

The function of feeding chases in the chinstrap penguin, *Pygoscelis antarctica*

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Abstract. Crèching chinstrap penguin chicks chase their parents on the run before being fed. This characteristic behaviour of *Pygoscelis* penguins has been interpreted in several ways. In an observational study of several colonies in a rookery on Deception Island, South Shetlands, the frequency and duration of feeding chases in families with one and two chicks were compared. Significantly more feedings occurred outside the crèche in two-chick than in one-chick families. Chases were significantly more frequent and prolonged in families with two than in those with single chicks. This difference was independent of the number of chicks present in the interactions (one or two siblings in two-chick families). Chases during feedings by single chicks were significantly less frequent and prolonged than those by one chick when its sibling was absent. Siblings chasing more intensively obtained more feedings. There was no increase in chasing effort with chick age. These results suggest that feeding chases allow parents to regulate food distribution between siblings according to their needs or hunger but they could also allow brood reduction in times of food crises.

In *Pygoscelis* penguins (gentoo, *Pygoscelis papua*, Adélie, *P. adeliae* and chinstrap) chicks are left on their own at the age of 3–4 weeks. They then form more or less dense aggregations called crèches, waiting for the parents to return from the sea to feed them. Crèches are presumed to have protective (weather, predators) and social functions (Sladen 1958; Spurr 1975; Davis 1982; Lishman 1985). Feeding interactions are frequently associated with chases, where running parents are closely followed by their chicks (for a full description of this behaviour in *Pygoscelis* see Thompson 1981; Lundberg & Bannasch 1983). Chases end by parents feeding the following chicks or leaving them behind. In these penguin species, parents may raise one or two chicks.

Several hypotheses about the function of these chases have been proposed.

(1) Chases are induced by parents to separate their own chicks from the rest of the crèche and thus avoid competition from strange chicks or interference by territorial adults (Sladen 1958; Penney 1968; Müller-Schwarze & Müller-Schwarze 1977).

(2) Chases contribute to parent–chick recognition. Parents would recognize their chicks by their propensity to run after them (Volkman & Trivelpiece, personal communication, cited in Lundberg & Bannasch 1983).

(3) Chases temporarily separate siblings in families with two chicks, avoiding unnecessary and wasteful competition and ensuring the efficient successive feeding of both chicks (Müller-Schwarze & Müller-Schwarze 1977; Thompson 1981).

(4) Chases lead to preferential feeding of the hungriest chick, if hunger leads to more intense chasing, as Richdale (1957) showed for yelloweyed penguins, *Megadyptes antipodes*, with respect to begging (parents fed preferentially the most intensively begging chick which was frequently the hungrier one).

(5) Chases lead to preferential feeding of the strongest chick when food is scarce, as Lundberg & Bannasch (1983) proposed based on the theory of parent–offspring conflict (Trivers 1974).

(6) Chases are the result of parents not being able to cope with the intense begging activity of their chicks (Lundberg & Bannasch 1983).

(7) Provoking a feeding chase allows the parents to evaluate how hungry the chick is and to determine how much of the stomach contents to give to

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the chicks (Thompson 1981). This mechanism of apportionment of food between parent and chicks would work independently of whether there are one or two chicks.

(8) Chases are an expression of parent-offspring conflict prior to chick independence. Parents would become increasingly reluctant to feed chicks, which in turn would be interested in maintaining the level of parental contribution (Trivers 1974). We would then expect an increase in chasing intensity with chick age until independence.

(9) Chases are secondarily an expression of muscle training, leading chicks to explore new ground or contributing to social experiences during the period before independence (Sladen 1958; Müller-Schwarze & Müller-Schwarze 1977).

In the present observational study of crèching chinstrap penguins, we have evaluated several predictions derived from these hypotheses by recording the frequency and duration of chases, the relationship between chases and feedings and the location of feedings in relation to the colony in families with one and two chicks.

METHODS

The study was conducted at the Vapour Col chinstrap rookery on Deception Island, South Shetlands (63°00' S, 60°40' W), during January–February 1991. The number of breeding pairs in this rookery was estimated as 10 000 in 1967 (Croxall & Kirkwood 1979) and 7500 in 1987 (Shuford & Spear 1988). For the study, we selected three colonies on relatively flat ground at the northern edge of the rookery and close to the shore (50–200 m). Colonies 1–3 comprised roughly 150, 160 and 100 chicks during the crèche stage.

We captured 37 whole family groups at the end of the guard phase, and assigned chicks to the adults guarding and feeding them. Of these families, six adults were not captured as they were never observed in the colonies. We selected approximately the same number of families with one and two chicks in each colony (five and seven in colony 1, six and six in colony 2 and six and seven in colony 3). The original clutch size was unknown, and some one-chick families were probably the result of the previous death of one chick. Adults and chicks were banded with plastic flipper bands marked with an individual alpha-numeric code. The bands could be easily read with binoculars from 40 m. Most observations were made from distances of 10–50 m. The

following measurements were taken while banding: bill length (from feathered edge to tip), bill depth (at anterior end of the nares), flipper length (anterior edge), length of longest rectrix and body weight (with spring balances accurate to the nearest 50 g).

During the crèche stage, we observed the interactions between parents and chicks during feeding visits by adults. We selected at random banded adults approaching the colonies and followed their behaviour until they departed for the sea. For each selected feeding visit, we recorded on tape the following data: the number and identity of chicks interacting with the adult; the number of begging bouts by individual chicks and the number of feedings received; whether feedings occurred inside or outside the colony; the number and duration of chases by individual chicks as well as the direction of these chases; and aggressive interactions between adult and chicks. Chases were classified as being before the first feeding, during feedings and after the last feeding in each parental visit. We also noted whether one or both chicks in families of two participated in the feeding interaction, as chicks occasionally did not react to the arrival of their visiting parent.

In cases with more than one visit by the same adult, we used means of individual parents as independent observations. Observations of members of a breeding pair were considered as independent, since feeding chases seem to be initiated by adults and mates apparently do not co-ordinate feeding visits. The Wilcoxon–Mann–Whitney test (Siegel & Castellan 1988), hereafter referred as the Wilcoxon test, was used to test differences between independent samples, whereas the Wilcoxon signed-ranks test was used for matched-pairs comparisons when appropriate. All tests are two-tailed at the 0.05 significance level unless stated otherwise. Means are presented with standard deviations.

RESULTS

We recorded 59 visits of adult penguins returning from the sea to feed their offspring. From these, 19 corresponded to adults with one chick (10 adults from eight different pairs) and 40 corresponded to adults with two chicks (22 adults from 15 different pairs). We observed 374 instances in which the focal adult penguin was chased by its offspring, of which 41 were of adults with one chick and 333 of adults

with two chicks. The average number of feedings per visit was 17.0 ± 8.3 in one-chick broods and 17.7 ± 5.8 in two-chick broods.

Parents might induce feeding chases to separate their offspring from other chicks to avoid competition. If so, adults should lead their offspring out of the crèche before feeding. This was clearly not the case as most feedings occurred inside the crèche in both one-chick (median of percentage of feedings inside crèche per interaction = 100%, range = 66.7–100%, $N = 10$) and two-chick families (median = 52.6%, range = 0–100%, $N = 22$). Although the difference between these medians is significant (Wilcoxon test, $Z = -3.82$, $P = 0.0001$), the need to separate offspring from other chicks in the crèche should be independent of brood size.

If chases are a means whereby parents recognize their own chicks, we have to assume that strange chicks cannot be recognized in a less costly way. Vocal cues allow chick discrimination by parents in the related Adélie penguin (Penney 1968; Davis & McCaffrey 1989). We frequently observed begging by chicks to adults other than their parents (even to other chicks), but they were often aggressively repelled by the adults or even by the adults' own chicks. Even when parasitic attempts included participation in chases (41 chases by nine chicks in six visits by adults), they did not obtain any of the 1031 feedings observed. The rarity of these instances makes the recognition hypothesis implausible. Incidentally, one chick was observed efficiently parasitizing non-focal adults on two occasions (this individual was observed frequently begging to other adults). Also, the prevalent chasing after the first feedings (i.e. after its putative function had been fulfilled) would indicate that some function other than recognition must be involved.

If feeding chases serve to separate chicks in two-chick families in order to avoid wasteful competition, we would expect most chases to be accompanied by separation of chicks and thus by feedings with only one chick present. Of 65 chases (defined here as bouts of chases ending with a food transfer) in which two chicks participated, 37 ended with only one chick begging and getting food from its parent, while in 28 cases the two chicks were present during the subsequent feeding interaction. This frequency distribution does not differ significantly from a random outcome (chi-squared one-sample test, $P > 0.20$). Separation of siblings may be a result of chasing due to asymmetries in chick

motivation or endurance (due to hunger), or caused by random events such as aggression from adults or other chicks in the crèches (personal observations). However, it appears unlikely that separation is the main function of chases.

Feeding chases could be a mechanism to determine the apportionment of stomach contents between parent and chick(s) depending on how hungry the latter are. This mechanism would work if chasing effort by chicks is a good index of hunger (each adult feeds the chicks independently of its mate and does not know when the chicks have received their last feeding). In that case, chases should be induced by parents independently of family size and would be most important prior to actual feeding. Once hunger state has been ascertained by chases, further chasing would be wasteful. However, chases were more frequent after first feedings than before for 29 adults out of 32 (Wilcoxon matched-pairs signed-ranks test, $Z = 4.15$, $P = 0.00003$).

In addition, chases were significantly more frequent and prolonged in families with two chicks than in families with one chick (Table I). The differences in frequency and duration are especially marked for chases occurring during feeding and least pronounced for chases occurring after feeding. If chases are merely a consequence of competition between chicks, we would expect a difference in families of two in the number and duration of chases depending on whether one or two chicks participated, with more intense chasing with two chicks present. There were no significant differences between interactions with one and two chicks present (Table II). This result suggests that there is something inherently different in parent-chick interactions in families with one and two chicks. Chases may be more frequent and prolonged in families with two chicks owing to their greater hunger determined by parental feeding limitations. To compare chick condition in one-chick and two-chick families, we performed an ANCOVA on body weight using the cube of bill length as the covariate to control for differences in chick age. The cube of bill length had a significant effect on body weight ($F_{1,48} = 10.28$, $P = 0.024$). Although chicks of one-chick families were heavier at capture (3483 ± 591 g, $N = 15$ versus 3178 ± 388 g, $N = 36$), the difference was not quite significant ($F_{1,48} = 3.51$, $P = 0.067$).

The interactions in two-chick families with only one sibling present also allow us to test whether

Table I. Test of differences between frequency and duration of chases in families with one and two chicks

	Single chick		Median	Two chicks		Median	Wilcoxon tests	
	$\bar{X} \pm \text{SD}$ (<i>N</i> = 10)			$\bar{X} \pm \text{SD}$ (<i>N</i> = 22)			<i>Z</i>	<i>P</i>
Total chases	2.1 ± 2.1		1	9.0 ± 7.4		7	3.6	0.0003
Chases before first feeding	0.1 ± 0.3		0	2.3 ± 7.1		0	1.9	0.052
Chases during feedings	0.5 ± 1.1		0	4.6 ± 4.1		4	3.5	0.0005
Chases after last feeding	1.5 ± 1.8		1	2.1 ± 1.5		2	1.3	0.18
Total duration (s)	17.3 ± 24.0		9.2	134.7 ± 142.4		96.2	3.7	0.0002
Duration of chases before first feeding	0.4 ± 1.3		0	39.0 ± 132.8		0	2.0	0.046
Duration of chases during feedings	2.4 ± 5.9		0	54.8 ± 58.2		45.5	3.7	0.0002
Duration of chases after last feeding	14.5 ± 23.0		9.2	40.9 ± 37.4		31.3	2.0	0.041

Table II. Tests of differences in frequency and duration of chases in families with two chicks when one or both siblings participate in the interaction

	One chick present		Median	Two chicks present		Median	Wilcoxon tests	
	$\bar{X} \pm \text{SD}$ (<i>N</i> = 6)			$\bar{X} \pm \text{SD}$ (<i>N</i> = 20)			<i>Z</i>	<i>P</i>
Total chases	6.2 ± 6.3		5	9.4 ± 7.5		7	1.3	0.198
Chases before first feeding	1.5 ± 3.7		0	2.4 ± 7.4		0	0.9	0.366
Chases during feedings	3.7 ± 2.7		3.5	4.6 ± 4.3		3.5	0.09	0.927
Chases after last feeding	1.0 ± 1.3		0.5	2.4 ± 1.5		2.2	1.9	0.061
Total duration (s)	57.7 ± 48.0		64	147.3 ± 150.5		154	1.7	0.092
Duration of chases before first feeding	9.8 ± 24.1		0	40.5 ± 139.4		0	0.9	0.366
Duration of chases during feedings	28.0 ± 22.6		28.5	57.1 ± 63.5		50	0.9	0.339
Duration of chases after last feeding	19.8 ± 27.8		6.5	45.1 ± 37.5		34.2	1.5	0.126

Four individuals were observed in both situations.

feeding chases are only the expression of the need by parents to control feeding because of the aggressive begging behaviour of chicks. In that case, we would not expect any difference in chasing activity between interactions with chicks of one-chick families and interactions with one chick present of two-chick families. This prediction is based on the assumption that the difficulty in controlling food delivery depends on the number of chicks present independently of family type. There is, however, a significant difference in the frequency (Wilcoxon test, $Z = 2.3$, $P = 0.019$) and duration ($Z = 2.4$, $P = 0.017$) of chases during feedings between the two situations (Tables I and II). This result could be explained if single chicks were easier to control than chicks in families of two owing to

their better condition. However, the lack of a marked difference in condition at capture makes this explanation unlikely.

In families of two the parent must decide how to distribute the food between chicks. Even when only one chick is present, the parent has to consider the possibility of the second chick appearing at any moment. Thus, the high frequency and duration of chases during feeding when only one chick appears suggests that the adult is reluctant to give all its food to only one of its offspring. The parent could use chasing effort as an estimate of chick needs and give more food to the hungriest chick. In 20 of 27 interactions with two chicks present, the chick chasing for the longest total time obtained more feedings (binomial one-tailed test, $P = 0.0107$). The

Table III. Tendencies in chasing frequency and duration and in the number of feedings, begging bouts by chicks and acts of aggression by parents towards chicks in relation to chick age

	Increasing	Decreasing	No change
Total number of chases	11	14	1
Chases before first feeding	6	5	15
Chases during feedings	10	10	6
Chases after last feeding	9	11	6
Total duration	9	17	0
Duration of chases before first feeding	9	4	13
Duration of chases during feedings	9	12	5
Duration of chases after last feeding	9	14	3
Feedings	12	13	1
Begging bouts	12	13	1
Parental aggression	7	13	6

relationship between chasing effort and feedings obtained is even more marked when chases occurring after the last feeding are excluded (in 18 of 21 cases the chick with the longest duration of chases got more food: binomial one-tailed test, $P=0.0027$). We have excluded from analysis cases when both chicks chased the parent for the same amount of time. In a two-chick family with only one feeding adult, one chick was found dead with a very low weight. In both observations of this family prior to the death of the chick, the surviving sibling was the one chasing most intensively and obtaining all the feedings. Chasing could have worked in this case as a mechanism for brood reduction.

If chases are an expression of a parent-offspring conflict about the level of parental investment (Trivers 1974), we would expect an increase in chasing effort by chicks with age owing to the increasing reluctance by parents to maintain a certain level of investment. We have observations on different days (two to five observations separated by 1–8 days) for 26 chicks. There is no tendency for chasing frequency and duration to increase with chick age (Table III). Other indicators of conflict would be the frequency of feedings (decreasing trend with age), the number of begging bouts (increasing trend) and the number of acts of parental aggression directed towards chicks (increasing trend). No such trends can be detected (Table III).

Although exploration of the surroundings of the colony and gradual familiarization with the shoreline before independence could be secondary

Table IV. Direction of chases (towards seashore, away from seashore or lateral to seashore) in the three colonies studied

	Colony 1	Colony 2	Colony 3
Towards sea	87	28	16
Away from sea	48	18	4
Lateral	87	53	14

functions of chases, they are clearly not its main function. Chases were not primarily directed towards the shore (Table IV). Also, chicks did not remain for long away from the crèche exploring new ground, but returned to the colony soon after the feeding interaction (of 46 interactions when chases led out of the crèches, only three were not followed by the immediate return of the chicks to the crèches). Single chicks or groups of chicks moved between crèches when adults were at sea and no feedings were taking place. Finally, locomotory training by chicks can be observed throughout the day and without the presence of parents, with chicks running and beating their flippers during intense bouts of activity.

DISCUSSION

The chases observed in chinstrap penguins cannot be explained by the need to separate offspring from other competing chicks, as a means of parental

recognition of offspring, or as the outcome of the inability of parents to control feeding. Feeding chases were comparatively rare in one-chick families with the consequence that feedings very seldom occurred outside the crèche. In two-chick families chases were frequent and led chicks outside the crèche, independently of the number of chicks present in the interaction. The clear difference between family types cannot be explained by these hypotheses. The lack of apparent increase in chasing tendency with chick age does not support the hypothesis of chases being the result of a parent-offspring conflict as observed in other species (Davies 1976, 1978; Woodward 1983; Moreno 1984; Edwards 1985). Locomotory training and spatial exploration by chicks may be secondary functions, but do not require chases to develop.

The difference in chasing effort between single chicks and chicks in families of two indicates that chasing in chinstrap penguins is related to the need by parents to regulate food distribution between siblings. This interpretation is supported by the fact that chases are frequent even when only one chick is present in two-chick family interactions. If chases were an expression of competition between siblings or of the need by parents to separate siblings in order to avoid such competition, we would expect a marked behavioural difference between interactions with one or two siblings present. There was no such difference. Separation of siblings is a frequent outcome of chases as in Adélies (Thompson 1981), but is apparently not the main function for which they evolved. However, competition is obvious during feedings and its avoidance could be a secondary function of chases, as krill is often wasted due to competition (krill on the ground is never picked up by penguins). In Thompson's (1981) study it is not clear if the difference in chasing effort in interactions with one and two chicks refers to different family types or just to number of chicks present, which makes comparison with our results difficult.

Although the hunger state of chicks was unknown to us, it appears reasonable to assume a positive relationship between hunger and chasing effort by chicks, as shown for Adélies by Thompson (1981). In that case, chasing would tend to regulate food distribution in favour of the hungriest sibling, given the positive association between chasing effort and number of feedings obtained. The function of ascertaining hunger state is not incompatible with

that of favouring the strongest chick in food crises as proposed by Lundberg & Bannasch (1983). At a certain point of deterioration in chick condition due to food shortage or disappearance of one parent, chasing effort would indicate the survival probability of the different siblings as the weakest would be unable to follow in the chases. In that situation, chasing would accelerate a brood reduction necessary to adjust brood size to parental capacity.

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