Determinants of Feeding Chases in the Chinstrap Penguin *Pygoscelis antarctica*

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Summary: Feeding interactions between parents and chicks in pygoscelid penguins are frequently associated with chases. We tested alternative predictions derived from two functional hypotheses proposed to explain feeding chases: (1) the harassment of the parent by two begging, competing chicks is stressful and makes the parent run away to avoid stress ('harassment avoidance hypothesis') and (2) chases are initiated by parents to separate the two chicks before feeding them in order to avoid inter-sibling competition, and thus to increase food transfer efficiency ('efficient food transfer hypothesis'). In an observational study of Chinstrap Penguins *Pygoscelis antarctica* during the crèche stage, we found that feeding chases were initiated in the presence of two begging chicks independently of their competitive disposition. When the chicks competed, parental visits lasted longer, and parents took longer time to transfer a given number of feedings, than when there was no competition. In chases inducing chick separation, the duration of adult running bouts was determined by the time it took to separate them. This would not be the case if feeding chases were initiated to avoid harassment by two competing chicks. Feeding chases initiated by parents appears to be a behaviour tending to separate the two chicks in order to feed them more efficiently, which results in shortening the time spent by parents in the colony. Additionally, we found some evidence indicating that through the feeding chases parents could also gain information on the nutritional needs of their chicks.

A characteristic of pygoscelid penguins is that feeding interactions between parents and chicks are frequently associated with chases, where running parents are closely followed by their chicks (Thompson 1981; Lundberg & Bannasch 1983; Bustamante et al. 1992). In a previous observational study of crèching Chinstrap Penguins *Pygoscelis antarctica*, Bustamante et al. (1992) were able to discard several of the hypotheses suggested in the literature to explain this behaviour. Chases were not obviously related to separation of own from other chicks as previously proposed (Sladen 1958; Penney 1968; Müller-Schwarze & Müller-Schwarze 1977). Parent–chick recognition was not dependent on chasing activity. Chasing effort did not increase with chick age, as would be predicted if chases were an expression of parent–offspring conflicts (Trivers 1974).

The clear association of intense chasing with two-chick families in contrast to one-chick families indicates that chasing may be a way for parents to separate their chicks to feed them more efficiently (Muller-Schwarze & Muller-Schwarze 1977). However, this difference may be simply the expression of an inherent difference (e.g. due to age or experience, Ainley et al. 1983) between parents tending one or two-chick broods. That the association of chases to broods of two

chicks is the response to the interaction of one parent with two chicks was shown experimentally in Chinstrap Penguins through the temporary removal of one sibling, which led to a reduction in the intensity of chasing similar to that shown by one-chick parents (Moreno et al. 1996). However, the question still remains if chases result from a reflex reaction by parents trying to avoid harassment by two begging chicks ('harassment avoidance hypothesis', Lundberg & Bannasch 1983), or have the function of feeding the chicks more efficiently ('efficient food transfer hypothesis', Müller-Schwarze & Müller-Schwarze 1977). In the first interpretation, competing chicks force the adult to run away. Thus, chases initiated by adults are a direct reaction to chick behaviour but not intended to avoid inter-sibling competition (Lundberg & Bannasch 1983). In the second case, parents are trying to separate chicks in order to avoid intersibling competition and thus to feed them efficiently one at a time and shorten the time spent at the colony. Although the first hypothesis may be considered as a proximate explanation and the second is based on ultimate or functional arguments, they are still exclusive if we consider harassment avoidance as a function through its effect on the immediate well-being of the parent. Also, the initiation of chases could be

stimulated by proximate factors other than harassment by chicks (acoustic stimulation, proximity between siblings and to the parent, etc.). Thus, both the function and the proximate stimulus are different in the two hypotheses.

From the 'harassment avoidance hypothesis' we should expect that: (1) the initiation of chases is associated with manifestations of active competition between siblings and not merely to the proximity between them, and therefore that chases should not be initiated if there is no competition; (2) the duration of chases is independent of the time it takes to separate the two chicks and only depends on the intensity of the parental reaction; and (3) the propensity to feed after a chase is not dependent on whether chicks are separated, but merely on whether or not the chicks compete. From the 'efficient food transfer hypothesis' we should expect that: (1) chases are initiated even when the two chicks are not actively competing but are close together and close to the adult; (2) the duration of chases depends on the time it takes to separate the two chicks; and (3) parents should feed more frequently after a chase if chicks have become separated than if they are together.

We have tested these predictions derived from the 'efficient food transfer' and 'harassment avoidance' hypotheses observationally. We have followed the interactions between feeding parents and their chicks during the crèche phase, as feeding chases take place predominantly during this phase (Thompson 1981; Lundberg & Bannasch 1983; Bustamante et al. 1992).

Methods

The study was conducted at the Vapour Col Chinstrap Penguin colony (20 000 breeding pairs) on Deception Island, South Shetlands (63°00′S. 60°40′W), during the breeding season of 1992–93. We selected a sub-colony of 120 pairs on relatively flat ground at one edge of the colony and 200 m from the shore. All parents were banded with numbered standard metal flipper bands for Chinstrap Penguins (Lambournes Ltd.), while chicks of families with two chicks were individually identified with plastic flipper bands marked with alphanumeric codes, which could be easily read with binoculars from less than 40 m.

During the guard phase, chicks are restricted to and are fed on the nest, limiting the possibility of chases developing. Thus, only observations of chicks in the crèche phase were considered. The following data were recorded on cassette tapes for each feeding visit: beg-

gings by and feedings to each chick (begging bouts were separated by more than 5 s); expressions of sibling competition classified as pushing sideways with their flippers against each other, pushing its sibling from behind, interposition of one chick by placing itself between its sibling and the parent, and interrupting a food transfer to its sibling by introducing the bill in its parent's beak (hereafter considered as competitive interactions). In visits with feeding chases, we noted the distance between siblings immediately before and after each chase, as well as the distance between the adult and each chick. We recorded if the initiation of chases was associated with begging or with expressions of sibling competition. The duration of a feeding visit was also recorded, from the time the parent arrived at the colony until it departed to the sea. Furthermore, in one randomly selected chase of each visit, we noted the times from beginning of the chase to the separation of the siblings by more than 1 m and until the parent stopped running.

Data were log-, squareroot- or arcsin-transformed when analysed with parametric statistical tests in order to meet their assumptions. We only included one observation per family when performing parametric tests. Nevertheless, statistical tests were not employed when analysing data of frequency of occurrence of particular events due to the pseudoreplicative nature of observations (several records for the same visit and parent). In a few instances some variables were not recorded, which explains why sample sizes differ between estimates of percentages. Mean values are presented ± 1 s.d.

Results

Timing and frequency of chases

The earliest age at which we observed feeding chases in our sample of families was 32.8 ± 2.5 days ($n = 10$ earliest families). Competitive interactions were first observed at an average age of 30.3 ± 1.2 $n = 10$) days of age, which was shortly before the mean creching age (35.0 ± 3.0 days, $n = 99$). Chases occurred in 74.5% of parental visits during the crèche phase ($n = 55$).

Determinants of chase initiation and duration

Chases were initiated in 94.2% of 515 cases when chicks were less than 1 m apart and away from their parent. At the end of chases, siblings were in close proximity to each other in 72% of them, 1-3 m apart in

18% of them, and in 10% of the cases they were separated by more than 3 m. Of the chases initiated when the two chicks were in close proximity to their parent (< 1 m), in 25% of the cases ($n = 485$) there was only one chick begging, in 52% the two siblings begged simultaneously without competing, and in 23% the two siblings begged simultaneously and actively competed.

When there were no competitive interactions between chicks, the total number of feedings transferred during each parental visit (17.50 ± 9.21, $n = 14$) was similar to that of feedings when there were competitive interactions (20.85 ± 6.10, $n = 41$) ($t = 1.94$, $d.f. = 53$, $P = 0.06$). However, in those parental visits when there were no competitive interactions, the number of feeding chases before the last feeding (2.50 ± 2.57, $n = 14$) was significantly lower than when there were competitive interactions between both chicks (5.73 ± 5.80, $n = 41$) ($t = 2.37$, $d.f. = 53$, $P = 0.02$).

By starting to run, parents may try to avoid competitive interactions between chicks if these interactions imply a time cost for parents trying to shorten feeding visits. In fact, there was a significant relationship between the number of competitive interactions and the number of feeding chases during each parental visit ($r = 0.29$, $n = 55$, $P = 0.03$). We tested for differences in the duration of parental visits depending on whether or not there were competitive interactions between the chicks using an Analysis of Covariance (ANCOVA), with the number of feedings transferred by adults to chicks as covariate. The factor x covariate interaction, indicating homogeneity of slopes, was not significant ($F = 0.27$, $d.f. = 1,47$, $P = 0.61$), and was not included in the final analysis. The result of the ANCOVA indicated that those visits in which there were competitive interactions among chicks lasted longer (963.00 ± 434.14 s, $n = 40$) than those in which there was no competition (715.46 ± 262.96 s, $n = 11$) ($F = 4.01$, $d.f. = 1,48$, $P = 0.05$) and that parents took longer time to transfer a given number of feedings when there were competitive interactions among their chicks than when there were no such interactions ($F = 16.21$, $d.f. = 1,48$, $P < 0.001$).

There was a close association between the time from the beginning of the chase to the separation of siblings by more than 1 m, and the total time spent running by the parent in a chase that resulted in chick separation (Fig. 1) (*Parent running time* (in s) = 3.8 + 0.91 x *sibling separation time* (in s); $r = 0.81$, $n = 62$, $P < 0.001$). The time from sibling separation until the parent stopped running was independent of the time from beginning of the chase to separation (*Running time after*

separation (in s) = 3.08 – 0.09 x *sibling separation time* (in s); $r = 0.12$, $n = 62$, $P = 0.35$). Both relationships indicate that parents kept running until their chicks were separated, and stopped after running further for a constant time (roughly 3 s). Sibling separation led in some instances to feeding to the closest chick but this was not always the case. Removing the effect of time until chick separation on adult chase duration by means of an ANCOVA (effect of covariate: $F = 122.4$, $d.f. = 1,59$, $P < 0.001$), to finish the chase by feeding or not had a significant association with adult chase duration ($F = 4.87$, $d.f. = 1,59$, $P = 0.03$; Fig. 1). This effect is probably due to the fact that parents running too short a distance after chick separation (2.6 s *vs* 3.9 s) did not manage to guarantee a sufficient inter-sibling distance to allow food transfer.

Determinants of food transfer

During the crèche phase, the most fed sibling received $70.32 \pm 15.64\%$ ($n = 55$) of the feedings transferred during each parental visit. The number of feedings received was positively associated with begging intensity (for the most fed chick: $r = 0.69$; for the least fed chick: $r = 0.92$; $n = 55$ and $P < 0.001$ in both cases). There was no food transfer in 89.9% ($n = 335$) of cases of simultaneous begging by two competing chicks and in 83.2% ($n = 666$) of simultaneous begging without competition.
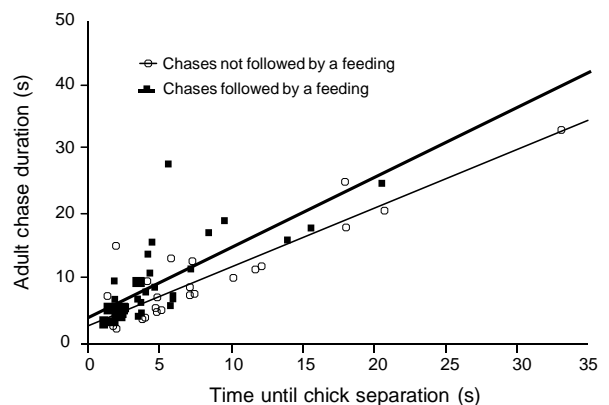

Figure 1 Duration of the run by parents as a function of the time it took until sibling separation. The two regression lines represent chases followed or not followed by a feeding. The regression equations are: y = 3.87 + 1.09x (feeding, $F = 42.64$, $P < 0.001$, $r = 0.75$, $n = 35$), and y = 2.63 + 0.91x (not feeding, $F = 95.47$, $P < 0.001$, $r = 0.89$, $n = 27$).

Of the chases ending with siblings separated by more than 3 m ($n = 55$), 81.1% of the cases were followed by feedings. Conversely, of the chases ended with siblings in close proximity of each other (< 1 m; $n = 231$), only 16% were followed by feedings. Thus, the consequences of the chase with respect to feeding depended on the inter-sibling distance after a chase.

In addition to separating the chicks, feeding chases could be used by parents as an indication of the nutritional needs of chicks. This could explain why, in the presence of only one chick, feedings after a chase occurred more frequently (82%, $n = 111$), than feedings when no chase had intervened but the chick begged for food (35%, $n = 1765$).

Discussion

Several authors have proposed that feeding chases in pygoscelid penguins have the function of separating competing siblings in order to promote efficient food tranfer (Müller-Schwarze & Müller-Schwarze 1977; Thompson 1981; Moreno et al. 1996). However, the costs to parents of trying to feed the two chicks while together are not apparent. On the other hand, Lundberg & Bannasch (1983) suggested that feeding chases could be initiated in order to avoid harassment by large competing chicks, without having any further function. Although their hypothesis may be considered as a proximate one, and efficient food transfer has a clear functional meaning, both hypotheses may be considered ultimate if harassment stresses the parents and thus has immediate effects on their well-being. Here we have tried to tease apart as much as possible the observational implications of both hypotheses.

Previous studies of pygoscelid penguins have shown that feeding chases occur mainly when chicks have entered the crèche stage (Thompson 1981; Lundberg & Bannasch 1983; Bustamante et al. 1992). However, chases do not increase in frequency with chick age once the chicks are in crèches (Bustamante et al. 1992), as would be predicted by the 'harassment avoidance hypothesis' (Lundberg & Bannasch 1983) given the increase in the size of chicks. Other predictions derived from this hypothesis are not met in our study. First, many chases were initiated without clear signs of inter-sibling competition. Second, the time that the parents ran was determined by the time until chick separation, which would not be the case if parents were just trying to avoid being harassed by two begging chicks. And third, parents apparently avoid delivering food in the presence of two begging chicks independently of their competitive disposition, as indicated by the low proportion of cases of simultaneous begging without competition ending in feedings.

The predictions derived from the 'efficient food transfer hypothesis' are met in our study. As predicted, chases were initiated in the presence of two begging chicks, even when they were not competing. By starting a chase, parents could preclude the competitive interactions among chicks in order to transfer the food to them as quickly as possible. This might be feasible if after the chases parents manage to separate their offspring. There is a time cost for parents in not avoiding competitive interactions among their chicks, as shown by the longer time it takes to transfer a given number of feedings when chicks compete. There seemed to be a tendency for parents to shorten the duration of feeding visits as much as possible, because they almost always departed from the colony after the last feeding to their chicks. In a previous study of Chinstrap Penguins, we also showed that feeding proceeds more rapidly after chick separation than before during a feeding visit (Moreno et al. 1996). Again as predicted, the duration of adult running bouts was closely linked to the time until chicks became separated, implying that sibling separation was the end sought by the parents. Finally, parents seemed to avoid transferring food after a chase if their running time after separation was too short, which may be due to a short inter-sibling distance. In fact, parents tended to refrain from delivering food after chases when chicks remained close together.

The present results suggest that chases are not merely the consequence of harassment of parents by their competing chicks, but a behaviour tending to separate the two begging siblings in order to feed them one at a time (Moreno et al. 1996). The great mobility of chicks in crèches as well as sibling competition has apparently led to the development of such a costly and characteristic behaviour as the feeding chases of pygoscelid penguins. In species of penguins with less developed creching behaviour, parents with two chicks are able to control the food transfer, i.e. by preventing chicks from gaining direct access to the bill with their flippers (Seddon 1990; Boersma 1991; Seddon & van Heezik 1991). In Chinstrap Penguins, the presence of two competing chicks pushing against each other and simultaneously begging by pecking at the parent's bill may impede efficient regurgitation. Chases contribute to separate chicks and allow a more efficient food transfer, usually to the most persistent chick. If persistence is associated with

hunger, chasing could regulate food distribution between siblings (Bustamante et al. 1992). A consequence of chasing behaviour is the unequal distribution of food between siblings in each feeding visit, leading to exclusive feeding of one in some cases. These differences in food allocation may be evened out during successive parental visits if the hungrier chick tends to run more, but may be of critical importance for chick survival during food crises (Moreno et al. 1994). Additionally, through the feeding chases parents could also gain information about the nutritional needs of their chicks.

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