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Feeding Behavior, Size Asymmetry, and Food Distribution in Magellanic Penguin (*Spheniscus magellanicus*) Chicks

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How food is distributed among siblings has long been of theoretical importance because the interests of siblings differ (Trivers 1974). The manner in which food is apportioned among siblings appears to be important in the determination of chick mortality patterns. One of the factors that could be affecting this food distribution is the size relationship between siblings. Penguins vary in their degree of hatching asynchrony, egg-size dimorphism, and fledging success (Lamey 1990). In *Spheniscus* penguins, hatching asynchrony creates size asymmetries that can lead to brood reduction (Lamey 1990, Boersma 1991, Boersma and Stokes 1995).

Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina, show high variability in breeding success among years, mainly as a result of changes in food availability (Boersma et al. 1990). During years with low food availability, most pairs raise no offspring or only one as a result of the starvation of one or both chicks (Boersma and Stokes 1995). When one sibling dies, the surviving chick receives all the food brought to the nest by the parents, resulting in an increased growth rate (Boersma 1991). We describe the feeding behavior of Magellanic Penguin chicks, quantify the way food brought to the nest is apportioned among siblings, and analyze how this distribution relates to chick size asymmetries.

Study area and methods.—The study was conducted in the Punta Tombo Provincial Reserve, Chubut, Argentina (44°02'S, 65°11'W), during January 1990 and 1991. Punta Tombo is the site of the largest continental colony of Magellanic Penguins (Boswall and McIver 1975), with 225,000 breeding pairs (Boersma et al. 1990). Magellanic Penguins have a seasonal breeding schedule in which they begin returning to the colony in late August and early September, and lay two eggs in October that are laid three to four days apart (Boersma et al. 1990). Eggs are always nearly equal in size with an average difference of 5 g between the larger and smaller eggs (Boersma and Stokes 1995). Chicks hatch in November approximately two days apart, and fledge in late January and February. Both adults defend the nest site, incubate eggs, and feed the chicks. Their prey include small fish such as anchovies (*Engraulis anchoita*), hakes (*Merluccius hubbsi*), silversides (*Austroaterina sp.*), and squids (*Illex* sp.; Gosztonyi 1984). Chicks used in this study were between the ages of 35 to 80 days.

We made observations during the morning between 0700 and 0900, and during the evenings between 1800 and 2200, which are the times of peak activity in the colony (Boersma unpubl. data). We chose nests by following an individual, at a distance of 5 to 20 m, that was returning from the sea to its nest. We followed an average of seven penguins per day during 30 and 20 days in January 1990 and 1991, respectively. To determine if chicks were fed inside or outside nests, we sampled 76 bush and 34 burrow nests along four transects. We counted the number of feeding events inside and outside nests.

Once an adult arrived at a nest, we weighed both chicks with 3- and 6-kg spring scales (25- and 50-g increments) and estimated mass to the nearest 10 g. Chicks in January generally weigh more than 1 kg. We marked the larger chick with a dark spot on the throat. We made feeding observations from behind bushes 3 to 7 m away. During the feeding, we recorded the position and behavior of the chick that received food and considered a meal had ended when 10 min had elapsed from the last regurgitation. We then reweighed both chicks and marked them with fiber-tape bands. Chicks waited as long as 5 min to resume begging. We checked the nests where observations were made, and weighed the chicks every five days until the end of the breeding season to determine changes in size asymmetries.

We defined the amount of food brought to the nest as the sum of the mass gain by both chicks at the end of the meal. To describe the size relationship between siblings we used an "asymmetry index" (AI), defined as the mass of the smaller chick as a percentage of the mass of the larger chick. We defined a reversal of AI when the size asymmetry changed between nest checks. The index is 100% when siblings are equal in mass. We defined asymmetric broods as the ones with an index lower than 75%, and symmetric broods as the ones with an index equal or higher than 75%. To analyze the distribution of food between siblings as a function of time during the meal, we divided each meal in four stages. We defined each stage as the period of time in which the parent distributed 25% of the total feeds between both siblings.

Results.—Of the total penguins followed to their nest ($n = 172$), only 23% had a two-chick brood. The

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TABLE 1. Percent of meal as indicated by percent of regurgitations and percent mass gain (±SD, with *n* in parentheses) of larger chick in asymmetric and symmetric broods.

	Percent regurgitations	Percent mass gain
Asymmetric	77.8 ± 14.4 (13)	75.1 ± 18.7 (12)
Symmetric	49.1 ± 11.7 (13)	51.2 ± 11.3 (23)

remaining 77% led to empty nests or nests with only one chick. We observed feeding behavior in 26 of the 39 nests with two chicks (20 bush and 6 burrow nests). In the remaining 13 nests we could not see adult-chick interactions. We weighed chicks before and after feeding in 35 nests.

Most chick feedings occurred outside the nest in both bushes (80%, $n = 76$, $X^2 = 27.84$, df = 1, $P = 0.001$) and burrows (88%, $n = 34$, $X^2 = 19.88$, df = 1, $P = 0.001$). For bush nests, the percentage of feedings occurring inside and outside the nest varied with bush size (Fisher exact test, $P = 0.015$). In small bushes, chicks were fed outside 96% of the time ($n = 25$), while in big-bush nests chicks were fed outside in 65% of the cases ($n = 20$).

Once the adult started regurgitating to one chick, the other chick typically tried to obtain some food, often interrupting the food transfer. We observed at least one of these interruptions in each of the nests sampled during 1991 ($\bar{x} = 12.7$ ± SD of 25.0, $n = 9$, range 1-79). As a result of interruptions, adults stopped regurgitating or some food was dropped. Once food was dropped, it was not retrieved by either chicks or adults. No pecking or aggressive interactions were observed in any of the 39 broods.

The amount of food brought to the nest varied, with a mean of 739.0 ± 271.1 g (range 5-1,400, $n = 35$). The mean number of total regurgitations per visit to both chicks was 20.6 ± 8.9 (range 4-48, $n = 26$). Larger chicks received significantly more regurgitations than smaller chicks (Wilcoxon test, $z = -2.76$, $n = 26$, $P = 0.005$). Similarly, the mass gain for larger chicks at the end of the feeding period was significantly higher than for smaller chicks (Wilcoxon test, $z = -2.45$, $n = 35$, $P = 0.014$). Average mass gain per meal was 424.6 ± 178.4 g for the larger chick ($n = 35$) and 314.4 ± 174.8 g for the smaller chick ($n = 35$).

The mean percentage of feeds per meal obtained by the larger chick in asymmetric broods differed significantly from the mean percentage of feeds obtained by the larger chick in symmetric broods (Mann-Whitney *U*-test, $U = 11.0$, $n = 13$ and 13, $P < 0.001$; Table 1). The mean percentage of mass gained per meal by the larger chick was significantly higher for asymmetric than for symmetric broods (Mann-Whitney *U*-test, $U = 46.5$, $n = 12$ and 23, $P < 0.002$; Table 1). Similarly, the differences in both the number of regurgitations received and the mass gained by each sibling during the meal were positively correlated with an increase in within-brood size asymmetry (no. regurgitations, $r = -0.66$, $P < 0.001$, $n = 26$; mass gain, $r = -0.58$, $P < 0.001$, $n = 35$).

TABLE 2. Food distribution (percent of feeds) between larger and smaller chicks in asymmetric ($n = 13$) and symmetric ($n = 13$) broods, as function of time during a meal. Each stage defined as period of time during which parent fed both siblings 25% of total regurgitations.

	Stage of the meal (%)			
Chick type	0-25	>25-50	>50-75	>75-100
Asymmetric brood				
Larger	86.8	82.0	74.2	59.4
Smaller	13.2	18.0	25.8	40.6
Symmetric brood				
Larger	56.2	43.7	49.6	39.1
Smaller	43.8	56.3	50.4	60.9

The order in which chicks were fed varied among broods with different degrees of size asymmetry. In asymmetric broods, the first feeds were mostly to the larger chick, and the smaller chick received little food. The smaller chicks were increasingly successful in getting food later in the meal ($X^2 = 17.73$, df = 3, $P = 0.001$; Table 2). In symmetric broods, however, the distribution of food throughout the meal was relatively even and constant. When stages of the meal were compared, no significant differences were found in the number of regurgitations received by both chicks ($X^2 = 3.09$, df = 3, ns; Table 2). Moreover, in some cases the smaller chick obtained more food than the larger chick.

Chicks in symmetric broods (AI ≥ 75%, $n = 17$) varied little in their size relationship during the month, although size reversals did occur. Asymmetric broods (AI < 75%, $n = 6$) showed greater variation in their size relationships. In the two broods with the greatests size difference between the chicks (AI < 40%), both of the smaller chicks died.

Discussion.—Magellanic Penguin chicks hatch two days apart and size asymmetries usually develop (Boersma and Stokes 1995). There is considerable variability in the degree of size asymmetry between siblings by the late stages of the breeding cycle. During the late stage, which coincides with the peak food demands from chicks, many second chicks die (Boersma et al. 1990, Boersma and Stokes 1995). Factors that determine the way in which food is apportioned between siblings play a central role in chick survival.

Analysis of mass changes showed that heavier chicks receive more food (Boersma and Stokes 1995). Food distribution between chicks varies according to the size asymmetry of broods, suggesting that late in the chick stage the size of chicks is important in determining how much food each is fed. In symmetric broods, Magellanic Penguin chicks obtain food from the parent evenly throughout the meal.

Late in the Magellanic Penguin chick stage, when size differences are large, the larger chick gains a better position with respect to the adult and gets most of the food, so that there is an unequal distribution of the meal. It could be argued that the larger mass gain of larger chicks reflects a higher capacity to take food because of the larger body size. Smaller chicks, however, kept on begging, suggesting they did not get adequate food. The difference in mass gain between siblings after each meal increased with the degree of size asymmetry within broods, supporting the hypothesis that food distribution between siblings is mostly determined by chick size differences. In broods with large asymmetries the smaller chick usually starves (Boersma unpubl. data). Similar results were observed in the Jackass Penguin (*Spheniscus demerus*), where the likelihood of starvation by the smaller chick is significantly higher than for the larger chick (Seddon and van Heezik 1991a, b).

Our observations show that late in the chick stage, most food is obtained by the larger chick. Whether this is due solely to competition or is due to some degree of parental preference is not clear. Evidence for competition among siblings has been reported for several penguin species: Yellow-eyed Penguin (*Megadyptes antipodes;* Richdale 1957); Galapagos Penguin (*S. mendiculus;* Boersma 1976); Adelie Penguin (*Pygoscelis adeliae;* Davis and McCaffrey 1989); Jackass Penguin (Seddon and van Heezik 1991b); and *Eudyptes* penguins (Lamey 1990). Boersma (1991), however, suggested that food allocation between Magellanic Penguin chicks also may be the outcome of parental manipulation. This mechanism may be important when chicks differ less than 25% in mass. In older chicks when there are large differences in size, which appears to correlate with larger chicks being more mobile and vocal, competition between chicks probably is very important.

Whatever the mechanisms of food distribution involved, the size relationship between sibling chicks is an important determinant of which chick is fed. Larger chicks are more successful at getting food. Our results suggest that, in Magellanic Penguins, chick size asymmetries are important in determining meal size late in the chick stage. The degree of size asymmetries and food availability ultimately may explain why parents that have chicks with large size asymmetries rear no chicks or only one, but never two chicks.

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