THE EVOLUTION OF BEGGING

COMPETITION, COOPERATION AND COMMUNICATION

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CONTENTS

16.

FEEDING CHASES IN PENGUINS: BEGGING COMPETITION ON THE RUN?

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ABSTRACT

Feeding interactions in Pygoscelid penguins normally involve chases where a parent runs and is closely followed by its chicks. Several hypotheses have been advanced to explain this behaviour. Studies with chinstrap and Adélie penguins indicate that feeding chases are mostly associated with a one-parent/two-chick situation. Chases are almost absent in one-chick broods, or situations in which one sibling is removed from the crèche and only the remaining sibling begs for food. Data are consistent with the hypothesis that chases serve to separate siblings in two-chick broods in order to feed them more efficiently.

INTRODUCTION

Penguins are colonial seabirds nesting in burrows or in open nests and raising one or two chicks. The nestling period is divided into an initial guarding stage, in which the chicks remain at the nest and are guarded by one of the parents, and a crèche stage, in which both parents forage at sea simultaneously. At the latter stage, chicks move from the nest site and join other chicks of the colony in groups or crèches, with parents regularly coming ashore to feed. During the crèche stage these feeding interactions are frequently associated with chases in

which a parent runs and is closely followed by begging chicks. When an adult comes ashore it approaches its nest site and gives a series of display calls. If not already at the nest site, its chicks will emerge from the crèche, approach the vocalizing adult and beg for food. The adult may feed its offspring at this point or run off pursued by the begging chicks, which it stops intermittently to feed. It takes 10 to 15 minutes for an adult to feed one or two chicks about a kilogram of food, divided into 15 to 20 feeds. Chases can take place before the first feed, between consecutive feeds, or after the last feed as the parent leaves the colony or returns to the sea (Table 1).

Table 1. Comparison of feeding chases in Adélie, chinstrap and gentoo penguins. When two figures are given they correspond to one-chick and two-chick broods respectively.

	Adélie[1]	chinstrap[2]	gentoo[3]
Chick age at earliest chases (d)		32.8[5]	
Meal[*] duration (s)	584-673	779[6]	840
No. chases/meal	4.8-7.8	2.1-9.0	1.7
No. chases before first feed[†]	0.3-0.6	0.1-2.3	0.5
No. chases during feeds		0.5-4.6	0.3
No. chases after last feed		1.5-2.1	1.0
No. of feeds per meal	14.8-16.1	17.0-17.7	19
Mean maximum distance to the nest during a meal (m)	43.9-84.5[4]		

[1]Boersma & Davis 1997; [2]Bustamante et al. 1992; [3]Lundberg & Bannasch 1983; [4]Thompson 1981; [5]Moreno et al. 1998; [6]Moreno et al. 1996; [*]meal = complete feeding interaction from parent arrival to parent departure; [†]feed = each single ball of food transferred to a chick during a meal.

Limited forms of chases (or chicks following the adult before or after being fed) have been described occasionally in other species of penguins (Table 2), but frequent and well-developed feeding chases seem to take place only in the Adélie, chinstrap and gentoo penguins. These Pygoscelids raise one or two chicks, are open-nesters and have chicks that join crèches. Feeding chases are similar in the three species and occur once chicks join crèches at about two to five weeks of age.

Table 2. Published references and studies of feeding chases in penguins.

Species	References to feeding chases	Descriptive studies	Experimental studies
Emperor penguin *Aptenodytes forsteri*	1*		
King penguin *Aptenodytes patagonica*	2*		
Adélie penguin *Pygoscelis adeliae*	3,4,5	6,7,8	
Gentoo penguin *Pygoscelis papua*	9,10	7	
Chinstrap penguin *Pygoscelis antarctica*	11	7,12,13	14
Crested penguins *Eudyptes spp*.	15		
Erect-crested penguin *Eudyptes sclateri*	16		
Fiordland crested penguin *Eudyptes pachyrhynchus*	17*		
Jackass penguin *Spheniscus demersus*	18		
Yellow-eyed penguin *Megadyptes antipodes*	19		

1 Prévost 1961; 2 Stonehouse 1960; 3 Sladen 1958; 4 Taylor 1962; 5 Penney 1968; 6 Thompson 1981; 7 Lundberg & Bannasch 1983; 8 Boersma & Davis 1997; 9 Pettingill 1964; 10 Van Zinderen Bakker 1971; 11 W.J.L. Sladen personal communication in Thompson 1981; 12 Bustamante et al. 1992; 13 Moreno et al. 1998; 14 Moreno et al. 1996; 15 J. Warham personal communication 1971 in Thompson 1981; 16 Warham 1972; 17 Warham 1974; 18 Kearton 1931 in Thompson 1981; 19 Richdale 1957 in Thompson 1981; * the behaviour described could be a feeding chase, but is not defined as such by the author.

In other penguin species that raise a single chick and have open nests and crèching behaviour, (genus *Aptenodytes* and *Eudyptes*), the chick may follow its parent out of the crèche for a short distance (5-10 m) before being fed. This is probably to avoid disturbance from other chicks or adults, but this behaviour has not been studied in detail. In species of penguins raising one or two chicks, nesting in burrows and with less developed crèching behaviour

(e.g. genus *Spheniscus*), parents seem to control the transfer of food by using their flippers to counteract sibling competition (Boersma 1991) and chases are rare (Seddon 1990; Seddon & Van Heezik 1991).

HYPOTHESES TO EXPLAIN THE FUNCTION OF FEEDING CHASES

Chases Prevent Competition or Interference from Foreign Chicks or Adults

First proposed by Sladen (1958) and later by others (Penney 1968; Müller-Schwarze & Müller-Schwarze 1977), this hypothesis suggests that chases are initiated by parents to separate their chicks from the rest of the crèche and thus avoid competition from foreign chicks or interference by territorial adults. The hypothesis predicts that (1) feeding chases should be more common in species with crèching behaviour than those without; (2) within species, feeding chases should be more common when breeding at higher densities; and (3) feeding chases should lead chicks out of the crèche where feeding can take place in the absence of competition or interference.

In relation to the first prediction, feeding chases are common in Pygoscelids, but are not so common or well developed in *Aptenodytes* or *Eudyptes* species that also form crèches. Species that normally do not form crèches like *Spheniscus spp*., yellow-eyed penguins and little penguins (*Eudyptula minor*) do not have feeding chases. Regarding the second prediction, no studies have tested the prevalence of feeding chases at different breeding densities or in crèches of different sizes within a species. In relation to the third prediction, in chinstrap penguins chases do not always lead out of the crèche. Almost all feeds occurred inside the colony in one-chick families, as do at least half of those in two-chick families (Bustamante et al. 1992). Similarly, in Adélie penguins feeding away from the colony is more common in two-chick than one-chick situations (Boersma & Davis 1997). As interference from foreign chicks should not be dependent on brood size, this hypothesis cannot explain why in one-chick broods feeding outside the colony is less frequent and feeding chases are less frequent (Bustamante et al. 1992; Boersma & Davis 1997), and why similar patterns were found in two-chick broods following the temporary experimental removal of one chick (Moreno et al. 1996).

Summing up, observational data do not provide much support for the hypothesis that feeding chases occur because they reduce competition from foreign chicks or interference from territorial adults.

Chases Facilitate Parent-Offspring Recognition

Parents could potentially recognise their chicks by the latter's propensity to run after them (N.J. Volkman & S.G. Trivelpiece personal communication, cited in Lundberg & Bannasch 1983). This hypothesis predicts (1) that chases should be more common in species with crèching behaviour because chicks that abandon the nest site cannot be recognized by their location. It also predicts (2) that chases should be independent of brood size, as the need to recognize offspring once they are in a crèche is independent of whether there are one or two chicks; and (3) chases should take place before the first feed. In accordance with the first prediction chases are present in species with crèching behaviour, but are not common in all of them (see above). Contrary to the second prediction chases are also clearly associated with two-chick broods. In addition, in contradiction to the third prediction many feeding chases in the chinstrap (Lundberg & Bannasch 1983; Bustamante et al. 1992), Adélie (Lundberg & Bannasch 1983; Boersma & Davis 1997) and gentoo penguins (Lundberg & Bannasch 1983) take place after the first feed (i.e. after any offspring recognition would already have taken place).

If chases are a means whereby parents recognize their own chicks, we have to assume that chicks cannot be recognized in a less costly way. Vocal cues, however, allow offspring to recognize their parents in the Adélie penguin (Penney 1968; Davis & McCaffrey 1989). Although chicks may beg for food from adults other than their parents, they are often aggressively repelled both in the chinstrap penguin (Bustamante et al. 1992) and in the Adélie penguin (Boersma & Davis 1997). This demonstrates that adults recognize foreign chicks by means other than the chase. Even when foreign chicks participate in chases, they very rarely obtain any food, indicating that they are not able to deceive the adults. In chinstrap penguins, Bustamante et al. (1992) observed nine individually marked chicks participating in feeding chases with adults that were not their parents and none obtained a feed. In conclusion, predictions from this hypothesis are not supported by observational evidence and it is unlikely that feeding chases are necessary for offspring recognition.

Chases Reduce Sibling Competition and Improve the Efficiency of Food Transfer

Müller-Schwarze and Müller-Schwarze (1977) and later Thompson (1981) suggested that chases temporarily separate siblings in two-chick broods, avoiding unnecessary and wasteful sibling competition and ensuring the

efficient feeding of both chicks. This hypothesis predicts that (1) chases should be uncommon in species raising a single chick. (2) In those raising two chicks chases should be more common in two-chick broods than in one-chick broods, in which no sibling separation is necessary. (3) Parents should also be more inclined to run when their offspring are closer together than when they are further apart (as they can feed one chick without interference from its sibling). (4) Feeding chases should not take place if only one of the chicks from a two-chick brood is present at the arrival of the parent. (5) Chases should tend to separate siblings and parents should wait until siblings are separated before they start feeding one chick. (6) Chases should create a symmetric distribution of food within the brood.

Feeding chases are rare or less developed in *Aptenodytes* and *Eudyptes* species that raise only one chick, in accordance with our first prediction. In agreement with the second prediction, both in the Adélie (Thompson 1981; Boersma & Davis 1997) and in the chinstrap penguin (Bustamante et al. 1992) chases are more frequent in two-chick than in one-chick broods. Supporting the third prediction feeding chases in the Adélie penguin are more likely to occur when siblings are less than 0.5 m apart than when they are farther apart (Boersma & Davis 1997). The fourth prediction is supported by an experimental study by Moreno et al. (1996) which showed that chases did not take place when only one sibling of a two-chick brood was present at the arrival of the adult. Bustamante et al. (1992) found that chases in which the two siblings participated ended with the separation of the chicks before being fed in only half of the instances, which to some extent in disagrees with prediction number 5. However, better data by Moreno et al. (1996) demonstrated that chasing intensity drops dramatically and food transfer rate increases after siblings are separated, thereby supporting prediction number 5 (Figure 1). In support of the last prediction, Boersma & Davis (1997) showed that in Adélies the chick that is fed tends to alternate after each feeding chase, and one sibling monopolized all feeds in only 12% of meals. They suggested that chases create a more symmetric distribution of food within the brood.

Observational and experimental data are in strong agreement with the predictions from this hypothesis. The hypothesis does not explain why, apart from Pygoscelids, other species raising two chicks do not rely on feeding chases to reduce sibling competition and transfer food efficiently. A possible reason why temperate species of penguins do not exhibit feeding chases is the difference in food availability. At the high latitudes where Pygoscelid penguins breed, food is more abundant than it is at lower latitudes. There is a considerable amount of evidence that food is often limited for temperate penguins (Boersma 1978; Boersma et al. 1990). When food is more limited

feeding chases might become too energetically costly, so it may not be surprising that temperate penguins do not have well-developed feeding chases.

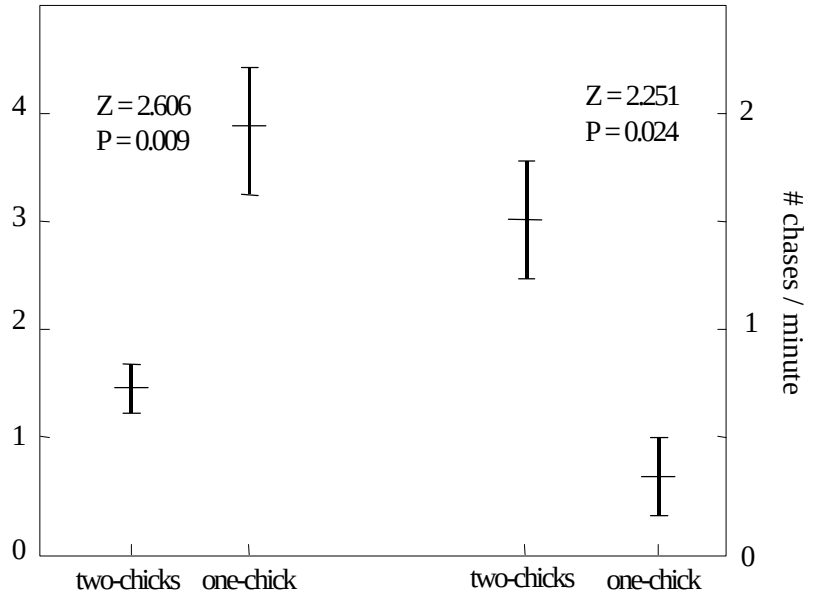

Figure 1. Effects of sibling separation on feeding and chasing rates in the chinstrap penguin. Modified from Moreno et al. (1996). Two-chicks refers to the first part of a feeding chase, when both chicks were chasing, whereas one-chick refers to the final part of a chase when only one chick still followed the parent. Results of Wilcoxon matched-pairs tests; n = 9.

Chases Facilitate Brood Reduction

In direct opposition to the previous hypothesis, feeding chases could be a mechanism to create asymmetries and facilitate brood reduction if they lead to preferential feeding of the strongest chick when food is scarce (Lundberg & Bannasch 1983). In any case, feeding chases cannot be considered as the main brood reduction mechanism in Pygoscelid penguins because they do not occur during the guarding stage, when brood reduction is common, and can only operate at the crèche stage, when chick mortality is low.

Most of the general predictions of this hypothesis are the same as those of the 'Efficient Food Transfer Hypothesis' (see above). They only differ in that

this hypothesis predicts an increase in feeding chase intensity and more asymmetric food distribution within broods when food is limited.

As with the 'Efficient Food Transfer Hypothesis', the observational data are in agreement with the general predictions of this hypothesis. There are, however, no adequate data to test if chases are more frequent, or food distribution more asymmetric, when food is limited. In the Adélie penguin, Boersma and Davis (1997) found that the largest chick was fed first more often in broods where size differences were obvious, but the larger chick did not obtain a greater number of feeds. Bustamante et al. (1992) describe a case of brood reduction during the crèche stage in a situation in which a single adult was feeding two chicks. On two occasions chick A chased the most and obtained all the feedings. Chick B was found dead a few days later with a very low weight indicating starvation.

Mortality during the crèche stage was rare in the Adélie at Cape Bird and chicks over 30 days had very little likelihood of dying (Davis & McCaffrey 1986). In this situation, feeding chases played no role in brood reduction. On the other hand, chicks in two-chick broods of chinstrap penguins at Deception Island had a 0.6% daily mortality rate during the crèche stage (Moreno et al. 1994), and most mortality was due to starvation. Under this scenario feeding chases could facilitate brood reduction by providing an asymmetric distribution of food.

Observational evidence does not allow us to reject this hypothesis completely, but brood reduction being so uncommon during the crèche stage suggests that it cannot be the main cause of feeding chases.

Adults Initiate Chases to Avoid Harassment by their Chicks

Lundberg and Bannasch (1983) suggest that chases could be the result of parents being unable to cope with the intense begging activity of their offspring. Chicks are always fed in front of the adult while begging at the tip of the parent's bill. Chicks push against each other to gain a feeding position and frequently interrupt feeds by pushing in front of the chick being fed.

Although this hypothesis is usually considered as a proximate cause of feeding chases, harassment avoidance could be considered a function in itself, if harassment had a negative effect on the well-being of the parents (Moreno et al. 1996). Also, factors other than harassment by chicks (acoustic stimulation, proximity between siblings and to the parent) could be the proximate factors that initiate feeding chases.

Specific predictions from the 'Harassment Avoidance Hypothesis' are that (1) feeding chases should increase with chick age, because heavier competing chicks will be more difficult to separate; (2) the initiation of chases should be associated with active competition between siblings (siblings pushing against each other to gain a feeding position) and not merely with the distance between them; (3) duration of chases should be a consequence of the intensity of parental reaction, with no relation to the time it takes to separate the two siblings; (4) the propensity to feed after a chase should not depend on whether siblings have become separated, but merely on whether or not they compete.

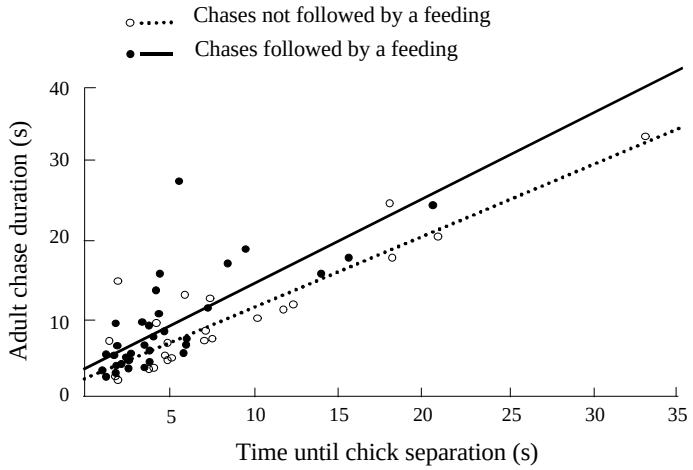

Figure 2. Time parents spent running as a function of the time it takes for the siblings to be separated during a feeding chase. Data are from chinstrap penguins in Deception Island (modified from Moreno et al. 1998). The two regression lines represent chases followed by a feeding ($y = 3.87 + 1.09x$, $F = 42.64$, $P < 0.001$, $R = 0.75$, $n = 35$), and chases not followed by a feeding ($y = 2.63 + 0.91x$, $F = 95.47$, $P < 0.001$, $R = 0.89$, $n = 27$).

In chinstrap penguins chases do not increase with chick age (Bustamante et al. 1992) and chases are frequently initiated without clear signs of sibling competition; when siblings are less than 1 m apart and away from their parent (Moreno et al. 1998). The time the parent spends running is determined by the time it takes until siblings are separated, which would not be the case if the parent ran just as a reaction to harassment by chicks. If the parent stops briefly (i.e. less than four seconds) after chicks become separated, the second chick will frequently catch up, but the chase will not be followed by a feeding (Figure 2). Parents avoid delivering food in the presence of two begging

chicks, independently of their competitive disposition (Moreno et al. 1998). In the Adélie penguin, feeding chases were more likely to occur when siblings were less than 0.5 m apart than when they were further apart (Boersma & Davis 1997).

The specific predictions of this hypothesis are not supported by the observational data from the chinstrap penguin; the only species for which data to test the predictions are adequate.

Chases Allow Parents to Assess the Nutritional Status of their Offspring

By provoking a feeding chase the parent could evaluate how hungry the chicks are and thereby determine how much food to give them (Thompson 1981). The parent could decide how much food to give its offspring and how much to keep and, in the two-chick situation, how to divide the food between the two chicks. Information regarding nutritional status is required because adults feed chicks independently of their mates and do not know when each chick has received its last feeding. In addition, feeding frequency by penguins is low (usually less than once per day), making it difficult to track changes in offspring need.

The hypothesis predicts that (1) chasing effort by chicks is a good index of hunger. (2) Feeding chases should take place both in species raising one chick and those raising or two chicks; and (3) in those typically raising two chicks, in both one-chick and two-chick broods.

Thompson (1981) showed experimentally in Adélie penguins that chick persistence in a chase was a function of the time since the last feed, in agreement with prediction number 1. This relationship between hunger and persistence has also been observed in chinstraps (J. Moreno personal communication). Bustamante et al. (1992) indicate that this hypothesis predicts that chases should be most obvious prior to the first feed of a meal, which was not the case in their study of chinstrap penguins. Once chick hunger state has been ascertained, further chasing seems wasteful, but parents could still use chases between successive feedings as a way of testing if the amount of food transferred to that chick has reduced its hunger level. The apparent lack of feeding chases in single-brooded species contradicts the second prediction. In partial agreement with the third prediction there are some chases in one-chick broods, as observed both in the Adélie (Boersma & Davis 1997) and in the chinstrap penguin (Bustamante et al. 1992), which take place mainly after the first feeding. This hypothesis predicts (4) that a

chick that has been recently fed should not be as persistent in a chase as a sibling that has not been fed. There are currently no data to test this prediction, but Bustamante et al. (1992) observed that in some instances (6 out of 26) the arrival of a parent of a two-chick brood elicited no response from one of the siblings. This chick could have been satiated and therefore not interested in chasing.

This hypothesis could explain why some feeding chases take place in one-chick broods of Pygoscelid penguins. If this was the main reason for feeding chases to evolve, however, one would expect them to be as frequent as in the two-chick broods, and to appear in species raising only one chick.

Chases are an Expression of Parent-Offspring Conflict

Chases could be an expression of parent-offspring conflict prior to chick independence. Parents will become increasingly reluctant to invest in (i.e. feed) chicks, which are themselves interested in maintaining the level of parental contribution (Trivers 1974). This hypothesis predicts (1) an increase in chasing intensity with chick age. It also predicts (2) that other indicators of parent-offspring conflict, such as frequency of begging or parental aggression toward chicks, should increase with chick age and the frequency of feedings should decrease. It does not predict that (3) there should be differences in feeding chases between species that raise one or two chicks, nor (4) between one- or two-chick broods. In the chinstrap penguin, Bustamante et al. (1992) found no significant increase in feeding chases or in any other indicator of parent-offspring conflict with chick age and no significant decrease in feeding frequency with chick age, in disagreement with predictions 1 and 2. No other studies have investigated in detail other expressions of parent-offspring conflict in penguins. The lack of chases in species raising a single chick and the low incidence in one-chick broods, although not inconsistent with this hypothesis, do not provide strong support.

Chases are a Secondary Expression of Other Evolutionary Pressures upon Chicks

Chases could be a secondary result of muscle training, exploring new ground, finding the location of departure routes to the sea or acquiring social experiences during the period before independence (Sladen 1958; Müller-Schwarze & Müller-Schwarze 1977; Thompson 1981). Although all of these

could be secondary consequences of feeding chases, none of them are clearly the main cause. Thompson (1981) found that chases in the Adélie penguin were directed preferentially to the beach that would be used as a departure route at fledging, but Bustamante et al. (1992) found no clear association between feeding chase direction in the chinstrap penguin and the location of the departure beach. In addition, chicks did not remain away from the crèche exploring new ground, but instead returned to the colony soon after the feeding interaction. Single chicks or groups of chicks also moved between crèches when no feeding chases were taking place, so chases are not a requirement for exploratory behaviour. Finally, locomotor training by chicks can be observed throughout the day, with chicks running and beating their flippers during intense bouts of activity in the absence of parents or any association with feeding chases.

DISCUSSION

Of the different hypotheses advanced to explain the occurrence of feeding chases in Pygoscelid penguins, several are clearly not supported by observational or experimental data. Feeding chases do not reduce competition from foreign chicks or territorial adults nor do they facilitate parent-offspring recognition. They are also not a clear expression of parent-offspring conflict. Harassment of parents by offspring does not seem to be the main proximate cause of feeding chases and the data provide little support for the hypothesis that feeding chases are a secondary result of other adaptive processes.

Feeding chases do appear to separate offspring in two-chick broods, so parents can feed them more efficiently. Observational and experimental data are in agreement with this hypothesis (Bustamante et al. 1992; Moreno et al. 1996, 1998; Boersma & Davis 1997). Efficient feeding is necessary, because food is sometimes dropped and never retrieved when parents try to feed two siblings that are begging and pushing against each other. Feeding chases are more common in two-chick compared to one-chick broods. They are also more common when both siblings of a two-chick brood are present compared to when only one sibling is present. Feeding visits by parents take longer, and parents need more time to transfer the same amount of food, when there are competitive interactions between chicks. Parents start to run as a direct consequence of the distance between siblings and stop as soon as siblings become separated. Chasing rate declines and food transfer rate increases when siblings become separated compared to when they are together. This hypothesis also explains why feeding chases are rare in species rearing only

one chick (e.g. *Aptenodytes, Eudyptes*), but it does not explain why other species of penguin raising two chicks (i.e. yellow-eyed penguins, little penguins and *Spheniscus* penguins) do not rely on feeding chases for efficient food transfer. It could be that they use other means to reduce the costs of food transfer (e.g. using their flippers to counteract sibling competition; Boersma 1991). It is also possible that chases cannot develop in breeding colonies typically sited within areas of dense vegetation (e.g. yellow-eyed penguins, little penguins and *Speniscus* penguins), rugged topography (e.g. crested penguins) or inside caves (e.g. little penguins). Even in Pygoscelid penguins feeding chases tend to be uncommon when colonies are situated in rugged topography (J. Moreno personal communication).

Feeding chases might amplify existing chick asymmetries and additionally facilitate brood reduction in cases of food scarcity, but only during the second half of the nestling period. Although brood reduction could be an adaptive advantage, it is unlikely to be the primary reason for feeding chases. Brood reduction is only reasonable as an explanation of feeding chases in situations in which laying parents cannot easily predict food availability during the crèche period. Food supply could be difficult to predict because of fluctuations in food levels within the season or because of the death of one of the parents. In both situations, parents might not know during the initial breeding stages (incubation to guarding) whether they could raise one or two chicks to fledging. Most brood reduction in chinstrap and Adélie penguins takes place during the guarding stage, before feeding chases start (Davis & McCaffrey 1986; Moreno et al. 1994). This reduces the possible role of brood reduction as a general explanation for feeding chases in Pygoscelid penguins. Feeding chases could, however, still have a secondary brood-reducing function in some instances. For example, seal predation causes relatively high adult mortality in chinstraps at Deception Island and brood reduction during the crèche stage is common. Therefore, feeding chases could facilitate brood reduction in this case.

Feeding chases could possibly be used by parents to assess the nutritional status of their offspring. For instance, Thompson (1981) and J. Moreno (unpublished data) found that persistence in a chase by a chick is proportional to its hunger level. In this way, feeding chases could be one part of a costly begging display in Pygoscelid penguins. It has not been proved, however, that parents use this information either to regulate food distribution between siblings, decide how much food to keep for themselves, or to adjust provisioning effort. This hypothesis can explain why there are feeding chases in some one-chick broods (something not explained by the 'Efficient Food Transfer Hypothesis'). If feeding chases are part of a begging signal, they are probably one of the few cases of offspring solicitation in which the signal is

forcibly extracted from the offspring by the parents. This hypothesis also does not explain why feeding chases have only evolved in Pygoscelid penguins, and why other penguin species rely on alternative begging signals to assess the nutritional status of their offspring.

FUTURE DIRECTIONS

Current research on feeding chases in penguins has shown that they facilitate the efficient transfer of food from parent to offspring in two-chick broods of Pygoscelid penguins. It is still unclear, however, whether feeding chases could occasionally facilitate brood reduction, and if they are also a component of an honest begging signal. Future research should try to address why feeding chases do not occur in other species raising two chicks, for example in yellow-eyed penguins, little penguins or *Spheniscus* penguins, in which there should also be a need for efficient food transfer. It would also be interesting to know more about the feeding chases described in *Aptenodytes* and *Eudyptes* penguins.

Feeding chases are likely to be a costly behaviour. Penguins may spend up to 14% of the feeding visit in chases, and running necessarily entails some energetic cost for both parents and offspring. Chases take chicks away from the protection of the crèche, which might increase predation risk (Boersma & Davis 1997). Future studies should try to measure the cost of feeding chases, both in terms of the energetic cost of running and the increase in predation risk. The costs associated with the extra time spent during the feeding interaction and food dropped to the ground should also be determined. Unfortunately, this is not an easy task because parents will not feed their chicks when they are not allowed to run (e.g. if they are kept inside an enclosure; J. Moreno personal communication).

To know if feeding chases play a role in brood reduction, it would be necessary to compare situations in which food is and is not limited. Feeding chases should be more frequent in years when food is scarce, but one would have to experimentally control for chick hunger level (which would increase with decreasing food provision). It would be possible to study feeding chases and food distribution in two-chick broods in which one parent has accidentally died, or to perform experiments by temporarily removing one parent (although it may also be necessary to know if parents are aware whether their mate is still provisioning the chicks, other than through chick hunger level). Chicks could also be directly provided with extra food to manipulate hunger level.

Feeding chases could be used by parents to gather information on long-term offspring need. The important point is whether parents use such information in their provisioning behaviour. Future studies should address whether parents retain some food in their stomach when chasing persistence is low. This could be estimated with ultrasonography. In addition, it is of interest to determine whether parents modify the amount of time devoted to resting and foraging depending on the persistence of chick feeding chases. Studying in detail the feeding chases that take place in one-chick broods, which cannot be related to efficient food transfer, could give some indication of whether parents use feeding chases as an honest begging signal.

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