



Alloparental feeding in the king penguin

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We investigated allofeeding (feeding of offspring by adults other than their own parents) in the king penguin, *Aptenodytes patagonicus*, a long-lived pelagic bird that faces severe food shortages during its reproduction and in which parents leave their fasting chick in dense crèches. A 1-year monitoring of 103 breeding pairs and 70 chicks was carried out in a colony in the Crozet Archipelago. We examined whether allofeeding was common enough to alter survival costs or benefits for both the allofed chicks and the allofeeders. Twenty-two per cent of marked adults allofed more than 65% of all the chicks without repeatedly feeding the same chick. Allofeeding in king penguins benefited allofed chicks by increasing their survival, yet little or no fitness cost was detected among allofeeders. We identified proximal factors affecting allofeeding: (1) the breeding conditions of the population were not unusual; (2) allofeeding occurred mostly when parental provisioning was low; (3) alloparents did not respond to increased begging by regurgitating more meals; (4) allofeeders were mostly failed breeders, although successful breeders occasionally allofed; (5) when the colony was no longer organized into breeder territories, allofeeders preferentially fed chicks that had been reared by close neighbours at the time of brooding.

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Alloparental feeding occurs when one or several individuals provide temporary feeding to alien young. Allofeeding can also include full adoption of young when a 'foster parent(s)' provides exclusive care of another's offspring in the absence of one or both original parents (Riedman 1982). Allofeeding raises intriguing evolutionary questions, because it can be viewed as an altruistic and reproductively costly behaviour (Wilson 1975). Allofed offspring survival is promoted at the expense of the allofeeders, but the energetic or fitness costs are not experienced by the allofed offspring (Brown 1987). In this case, an 'intergenerational conflict' might appear, where offspring are selected to gain from alloparental feeding, but alloparents are selected not to provide such allofeeding (Pierotti & Murphy 1987).

Most of the 150 bird species that allofeed are seabird species that show several specific life-history traits and environmental constraints that promote allofeeding (Riedman 1982; Brown 1987; Heinsohn et al. 1990;

Arnold & Owen 1999). For example, seabird chicks are semiprecocial or altricial at hatching. They require prolonged periods of biparental care because of slow growth rates, and they endure long periods of parental absenteeism because of distant and unpredictable food resources. King penguins, *Aptenodytes patagonicus*, show all those life-history traits that may be favourable to alloparental feeding. As pelagic predators (Bost et al. 1997; Charrassin & Bost 2001), they leave their colony for long periods, and return periodically with food for the chick. Their breeding cycle takes over 14 months (Stonehouse 1960; Barrat 1976; Weimerskirch et al. 1992; Olsson 1996). The large size of the species (Stonehouse 1960), combined with a short window of food abundance during the austral summer (El Sayed 1988), make completing chick rearing impossible before the onset of winter, but only until the next summer. Breeders do not build a nest, but brood their egg and single chick on their feet for 53 days during the austral summer (Barrat 1976). Before the onset of winter, breeding territories no longer exist and chicks aggregate in dense groups called crèches (Stonehouse 1960; Davis 1982; Evans 1984; Tourenq et al. 1995). During the winter, feeding of their single chicks by parents is reduced and may not even occur from the beginning of autumn until

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the next spring (Stonehouse 1960; Barrat 1976; Cherel & Le Maho 1985; Cherel et al. 1987; Jouventin & Lagarde 1995). In king penguins, chick prewinter mass, crèching behaviour and the age of the chick are the key variables that explain winter survival (Stonehouse 1960; Barrat 1976).

We studied alloparental feeding in a king penguin colony by observing feeding exchanges between adults and chicks during one breeding cycle. We assessed whether allofeeding was common enough to alter survival costs or benefits for both the allofed chicks and the allofeeders. We verified whether the same alloparent fed repeatedly the same chick. We then explored in king penguins five hypotheses of behavioural mechanisms commonly associated with allofeeding in colonial seabird species: (1) occasional and unusual breeding conditions (such as changes in the breeding habitat or breeding success of a colony: Roberts & Hatch 1994), (2) young solicitation towards alloparents (Birkhead & Nettleship 1984; Mock 1984; Pierotti & Murphy 1987; Hebert 1988; Morris et al. 1991; Brown 1998), (3) suboptimal parental care (Pierotti & Murphy 1987; Hebert 1988; Morris et al. 1991), (4) breeding failure (Riedman 1982; Birkhead & Nettleship 1984; Jouventin et al. 1995) and (5) spatial proximity of breeding adults in colonies (Roulin 2002).

METHODS

This study was undertaken at Possession Island (Crozet Archipelago, 46°25'S, 51°45'E), which has a subantarctic climate (mean annual temperature and precipitation: 5°C, 2800 mm). Winter conditions prevail from April to November, when marine resources are at their minimum (Hart 1942; Foxton 1956).

We carried out an all-occurrence sampling of feeding events on one subcolony ($N = 200$ breeding pairs) in a central part of the 'La Grande Manchotière' colony ($N = 30\,000$ breeding pairs), from the beginning of incubation (December 1998) to the departure of the juveniles (February 2000). We also recorded the rate of crèching chick calls (average number of calls per minute) each time they encountered an adult (parent or alloparent) during the winter. Clear topographic features (slope and rocks) defined the limits of our subcolony and prevented mixing with the populations of other subcolonies.

We marked 74 breeding adults with no identified partner and 103 breeding pairs with a unique dye-mark code of Nyanzol-D (dark colouring) on their white underbellies. We also implanted a miniaturized transponder (TIRIS, Texas Instruments, Dallas, Texas, U.S.A.; Gendner et al. 1992; Le Maho et al. 1993; E. F. Prentice & D. L. Park, unpublished data, available at NWFSC, 2725 Montlake Blvd., Seattle, WA 98112-2097, U.S.A.) subcutaneously in the tail fold of each animal. We defined 'young chicks' as those with a parent, 'crèching chicks' as those with brown down in close association with other crèching chicks, and 'juveniles' as those with growing subadult feathers and no longer in the crèches. Breeding failure (offspring abandonment or mortality) may occur at the

egg stage, early chick age or crèching stage. Successful breeding was established by the departure of the juveniles to the sea. Chick mortality was determined either by seeing giant petrels (*Macronectes* sp.) kill starving chicks or by finding carcasses at a distance from the colony. Early marking of the young chicks was essential to associate a single chick with its biological parents. Among the 103 breeding pairs, 95 chicks were marked under the skin with a transponder and externally with an individual tag on their back (made by Floy Tag Inc., Seattle, Washington, U.S.A.) when they were 5–10 days old. During handling, each chick was replaced by a dummy egg to avoid parent abandonment. At the beginning of the crèching period (April), we banded and weighed the remaining 70 marked chicks. We removed bands from all marked juveniles just before their departure to the sea (from the end of the following December to the beginning of February). Daily observations were carried out with a spotting scope (20 × 60) and binoculars (10 × 50) in three blinds situated more than 7 m from the subcolony. Three pairs of antennae at the subcolony entrance detected all departures and arrivals of the transponded individuals (Descamps et al. 2002). A video system provided additional data (infrared video camera connected to a videotape recorder), especially at night.

Between foraging trips, adults regurgitated their stomach contents to one or more chicks in the colony while partly joining bills with them. Feeding transfers were considered to be alloparental when an adult provided food to a nonoffspring chick. To estimate the amount of food delivered to the chick, we established a semiquantitative scale of three meal sizes that were distinguishable at a distance: F (large meal), f (small meal), L (liquid similar to a thick mucus). To avoid disturbance in the subcolony under study, F and f masses were calibrated in another subcolony by weighing 30 chicks before and after feeding. These observations suggested the following mean ± SE mass for each meal size: F: 80 ± 2.5 g ($N = 51$); f: 80 ± 1.8 g ($N = 59$); L: 25 ± 1.2 g ($N = 43$).

We calculated the proximity of neighbouring breeders to each other using daily photographs of the subcolony and monitoring with the Animal Movement 2.04b extension (Hooge & Eichenlaub 1997) for ArcView 3.2c (ESRI 2000). We established a proximity index, where 1 corresponds to the nearest neighbour of a breeding pair and 15 means a neighbour 15 breeders away from the pair (maximum value obtained from the limited size of the subcolony under study).

All statistical analyses were performed using SAS software (SAS Institute 1998). For all data, normality was checked with the Kolmogorov–Smirnov test (Lilliefors option). When necessary, independent variables were log-transformed to improve normality and homoscedasticity. The alpha level of all tests was 0.05. For multiple analyses on similar hypotheses, we used the Bonferroni correction.

We used a multiple logistic regression model (Trexler & Travis 1993; Legendre & Legendre 2000) to test the null hypothesis that chick survival (binary variable) during winter did not differ by chick age (days), chick prewinter mass (g), number of winter parental and alloparental food events for each food meal class received by each

chick (F, f and L) and all possible interactions. All independent variables were standardized, and multicollinearity between each of those variables was nonsignificant. We used a multimodel inference procedure derived from the AIC procedure to select our model (Akaike 1973; Hurvich & Tsai 1991; Burnham & Anderson 1998; $\alpha = 0.05$; PROC LOGISTIC). If the 95% confidence intervals of the weighted average (β) for the estimates of one independent variable among all the selected models did not include 0, then this variable was considered to have an effect on the dependent variable.

Ethical Note

Our study was undertaken under the approval of the Ethical Committee of the French Polar Institute (IPEV) and of the Scientific Committee of IPEV, following the SCAR (Scientific Committee for Antarctic Research) code of conduct. The species under study is listed in Appendix III to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). The minimum number of birds needed for our study was a function of survival rate of the chicks, which was previously estimated by two pilot studies (N. Lambert & C. A. Bost, unpublished data).

RESULTS

In our subcolony, 25% of the adults (Table 1) performed alloparental feedings. The mean \pm SE number of allofeeding events per alloparent was 22.1 ± 9.5 during winter ($N = 583$). At least 91.43% of chicks were fed by their parents (64 of 70), although 65.71% of all the chicks (46 of 70) were also allofed. Each alloparent that failed to breed returned to the subcolony, on average, four times (± 1 , $N = 46$) and allofed different chicks each time.

Only 23 chicks survived to the onset of the fledgling period from the 70 chicks that were banded at the beginning of winter. A one-tailed t test indicated that chicks that survived were heavier at the beginning of winter ($\bar{X} \pm SE = 7.41 \pm 1.13$ kg, $N = 24$) than were nonsurvivors (6.70 ± 1.28 kg, $N = 44$; PROC TTEST: $t_{64} = -2.35$, $P = 0.02$). Chicks that survived were also allofed more than were nonsurvivors ($\bar{X} \pm SE$ number of allofeeding events: survivors: 10.12 ± 1.1 , $N = 23$; nonsurvivors:

4.28 ± 0.8 , $N = 47$; PROC TTEST: $t_{68} = -2.78$, $P = 0.01$; significant after Bonferroni correction at $0.05/2 = 0.025$).

The multimodel inference procedure showed that chick age, chick prewinter mass, parental L and alloparental L had no effect on chick survival (95% CI of their β included 0). However, we found a positive effect on chick survival of parental f ($\beta = 87.41$; 95% CI: 85.27–89.03), parental F ($\beta = 83.72$; 95% CI: 83.11–86.02), alloparental f ($\beta = 3.89$; 95% CI: 3.15–4.37), and alloparental F ($\beta = 3.27$; 95% CI: 2.92–3.72). Seven crèching chicks that lost meals because one or both of the parents allocated food to foreign young survived until the fledgling period. This was also the case for seven crèching chicks that never received alloparental meals. In both cases, all chicks returned to their natal colony after 2 years.

All observed allofeeders returned to the colony the year after and 2 years after allofeeding (their transponders were detected by the TIRIS antenna). We found no significant correlations between the number or the rate of crèching chicks calls and the number of alloparental meal classes given to the chick immediately after the calls (PROC CORR: number of calls: $r = 0.07$, $N = 125$, $P = 0.89$, $R^2 = 0.005$; rate of calls: $r = 0.04$, $N = 125$, $P = 0.61$, $R^2 = 0.001$) and one foraging trip after the calls (PROC CORR: number of calls: $r = 0.01$, $N = 17$, $P = 0.81$, $R^2 = 0.0001$; rate of calls: $r = 0.08$, $N = 17$, $P = 0.24$, $R^2 = 0.009$).

In our subcolony, the number and the types of alloparental meals varied from April to November (Fig. 1b). However, 81.98% of allofeeding events (478 of 583) occurred between May and September (Fig. 1b). This coincided with a decrease in parental feeding (Fig. 1a).

Mean \pm SE breeding success in the subcolony was $24.21 \pm 4.5\%$ ($N = 95$), which was not significantly different from the mean breeding success previously observed in king penguin colonies on Possession Island (Weimerskirch et al. 1992; $\bar{X} \pm SE = 30.6 \pm 4.2\%$; $\chi^2_1 = 0.05$, $P = 0.82$).

Only adults performed allofeeding. An average \pm SE of $81.4 \pm 2.43\%$ ($N = 57$) of allofeeders were failed breeders (Table 1). Parents that had lost their chick during winter did more allofeeding after the death of their chick than before (PROC UNIVARIATE for paired t tests: $t_{12} = 3.21$, $P = 0.03$; $\bar{X} \pm SE$ number of allofeeding events: before death: 9.10 ± 1.00 ; after death: 12.90 ± 2.10). We observed four events of allofeeding (0.68% of the total number of allofeeding events, $N = 583$) by two adults that had just completed their moult, and thus were no longer raising a chick.

The index of proximity between the breeding territory of allofed chicks and of adults that became their allofeeders was negatively correlated with the number of allofeeding meals received by those chicks during crèching (PROC CORR: $r_s = -0.90$, $N = 17$, $P = 0.001$). About 90% of alloparents for each chick were present within six breeding places, even though breeding territories and crèches were in different locations.

DISCUSSION

Our study provides information on a poorly documented stage of the king penguin's life cycle and is the first

Table 1. Percentage of marked alloparental feeders classified by breeding status in the king penguin subcolony under study (sample sizes in parentheses)

Breeding status	Percentage of alloparental feeders	Percentage of adult feeders of the subcolony
Successful breeders	18.64 (13)	52.47 (147)
Breeders failed at egg stage	48.31 (34)	25.21 (70)
Breeders failed at early chick stage	17.80 (12)	11.32 (32)
Breeders failed at crèching	15.25 (11)	11.00 (31)
Total	(70)	(280)

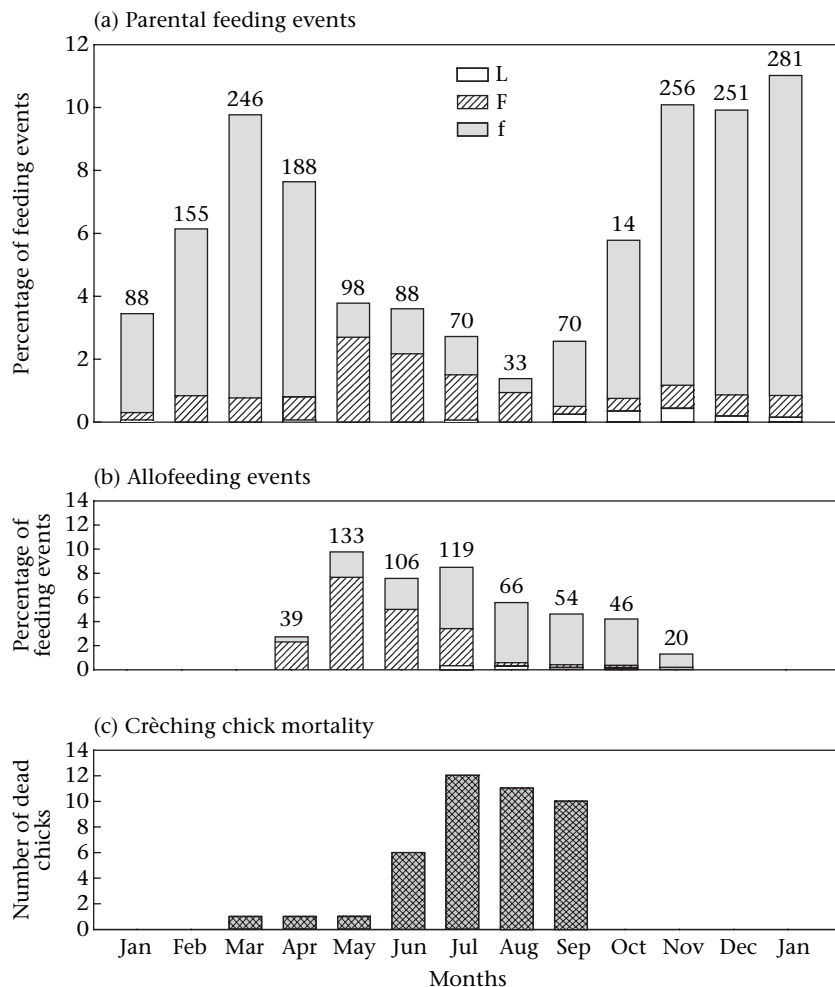


Figure 1. Relative importance of allofeeding events during the king penguin breeding cycle with regard to parental rearing, level of marine resources and crèching chick mortality in the king penguin subcolony under study. (a) Relative importance (%) of each meal class ($N = 1968$; sample sizes over bars) given by parents. Feeding classes are: f (feeding ≤ 80 g); F (feeding > 80 g); L (liquid feeding). (b) Relative importance (%) of meal class ($N = 583$; sample sizes over bars) given by alloparents. We adjusted the scale of the ordinate axis in (b) to be proportional to (a) by considering that winter allofeeding (F, f and L) represented 26.9% of the total amount of winter chick feeding. (c) Chick mortality ($N = 41$) during the crèching period.

extensive investigation of alloparental feeding in this species. We found that allofeeding among king penguins is common during the breeding cycle and that many allofeeders, especially failed breeders, may donate meals repeatedly, thereby enhancing allofed chick survival. Allofeeding in the king penguin does not correspond to adoption of the allofed chick, because allofeeders do not feed the same chick several times. Allofeeding might be considered a cost for the offspring that lost parental meals; however, all the chicks in this situation survived for at least 2 years after crèching. The alloparental cost of feeding foreign chicks (several grams) is minimal relative to the nutritional costs for an adult king penguin (several kilograms; Green & Gales 1990). Therefore, allofeeders might contribute to foreign chick survival without deleterious effects to themselves. All observed allofeeders returned to the colony the following year and after 2 years. Moreover, to our knowledge there is no published evidence of reduced survival or reduced future fecundity

of alloparents (Emlen et al. 1991). Alloparental and parental meal classes, except the liquid food class, enhanced winter survival of chicks, yet any direct benefits to alloparents are difficult to demonstrate, especially for failed breeders.

What mechanistic factors might influence alloparental feeding in the king penguin? Roberts & Hatch (1994) argued that unusual breeding conditions might influence allofeeding behaviour. Breeders in our king penguin subcolony, however, did not face abnormal breeding conditions; breeding success was close to the mean breeding success of the colony. In addition, two pilot studies confirmed the occurrence of allofeeding behaviour elsewhere in the colony (N. Lambert & C. A. Bost, unpublished data) and Stonehouse (1960) briefly described potential alloparental brooding in king penguin colonies on South Georgia Island ($54^{\circ}17'S$, $36^{\circ}30'W$). Other observations of alloparental behaviour were also made in other king penguin colonies in the Crozet Islands and also in the Kerguelen

Archipelago (49°20'S, 70°20'E; Dobson & Jouventin 2003; N. Lecomte & C. A. Bost, unpublished data).

In our study, the number and the rate of chick calls did not appear to influence the amount of allofeeding a chick received. Adults did not respond to increased begging by regurgitating more meals to the chick. It is well established that competitive siblings signal hunger to their parents by using begging behaviour (e.g. Leonard & Horn 2001). However, there are only two studies, with contrasting results, on begging behaviour in the absence of sibling competition, as in the case of the king penguin chicks. Granadeiro et al. (2000) concluded that begging rate had no effect on the provisioning rate in Cory's shearwater, *Calonectis diomedea*. Quillfeldt (2002) found a positive relation between the number of begging events and provisioning rates in Wilson's storm petrels, *Oceanites oceanicus*. Quillfeldt argued that the use of begging rates by Granadeiro et al. (2000) instead of the total number of begging calls by the chicks led to a difference between the two studies. However, in our study, these two parameters were used and we found no link between chick solicitation and alloparental response.

In many seabird species, a period of low parental rate of provisioning might be a factor allowing the expression of alloparental care (Pierotti & Murphy 1987). In our study, allofeeding occurred mostly during winter when parental absenteeism is high and food provisioning is low. During that period, crèching chicks and allofeeders are accessible to each other. However, before that, when the chicks were kept on the feet of their parents, no alloparent could gain access to neighbouring chicks because of the protection and the territorial behaviour of their parents.

We confirmed that allofeeders were mostly failed breeders, which is consistent with Stonehouse's (1960) earlier observations, although successful breeders were occasionally involved in allofeeding events. However, having a living chick to care for seemed to reduce the likelihood of allofeeding. Adults performed more allofeeding events after the death of their crèching chick than they did before their breeding failure. The pronounced occurrence of allofeeding at the beginning of winter might be explained by the high number of allofeeders that had just failed reproduction. Four adults that had started a new breeding cycle were also seen allofeeding. This observation suggests that the breeding status of allofeeders in king penguins is more variable than expected according to studies involving other species (Riedman 1982).

Finally, allofeeding in the king penguin seemed to be affected by the spatial proximity of breeding adults in colonies. Allofeeders preferentially fed crèching chicks that were reared by close neighbours at the time of brooding. Hence, the closer that a breeding neighbour was, the greater the chance that a chick would be allofed by this adult at the crèching stage. It is remarkable that the colony was no longer divided into breeding territories at the time of crèching. This observation suggests that allofeeders may recognize the chicks that they feed by a mechanism that has not been described. Further studies of chick recognition by adults during brooding are needed to explore this hypothesis.

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