

Parent–Offspring Interactions and Feeding Chases in the Chinstrap Penguin *Pygoscelis antarctica*

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Feeding interactions between parents and chicks in pygoscelid penguins frequently lead to “chases.” In a field experiment with Chinstrap penguins (*Pygoscelis antarctica*) on Deception Island, we showed that chases are almost nonexistent when a parent is met by only one of their chicks (the other was temporarily removed). Also, chasing intensity in the two-chick situation decreased after chick separation, whereas the rate of feedings increased. The initiation of chases could be due to the need of separating the two chicks before feeding them in order to increase feeding efficiency or, alternatively, be a reaction of the parent to the harassment from two begging, competing chicks.

Chinstrap penguin *Parent–offspring interactions* *Feeding chases*

In pygoscelid penguins chases often occur in feeding interactions, when parents run from their closely following chicks (Bustamante, Cuervo, & Moreno, 1992; Lundberg & Bannasch, 1983; Thompson, 1981). 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 behavior. Chases did not function to separate a parent’s chicks from others in the crèche, as previously proposed (Müller-Schwarze & Müller-Schwarze, 1977; Penney, 1968; Sladen, 1958); parent–chick recognition was not dependent on chasing; and chasing 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 fami-

lies indicates that chasing may be a way for parents to separate their chicks to feed them more efficiently (Müller-Schwarze & Müller-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. If chases involve the interaction of one parent with two chicks, the temporary removal of one sibling should lead to a reduction in the intensity of chasing to the level shown by one-chick parents.

In the present study of the Chinstrap penguin, we compared chasing intensity in the normal two-chick situation with an experimental situation where parents with two chicks are met by only one of them. In this way, we removed the possible effects of parental age, experience, or quality (Ainley et al., 1983).

Method

The study was conducted at the Vapour Col chinstrap penguin colony (20,000 breeding pairs) on Deception Island, South Shetland Islands (63°00'S, 60°40'W), during the breeding season 1991/92. One breeding group of 100 pairs on relatively flat ground at one edge of the colony and close to the shore (100 m) was selected. All parents were banded with numbered metal flipper bands (Lambournes Ltd.). Chicks from two-chick broods were individually identified with plastic flipper bands marked with alphanumeric codes. The codes could be read easily with binoculars from <40 m.

The temporary removal experiment was conducted when chicks were 37–44 days of age (mean 41 days). For the experiment, one chick from each family was removed from the crèche and kept in a pen that was visually and auditorally isolated from the colony. The interaction of visiting parents with the remaining sibling was observed, the retained chick being returned to the crèche at the end of the observation (after less than 12 h of separation). Approximately the same number of manipulated and unmanipulated families were observed each day. The order of experimental and control days for each family was randomly determined. We obtained observations of six individuals in both the control and experimental situations. Due to bad weather, several observations had to be interrupted. Therefore, for other individuals we have either experimental or control observations (seven controls and six experimentals). We compared the experimental sample against control observations using an unmatched statistical design (Mann-Whitney *U*-tests) in order to increase sample size and the representativeness of the results. The analyses were repeated with pairs as statistically independent units, without any change in the results. In cases with more than one visit by the same adult, we have used means as independent observations. Observations of members of the same mated pair were considered as independent (11 and 9 pairs in the experimental and control groups, respectively), because mates do not coordinate feeding visits (Taylor, 1962).

The following data were recorded for each

feeding visit: the total duration of feeding visits measured from arrival to departure of the adult from the colony; the number of feedings received by each chick; the number and duration of chases by the parent and by individual chicks and if they occurred before the first feeding, between the first and the last feeding, and after the last feeding in each visit. In control observations (two chicks), we divided the feeding visits into two parts according to whether the adult was followed by both or only one chick. As separation of siblings was a frequent outcome of chases (9 of 13 interactions), this division corresponds to the initial and final parts of feeding interactions. We compared feeding and chasing rates in the two situations with a matched statistical design (Wilcoxon matched-pairs test).

Results

Duration of feeding bouts and number of feedings did not differ significantly between parents feeding two chicks and those feeding one chick in an experimentally reduced brood (Table 1). Therefore, average food amount received per chick in broods of two was half the food obtained by one chick in experimentally reduced broods. Chasing activity before and during occurrences of parents feeding one chick was significantly lower than that observed when they were delivering food to two chicks (Table 1). In two observations not included in the control sample, both mates arrived simultaneously at the crèche. This resulted in markedly lower chasing activity (on average 1.5 chases with a total duration of 9 s). These values are close to those observed in the experiments (Table 1). Although anecdotal, these observations stress the association of chasing behavior with the one-parent-two-chick situation. Duration of chases after the last feeding was also lower in experimentally reduced broods (Table 1). This result may show that chicks in the experimental situation become satiated more quickly than in the normal two-chick situation (consistent with the lower feeding rate per chick in families of two chicks).

In 9 of 13 control visits, the two chicks chasing their parent became separated and only one of them followed its parent until the end of the feed-

Table 1. Characteristics of Feeding Interactions of Parents Feeding Two Chicks (Control Group) and Those Feeding Only One After Experimental Removal of One Sibling (Experimental Group), and Results of Mann-Whitney *U*-Tests

| | Control (<i>n</i> = 13) | | Experimental (<i>n</i> = 12) | | <i>Z</i> | <i>p</i> |
|---|--------------------------|--------|-------------------------------|--------|----------|----------|
| | Mean ± SD | Median | Mean ± SD | Median | | |
| Visit duration (s) | 778.6 ± 239.7 | 766 | 877.3 ± 388.3 | 840 | 0.4 | 0.707 |
| No. of feedings | 23.5 ± 6.9 | 23.5 | 22.0 ± 9.7 | 21.5 | 0.4 | 0.686 |
| Chase duration (s) | 100.2 ± 72.0 | 71.5 | 18.3 ± 22.3 | 14.2 | 3.7 | 0.0002 |
| No. of chases | 9.6 ± 4.7 | 8.5 | 1.5 ± 1.0 | 1.5 | 3.9 | 0.0001 |
| Duration of chases before first feeding (s) | 9.2 ± 15.9 | 0 | 0 ± 0 | 0 | 2.4 | 0.016 |
| No. of chases before first feeding | 0.6 ± 0.9 | 0 | 0 ± 0 | 0 | 2.4 | 0.016 |
| Duration of chases first to last feeding | 57.5 ± 46.4 | 47.5 | 4.6 ± 8.3 | 0 | 3.4 | 0.0008 |
| No. of chases from first to last feeding | 7.0 ± 4.5 | 7 | 0.4 ± 0.6 | 0 | 3.6 | 0.0004 |
| Duration of chases after last feeding | 33.5 ± 40.1 | 19 | 13.7 ± 22.9 | 6.8 | 2.3 | 0.024 |
| No. of chases after last feeding | 2.0 ± 1.6 | 2 | 1.0 ± 1.0 | 1 | 1.8 | 0.066 |

ing visit. In these cases, the parental feeding rate (feedings/time, from separation until last feeding) was higher when the parent was chased by only one chick (Fig. 1). In contrast, chasing rate (number of chases/min) was lower during the last part of the feeding visit (Fig. 1). Thus, chasing intensity drops after chick separation, whereas the feeding process becomes more efficient (higher feeding rates). Compared with the experimental one-chick situation, feeding rate in families of two was higher when only one chick took part in

chases [last part of control observations (mean ± SD): 3.8 ± 1.7; experimental: 1.9 ± 1.0; Mann-Whitney *U*-test, *Z* = 2.736, *p* = 0.006). The same trend was true of chasing rate (last part of control observations: 0.37 ± 0.51; experimental: 0.03 ± 0.04; *Z* = 2.106, *p* = 0.035). Thus, chasing rate among controls when only one chick participated was intermediate between that of parents delivering food to two chicks and the very low rates in the experimental one-chick situation.

Discussion

The results of the experiment are consistent with previous observations that parents with only one chick do not initiate chases (Bustamante et al. 1992; Müller-Schwarze & Müller-Schwarze, 1977; Thompson, 1981). Parents fed a chick just as often in the experimental one-chick situation and spent the same period of time interacting with one as with two chicks. However, parents were chased less when feeding their remaining chick and never ran before delivering the first feeding (chases after the last feeding are the expression of increasing parental reluctance to continue feeding). Chasing behavior is thus characteristic of one parent finding two chicks upon its arrival at the crèche, and does not depend on whether parents raise one or two chicks. In the usual two-chick situation, the separation of siblings during the chase leads to a

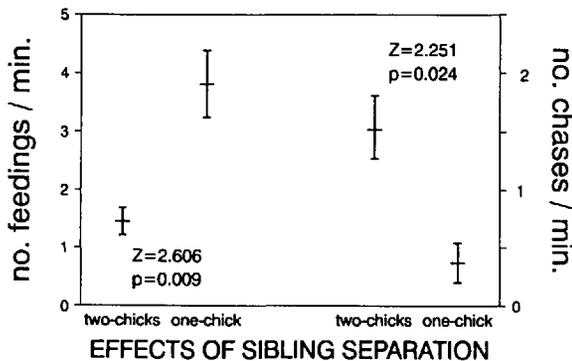


Figure 1. Effects of sibling separation on feeding and chasing rates. One-chick refers to the last part of chases when only one chick followed the parent, whereas two-chicks refers to the first part when both chicks were chasing. Sample size for each group = 9; results of Wilcoxon matched-pairs tests are also shown.

marked drop in chasing frequency, whereas the food delivery rate is increased. The fact that feeding proceeded more rapidly after chick separation occurred supports the notion that parents run in order to separate their chicks and increase feeding efficiency.

Sibling separation has a similar but weaker effect compared to experimental removal of one sibling. The difference may be due to the fact that parents are probably aware of the presence in the crèche of the nonparticipating chick. These observations support the notion that one function of chases is to separate competing siblings in order to promote efficient food transfer (Müller-Schwarze & Müller-Schwarze, 1977; Thompson, 1981). However, the costs to parents of trying to feed the two chicks while together are not apparent.

We suggest that chases function to separate the two begging siblings in order to feed them more efficiently one at a time. The great mobility of chicks in crèches as well as sibling competition has apparently led to the development of this energetically costly behavior. Among species of penguins in which crèching behavior is less developed (i.e., species that nest in burrows), parents are able to control the food transfer by preventing chicks from gaining direct access to the bill with their

flippers (Boersma, 1991; Seddon, 1990; Seddon & van Heezik, 1991). If persistence of chases is associated with hunger, chasing could also regulate food distribution between siblings, thereby reducing brood size when food is sparse (Bustamante et al., 1992).

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