duration (days) from arrival at colony to courtship with definitive partner, and from beginning of courtship to laying, from visual observations in summer 1993–1994**

<table>
<thead>
<tr>
<th></th>
<th>Arrival to courtship (days)</th>
<th>Courtship to laying (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males relieved by partner (N=43)</td>
<td>3±0.5 (0–11)</td>
<td>9±0.3 (5–11)</td>
</tr>
<tr>
<td>Deserting males (N=8)</td>
<td>4±1.1 (0–9)</td>
<td>9±1.1 (5–13)</td>
</tr>
<tr>
<td>Mann–Whitney U</td>
<td>154.5</td>
<td>161.5</td>
</tr>
<tr>
<td>Females relieving partner (N=47)</td>
<td>1±0.3 (0–6)</td>
<td>8±0.3 (1–12)</td>
</tr>
<tr>
<td>Female partner of deserting males (N=8)</td>
<td>2±0.7 (0–5)</td>
<td>9±0.7 (5–13)</td>
</tr>
<tr>
<td>Mann–Whitney U</td>
<td>152.0</td>
<td>154.0</td>
</tr>
</tbody>
</table>

Means are given±SE, with range in parentheses.
of the deserting birds was not altered, since their daily gain in body mass at sea was not significantly different from that of successful males (Table 5).

Table 4. Durations of stays in the breeding area and body mass variations, during courtship and incubation for males and females, based on automatic identification and weighing in summer 1993–1994.

<table>
<thead>
<tr>
<th>Period</th>
<th>Males relieved by partners</th>
<th>Deserting males</th>
<th>Females relieving partners</th>
<th>Female partners of deserting males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arrival in breeding area to departure to sea (days)</td>
<td>28.8±0.7</td>
<td>27.0±1.6</td>
<td>8.8±0.4</td>
<td>8.4±1.1</td>
</tr>
<tr>
<td></td>
<td>15.2–40.3</td>
<td>19.5–33.6</td>
<td>2.1–15.3</td>
<td>3.3–12.3</td>
</tr>
<tr>
<td></td>
<td>N=41</td>
<td>N=9</td>
<td>N=44</td>
<td>N=8</td>
</tr>
<tr>
<td>Mating to departure (days)</td>
<td>25.7±0.6</td>
<td>26.4±1.4</td>
<td>7.6±0.37</td>
<td>7.9±1.0</td>
</tr>
<tr>
<td></td>
<td>15.2–33.9</td>
<td>19.5–33.6</td>
<td>0.8–11.3</td>
<td>3.3–11.1</td>
</tr>
<tr>
<td></td>
<td>N=41</td>
<td>N=9</td>
<td>N=44</td>
<td>N=8</td>
</tr>
<tr>
<td>Incubation shift 2 (days)</td>
<td>18.2±0.4</td>
<td>19.3±0.5</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>13.1–25.7</td>
<td>18.1–22.7</td>
<td>N=39</td>
<td>N=9</td>
</tr>
<tr>
<td>Foraging trip (days)</td>
<td>—</td>
<td>—</td>
<td>18.0±0.4</td>
<td>22.8±0.7</td>
</tr>
<tr>
<td></td>
<td>—</td>
<td>—</td>
<td>13.0–25.6</td>
<td>18.9–26.7</td>
</tr>
<tr>
<td></td>
<td>N=44</td>
<td>N=9</td>
<td>N=44</td>
<td>N=9</td>
</tr>
<tr>
<td>Body mass at arrival (kg)</td>
<td>13.87±0.21</td>
<td>11.65±0.67</td>
<td>11.77±0.16</td>
<td>10.80±0.70</td>
</tr>
<tr>
<td></td>
<td>N=20</td>
<td>N=6</td>
<td>N=24</td>
<td>N=3</td>
</tr>
<tr>
<td>Body mass at mating (kg)</td>
<td>12.89±0.24</td>
<td>11.44±0.71</td>
<td>11.41±0.21</td>
<td>10.57±0.55</td>
</tr>
<tr>
<td></td>
<td>N=21</td>
<td>N=5</td>
<td>N=19</td>
<td>N=4</td>
</tr>
<tr>
<td>Body mass at departure (kg)</td>
<td>10.35±0.12</td>
<td>9.34±0.18</td>
<td>9.73±0.14</td>
<td>9.27±0.25</td>
</tr>
<tr>
<td></td>
<td>8.95–11.61</td>
<td>8.35–9.96</td>
<td>8.50–11.14</td>
<td>7.98–10.01</td>
</tr>
<tr>
<td></td>
<td>N=34</td>
<td>N=8</td>
<td>N=27</td>
<td>N=8</td>
</tr>
<tr>
<td>Body mass at return to colony (kg)</td>
<td>—</td>
<td>—</td>
<td>13.18±0.18</td>
<td>12.82±0.32</td>
</tr>
<tr>
<td></td>
<td>—</td>
<td>—</td>
<td>11.71–15.54</td>
<td>11.49–14.41</td>
</tr>
<tr>
<td></td>
<td>—</td>
<td>—</td>
<td>N=29</td>
<td>N=8</td>
</tr>
<tr>
<td>Mass gain at sea (kg/day)</td>
<td>—</td>
<td>—</td>
<td>0.20±0.01</td>
<td>0.16±0.01</td>
</tr>
<tr>
<td></td>
<td>—</td>
<td>—</td>
<td>0.11–0.31</td>
<td>0.12–0.21</td>
</tr>
<tr>
<td></td>
<td>—</td>
<td>—</td>
<td>N=19</td>
<td>N=7</td>
</tr>
</tbody>
</table>

Means are given±SE, with ranges.

Figure 3. Duration of sojourn in the breeding area and body mass variations between arrival at the colony for courtship and the end of incubation shift 2, in successful pairs (N=48) and pairs with males deserting because of depletion of their body reserves (N=10), according to automatic identification and weighing data in summer 1993–1994. Data on some variables were lacking for certain individuals and therefore sample sizes vary (see Table 4 for sample sizes).

Figure 4. Duration of sojourn in the breeding area and body mass variations between arrival at the colony for courtship and the end of incubation shift 2 for male number 153701. He was successfully relieved in 1992–1993 and 1993–1994, but failed in 1995–1996 because of depletion of his body reserves. In 1994–1995 (not shown), he arrived at the colony for courtship at 13.26 kg, but did not breed.

DISCUSSION

Our study shows that male king penguins may reach a low body mass at which they stop reproduction, either during courtship or incubation, and leave the colony to
replenish their body reserves. The building up of body reserves prior to the courtship and incubation fasts allows in the majority of cases a sufficient safety margin if it becomes necessary to wait for a female’s return. However, breeding failure caused by depletion of body reserves of males during incubation remained exceptional at only 3% of the incubation attempts. In these few cases, the depletion of body reserves of deserting males was due to the combination of a lower level of body reserves at the beginning of the fast and a longer trip duration at sea of their female.

Body Mass at Desertion and Critical Body Mass

The stimulus for birds to feed before their life is endangered is assumed to be due to an internal physiological signal triggered when fat stores are critically depleted, the so-called critical body mass (CBM; Le Maho et al. 1988; Groscolas 1990; Robin et al. 1998). The CBM is defined as the body mass at which a long-term fasting animal shifts its fuel catabolism from a stage of protein sparing (phase II) to a stage, still reversible, in which protein catabolism dramatically increases (phase III; Le Maho et al. 1981; Cherel et al. 1988; Cherel & Groscolas 1999). Because body mass varies with structural size, it is difficult to determine in undisturbed free-ranging king penguins whether the stimulus to desert the egg and to rebuild body reserves coincides with the CBM. The range of body mass at desertion, 8–10 kg, was related to the structural size of the birds. In a recent study with captive incubating males in the same colony at Possession Island, depletion of body reserves was induced by an experimental prolongation of incubation (Groscolas et al. 2000). Body masses at egg desertion averaged 8.78 kg and were similar to those in the present study. King penguins at South Georgia are bigger than at Possession Island (Stonehouse 1960; Barrat 1976). In our study of Possession Island birds, the bill length of males was shorter (123 ± 1 mm, N=274) than those measured by Stonehouse (1960) in South Georgia (137 ± 1 mm, N=70). This could explain the greater body mass of males at desertion (9.49 kg) at South Georgia (Olsson 1997). The CBM in nonbreeding captive male king penguins from Possession Island was 9.98 kg in one study (Cherel et al. 1988) and 9.65 kg in another (Cherel et al. 1994), but these authors selected the largest males at the time of catching (Y. Cherel, personal communication). These CBM values are similar to the body masses at desertion of the largest birds in our study (see Fig. 2). Male king penguins appear to desert the egg to feed after reaching the CBM. The internal signal for egg desertion may be related to a threshold in adiposity, although the mechanism of this signal remains unknown (blue petrels, Halobaena caerulea: Ancel et al. 1998; barn owls, Tyto alba: Handrich et al. 1993; emperor penguins: Robin et al. 1998). Video-recordings of captive king penguins showed that the behavioural changes reflecting the conflicting drives to feed or to incubate occur progressively after the birds reach the CBM over several days before definitive egg desertion (Groscolas et al. 2000).

Why did Males reach a Deserting Body Mass?

The decision to stop breeding and to go to sea might be controlled by the time spent courting and incubating without being related to the level of body reserves. However, male courtship varied from 5 to 11 days and incubation shift 2 varied from 13 to 26 days in 1994. Thus, the duration of the first fast of the males was highly variable and their body reserves provided flexibility in their fasting capacity. In our study, the males were able to anticipate a 1-month fast in 97% of cases by arriving with a mean body mass of 13.9 kg. This mass allowing the onset of breeding corresponds to what has been called upper threshold mass for other seabirds (Weimerskirch 1999).

In captive birds, depletion of the body reserves and desertion were induced by a prolonged incubation fast, on average 10 days longer than successful free-living birds (Groscolas et al. 2000). In our study of free-living birds, the desertions of males during shift 2 were not due to a prolonged fast, but to a lower amount of energy stored before the fast. Compared with successful males, deserting males with a mean body mass of 11.65 kg were already in poor body condition at the onset of courtship. However, none of these deserting males would have failed if their female had foraged as efficiently as those of successful pairs. Females that came back after their male deserted had foraged less successfully than females relieving their partner; their body mass increased less per day (0.16 versus 0.20 kg/day) and their trip duration was longer (23 versus 18 days) than females of successful pairs. Deserting males did not have a sufficient body reserve margin to wait a few days more than the mean duration for female relief. In contrast, relieved males

<table>
<thead>
<tr>
<th></th>
<th>Body mass at departure (kg)</th>
<th>Body mass at return (kg)</th>
<th>Trip duration (days)</th>
<th>Daily gain in body mass (g/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relieved males</td>
<td>10.19±0.16</td>
<td>14.12±0.17</td>
<td>19±0.4</td>
<td>200±9</td>
</tr>
<tr>
<td>Deserting males</td>
<td>9.39±0.20</td>
<td>14.20±0.42</td>
<td>22±1.1</td>
<td>220±15</td>
</tr>
<tr>
<td>Mann–Whitney U</td>
<td>42*</td>
<td>91</td>
<td>42*</td>
<td>83</td>
</tr>
</tbody>
</table>

Means are given±SE. *P<0.03.
weighed on average 1 kg more than deserting males, and
had a 10-day greater margin to wait for females to return.
The poorer condition of deserting males at the onset of
courtship cannot be attributed to their inexperience,
because none were newly recruited breeders. They had all
bred at least once before and the majority had suc-
cessfully incubated the year before. The interannual
comparison of male no. 153701, which deserted in 1996,
showed that this bird had reached an adequate body mass
for successful incubation in previous years. Notably, at
the beginning of courtship the body mass of deserting
males was close to the courtship body mass of 12.4 kg at
which some males interrupted their courtship to replen-
ish their body reserves. That males begin or put off
incubation in a window of less than 2 kg (13.9–12.4)
implies that body reserves are involved in determining
whether a bird engages in incubation. Thus, males
engaged in reproduction at ca. 12 kg may have just
enough body reserves to last the average incubation
length, but should succeed if their partner is only slightly
delayed. Yorio & Dee Boersma (1994) described a body
condition hypothesis where physical condition at the
start of incubation is the main cause of nest desertion,
and a nest relief hypothesis where delay in returning from
a foraging trip is the main cause. In our study, the
desertion of males was due to a combination of these
two factors.

We suggest that males with a body mass of 12 kg face a
conflict between engaging in incubation with no safety
margin and increasing their body reserves and conse-
quently breeding late in the season, that is, when marine
resources are decreasing. If the female is not delayed at
sea, relieved males are then able to replenish their body
reserves quickly, even to a higher level than at the
beginning of courtship, and can continue the breeding
cycle normally. In contrast, breeding later presages failure
as pairs laying after the end of January have almost no
chance of rearing their chick long enough for it to survive
the winter (Weimerskirch et al. 1992; Olsson 1996). The
synchronization of the king penguin population in
returning to the colony provides conditions for an ideal
free mate choice (Olsson 1998). Males breeding late risk
losing good mating opportunities.

The disadvantage of late laying may explain the larger
In our colony, the onset of the breeding season varied as
much as 6 weeks between years depending on the timing
of the moult. Over 10 seasons (from 1990–1991 to 1999–
2000), the peak of egg laying in this colony occurred four
times during the second half of November, three times
during the first half of December and three times during
the second half of December (unpublished data). In our
study, the 1993–1994 summer was the only season when
the egg-laying peak occurred during the second half of
December. The laying dates of deserting males occurred
after 25 December. Despite two of the deserting males
having arrived at the colony very early in this season (22
and 24 November), they interrupted their courtship, and
laying occurred only on 26 December and 19 January.
Similarly, the four successful males that started court-
ship with a body mass lower than 12.5 kg engaged in
incubation after 25 December. In contrast to deserting
males, their females were not late returning and these
pairs successfully fed a chick at least until the end of the
summer. If these birds had taken a break at the end of
December, laying would have occurred only at the end of
January, too late to rear a chick. The constraint for king
penguins to breed early in the season and to maximize
the chances of chick survival could explain why some
males commence incubation with limited body reserves
instead of breeding late.

We recorded no case of desertion during shift 4 (the last
male shift before hatching). However, when marine con-
ditions are exceptionally bad, a foraging trip during
incubation can last 1–2 months (M. Gauthier-Clerc, Y. Le
Maho & Y. Handrich, unpublished data). In this situ-
ation, the long delay to relief may induce the desertion of
80% of birds breeding late.

Survival and Restoration of Body Reserves after
Desertion

According to life history theory, there is a trade-off
between adult survival and reproduction, which in long-
ived species favours adult instead of offspring survival. In
our study, the majority of starved males were able to
replenish their body reserves at the same rate of body
mass gain as birds relieved by their partner. Similar results
were found in a study where egg desertion was experi-
mentally induced by preventing relief by the partner
(Robin et al., in press). These results are consistent with
the hypothesis that the most long-lived species accept
fewer risks when facing poor feeding conditions and
therefore can reduce reproductive effort to preserve their
future survival and future reproduction (Chastel et al.
1995). Captive male king penguins of this colony with a
body mass lower than 8 kg were in good health after
40–50 fasting days (Cherel et al. 1988, 1994). At 9 kg,
deserting adults therefore had an energy safety margin.
We also had two cases where birds had already reached a
body mass lower than their body mass at desertion
sometime in their life. This safety margin probably helps
the birds to optimize their survival probability, since they
have to cope with an unpredictable food availability
before reaching the polar front where the majority feed
during this period (Bost et al. 1997).

Our results support the hypothesis that there exist
internal metabolic signals linked to fat stores that induce
behavioural decisions in birds to engage in or stop breed-
ing. The desertion of king penguins to replenish body
reserves before their life is endangered, together with
their aptitude to forage as efficiently as successful
breeders, is also in accordance with life history theory
predicting that the trade-off favours parent survival over
current breeding success in long-lived birds.

Acknowledgments

This work was supported financially by the Institut
Francais pour la Recherche et la Technologie Polaires and
by additional grants from the EEC (grant on new tech-
niques in undisturbed animals), CNRS and Université
Louis Pasteur. M.G.-C. was supported by a doctoral grant from the MERNT. We are very grateful to E. Challet, J. B. Charrassin, T. Dahier, S. Eudes, G. Froget, Y. Ropert-Coudevil and E. Valentini, who collected data from the automatic identification and weighing system from 1991 onwards in Crozet and to R. Groscolas and two anonymous referees for improving the manuscript. We also thank H. Massinck and J.-P. Bruneval from Texas Instruments Holland and France, respectively, for enabling this first use of the TIRIS identification system on a wild animal.

References