

Ari Ueno · Tetsuro Matsuzawa

Food transfer between chimpanzee mothers and their infants

Received: 2 September 2002 / Accepted: 4 March 2004 / Published online: 3 July 2004
© Japan Monkey Centre and Springer-Verlag 2004

Abstract Food sharing among chimpanzees is known to occur particularly between mothers and infants and has been proposed to be a form of parental investment. To explore the function of food sharing, it is essential to know how and what is transferred to an infant from its mother. We investigated details of interactions leading to food transfer and characteristics of items transferred in three mother–infant (< 2 years old) pairs in captivity. We gave one kind of fruit or vegetable to a mother and observed interactions between the mother and her infant. Tested items consisted of familiar and novel foods for infants. Two patterns of direct food transfer, so-called sharing, were recognized: (1) “infant-initiated sharing” in which the infant attempted to take food and the mother did not resist, and (2) “mother-initiated sharing” in which the mother spontaneously offered a part of her food without the infant’s attempts to take it. There were clear differences in the characteristics of items transferred in these two patterns of sharing. In infant-initiated sharing, palatable parts of the same food that the mother was eating were transferred. In contrast, in mother-initiated sharing, only unpalatable parts of food in the mother’s possession were transferred. Mothers seemed to be reluctant to give nutritious foods to their infants during this study period. Infants, rather than mothers, were responsible for initiating and experiencing the diversity of adult foods in chimpanzees.

Keywords Food transfer · Food sharing · Mother–infant · Chimpanzee

Introduction

Chimpanzees are one of the non-human primates in which food sharing has been studied in great detail under both field and laboratory conditions (Hiraiwa-Hasegawa 1990a; McGrew 1975; Nishida and Turner 1996; Nissen and Crawford 1936; Silk 1978, 1979). In chimpanzees, it occurs both in mother–infant pairs and among adults. However, food sharing between mother and infant is different from that between adults in some ways (McGrew 1975; Silk 1978). Among adults, shared food is almost always limited to animal material. On the other hand, mothers frequently share not only animal food but also a variety of plant foods with their offspring. Previous studies have suggested that food sharing facilitates an infant’s learning of the diversity of adult foods available in its environment (Hiraiwa-Hasegawa 1990b; Lefebvre 1985). When the frequency of food sharing was compared between abundant or easy-to-process and rare or hard-to-process foods, it was revealed that rare or hard-to-process foods were shared more often and for longer period than abundant or easy-to-process foods in mother–infant chimpanzees (Hiraiwa-Hasegawa 1990b; Nishida and Turner 1996; Silk 1978). Chimpanzees take 3–4 years to complete weaning (Hiraiwa-Hasegawa 1990a), and until that time infants spend much time with their mothers, sharing intense physical and social bonds. For chimpanzee infants, mothers are likely the most accessible source of information about adult foods.

To explore the function of food sharing, it is essential to know how and what is shared. However, few studies have focused on this issue in detail (Nissen and Crawford 1936; Plooj 1984; Nishida and Turner 1996). Furthermore, even though previous studies mentioned the variety of patterns of food sharing, ranging from a

Electronic Supplementary Material Supplementary material is available in the online version of this article at <http://dx.doi.org/10.1007/s10329-004-0085-9>

A. Ueno (✉)
Section of Social Behavior, Primate Research Institute,
Kyoto University, 41 Kanrin, Inuyama,
Aichi 484-8506, Japan
E-mail: ueno@pri.kyoto-u.ac.jp
Tel.: +81-568-630546
Fax: +81-568-630564

T. Matsuzawa
Section of Language and Intelligence,
Primate Research Institute, Kyoto University,
Aichi, Japan

kind of theft to offering, they often did not analyze those patterns separately. This might be partly because chimpanzees were rarely observed to offer their foods voluntarily, in particular in the wild (e.g., Nishida and Turner 1996). In a preliminary report (Ueno and Matsuzawa 2003), we tried to clarify the details of interactions that lead to direct food transfer between a mother and infant in a group of captive chimpanzees. Based on the methods described in the preliminary report, we focused on collecting quantitative data of mother–infant interactions and identifying the characteristics of items transferred between them. The present study also discusses the implications and function of food sharing between chimpanzee mothers and infants.

Methods

Subjects

Subjects were three infants born in 2000 at the Primate Research Institute, Kyoto University, and their mothers (Table 1). This was the first time for all three mothers to give birth. Infants were nursed by their mothers, and they spent their daily life with their mothers and the other group members in the indoor facilities and outdoor compounds of the Primate Research Institute. The group consisted of 14 individuals: three adult males and five adult females in addition to the three mother–infant pairs. The group was divided into two or three parties each day for time sharing of a large outdoor compound.

The infants were subjects of a research project on the behavioral and cognitive development of chimpanzees (e.g., Matsuzawa 2003) and have had contact with human researchers about 6 days a week from just after their birth. They were fed various kinds of vegetables and fruits (e.g., carrots, bananas, apples, strawberries, and peaches) and monkey chow three times a day in addition to other food items (e.g., grapes, raisins, and peanuts) given as reward for other experiments. Infants started to eat solid foods occasionally from around 6 months of age. The portion size of their daily solid foods gradually increased, and infants had their own daily meals regularly beside their mothers from around 13 months of age. However, infants continued to suckle and sleep with their mothers during the night throughout this study period. Care and use of chimpanzees adhered to the “Guide for the Care and Use of Laboratory Primates of the Primate Research Institute (2002).”

Procedure

We conducted the study when the infants were less than 2 years old: Ayumu from 10 to 23 months of age, Cleo from 10 to 21 months of age, and Pal from 8 to 20 months of age. Each mother and infant pair was tested separately in a face-to-face situation by testers twice a week on average. We tested a variety of food items longitudinally, but only one kind of food item was tested in each trial. The test was carried out only once a day for each pair, 2–3 h after feeding time. This means that the inter-test interval was more than 24 h.

The tests were part of a series of experiments on behavioral and cognitive development. Each mother and infant pair was introduced to an experimental booth (1.8×1.8×2.0 m) from the outdoor compound. The tester entered the booth with the mother and infant and sat beside them. Then he passed a food item to the mother. A trial was terminated when the mother finished eating and possessed nothing in her mouth or hands. All interactions between mother and infant were recorded with two video cameras placed outside the booth and a camera (SONY, CCD-MC100) held by the tester inside the booth.

Tested food items

The food items tested on each subject pair are listed in Table 2. These items were fruits and vegetables including familiar items ($n = 22$ in total) and novel items ($n = 25$ in total) for the infants. Familiar items were foods that mothers and infants had often eaten before in their daily meals or as experimental rewards. Novel items were foods that infants had neither seen nor eaten before. Ten of the 25 novel food items were novel for both infants and mothers. Novel items were given only once, and familiar ones were given up to three times. Among the tests with familiar items, the tests with novel items were inserted about once every 2 weeks. The amount of food given was consistent across items and trials as defensible portions for mothers, ranging in weight from 50 to 300 g.

Data analysis

We analyzed the data of trials in which a mother ate a given food. In total, 56 trials including 41 different food items were analyzed for Ai–Ayumu (A-A), 18 trials

Table 1 Mother–infant subjects of the present study

Mother		Infant			Study period (age in years:months)
Name	Age	Name	Sex	Date of birth	
Ai	25	Ayumu	Male	24 April 2000	0:10–1:11
Chloe	21	Cleo	Female	19 June 2000	0:10–1:09
Pan	18	Pal	Female	9 August 2000	0:08–1:08

Table 2 Tested foods and the outcome of each trial in three mother–infant pairs. Food items are arranged in the order of vegetables to fruits. I, M, B, and – represent trial outcomes as follows: I infant-initiated sharing; M mother-initiated sharing; B both infant- and mother-initiated sharing within a trial; – no sharing. *Italic letters* indicate that more than two incidents of either infant-initiated or mother-initiated sharing occurred within the same trial

Food item	Mother–infant pair		
	Ai–Ayumu	Chloe–Cleo	Pan–Pal
Familiar			
Carrot	–, I		–, I
Eggplant	–, –		
Cucumber	–, –		–, I
Okra	I, –, I		
Green pepper	–, M		
Tomato	–, –		–, I
Onion	–		
Pepper	B		
Grape	M, M	–	
Strawberry	–, –, –		–, –, I
Apple	–, –, –		I
Japanese pear	–, –		
Banana	–, –		I
Ume	–		
Peach	I	–	
Persimmon	–	–	–
Grapefruit	–		–
Kiwi fruit	M, B	–	–, –
Mandarin	–		I, –
Gumdrop	–		
Blueberry		–	
Orange		I	
Total no. of different food items	20	8	10
Total no. of trials	35	8	17
Novel			
Paprika ^a	–	–	
Asparagus ^a	–		
Wax gourd	–		
Pekoros ^a	–		
Radish ^a	I		I
Maize	I	–	
Turnip			I
Watermelon	–	–	–
Honeytame ^a	–	I	
Pineapple	–		–
Mango	–	M	–
Fig	B	–	–
Cherry	–		
Litchi ^a	–		–
Loquat	–	–	–
Pear	M	M	M
Lemon	I		
Muscat	M		
Kabosu orange ^a	I		
Starfruit ^a	B		
Plum	–	–	–
Papaya	–		
Melon		–	
Hime-apple ^a			B
Kumquat ^a			–
Total no. of different food items	21	10	12
Total no. of trials	21	10	12

^a Novel for both mothers and infants; the others were novel only for infants

including 18 different food items for Chloe–Cleo (C-C), and 29 trials including 22 different food items for Pan–Pal (P-P; Table 2). The mothers and infants were given their normal diet throughout the period of testing.

From the video records, we scored the behavioral measures listed in Table 3 by the continuous recording method. We also scored incidents of direct food transfer from mother to infant and transferred food parts (fruit, seed, skin, calyx, or stalk). We also analyzed the palat-

ability of directly transferred food parts and made comparisons between familiar and novel food items and between the first and second half of the study.

Food sharing

Direct transfer of any part of a food item to the infant from the mother was considered as food sharing in the

Table 3 Mother's and infant's behavior in the context of mother's eating of food. *I* infant behavior, *M* mother behavior, *Y* observed at least once during the experimental period, *N* never observed during the experimental period

Behavior	Definition	Mother–infant pair		
		Ai–Ayumu	Chloe–Cleo	Pan–Pal
Approach (I)	Move close to mother within 30 cm distance	Y	Y	Y
Swing a hand (M)	Swing an empty hand in front of approaching infant with vocalizing, sometimes with slapping the infant	N	N	Y
Inspect (I)	Look at mother's face or food within 30 cm distance for more than 3 s, sometimes with protruding lower lip	Y	Y	Y
Attempt to take food (I)	Extend hand, try to mouth food, grasp mother or try to open mother's palm. Any of these behaviors separated by more than a 3-s interval was considered as an independent attempt	Y	Y	Y
Extend hands (I)	Put outstretched hands with palm open within 30 cm of mother's food or chewing mouth	Y	Y	Y
Try to mouth food (I)	Move with mouth open to within 30 cm of mother's food or chewing mouth	Y	Y	Y
Grasp mother (I)	Grasp mother's face or hand holding food	Y	Y	Y
Try to open mother's palm (I)	Grasp mother's palm holding food, and pull mother's fingers outward	Y	N	Y
Leave infant's attempts (M)	Do not reject infant's attempts but maintain the position while continuing the ongoing behavior or without moving	Y	Y	Y
Reject infant's attempts (M)	Drive off infant, conceal food or keep away food	Y	Y	Y
Drive off infant (M)	Push away or hold infant's face or hands, coinciding with infant's attempt	Y	Y	Y
Conceal food (M)	Cover the possessed food with hands or change position to turn the back on infant	Y	Y	Y
Keep away food (M)	Move mouth or hands holding food away from infant, coinciding with infant's attempt	Y	Y	Y
Point at mother's food (I)	Stretch out an index finger and move it within 30 cm of mother's food or chewing mouth	Y	Y	Y
Show facial expression (I)	Show grin- (Plooij 1984) or grimace-like facial expression (Goodall 1986) with nothing in mouth	Y	N	Y
Vocalize (I)	Vocalize "whimper" (Plooij 1984)	Y	N	Y
Poke infant (M)	Poke infant gently with fingers or a part of food	Y	Y	Y
Offer food (M)	Present a part of food close to infant with hands or mouth while looking at infant and maintain this position for more than 3 s or until the infant takes the food	Y	Y	Y
Receive offered food (I)	Take the offered food part with a mouth or a hand and then mouth it	Y	Y	Y
Ignore offered food (I)	Look at the offered food part, look aside, and do not take it	Y	N	Y
Scrounge (I)	Pick up a piece of food dropped on a mother's/an infant's fur or the floor from a mother's mouth and mouth it	Y	Y	Y

present study. When infants took away at least a part of the food directly from the mother (but did not necessarily eat it), we recorded the incident as sharing. Every direct transfer of a food part was counted as one incident of sharing; however, such transfers that occurred continuously within 3-s intervals of each other were recognized as one incident.

Palatability of transferred food parts

Directly transferred food parts were classified into two categories, palatable or unpalatable for the mother. Palatable items were defined as the same food parts eaten by mothers. Unpalatable items were food parts

that the mother did not eat during a trial, such as seed, skin, calyx, and stalk.

Results

Patterns of food sharing

The average trial length was 133 s (SD 98) for A–A, 106 s (SD 86) for C–C, and 187 s (SD 105) for P–P. After food was passed from the tester to a mother, the infant approached and inspected the mother from close proximity in 94% (97/103) of the trials. Then, mothers and infants showed various behaviors over the food as listed in Table 3. In the context of a mother's eating of

food, an infant took a part of the mother's food not only through food sharing but also through scrounging. Mothers often threw away a part of the food, such as seed, skin, calyx, and stalk. Such discarded food parts fell onto the mother's/infant's fur or the floor. Infants scrounged them not necessarily with interaction with their mothers (Table 3). In contrast to scrounging, food sharing necessarily involves interactions with the mother. We further focus on food sharing rather than scrounging.

Of the behaviors that immediately affect food sharing, we especially focused on six (Table 3): infant's attempts to take food, mother's leaving the infant as it attempts to take food, mother's rejection of infant's attempts, mother's offering, infant's reception of offered food, and infant's ignoring of offered food. All of the incidents of food sharing were assigned to one of two patterns, "infant-initiated sharing" or "mother-initiated sharing," according to the preceding interactions. Infant-initiated sharing is defined as food sharing that is initiated by the infant's attempts (Fig. 1a). Mother-initiated sharing is defined as food sharing that is initiated by the mother's offering (Fig. 1b). These two patterns of sharing were mutually exclusive. Multiple incidents of food sharing could occur in one trial. In total, 49 incidents of sharing were observed over 33 of the 103 test trials in the three mother–infant pairs. In 5 of the 33 trials with food sharing, both infant-initiated and mother-initiated sharing were observed within the same trial. In 6 trials, 2–3 incidents of either infant-initiated or mother-initiated sharing occurred within the same trial (Table 2).

An infant attempted to take the food from its mother in 62% (64/103) of the trials (Table 4). The mother rejected the infant's attempts to take some of the food in 78% of these trials (50/64). In 66% (33/50) of these trials, infants repeated their attempts after the rejection. As a result, an infant's attempts to take food succeeded in 23% (24/103) of the trials. This pattern of sharing, which was classified as infant-initiated sharing, was observed in 12 trials for A–A, 2 trials for C–C, and 10 trials for P–P.

Mothers offered a part of the food to their infants in 16% (16/103) of the trials (Table 4). Infants took the offered food parts in 88% of these trials (14/16). In the remaining 2 trials (one in A–A and another in P–P), the infant ignored the offered food parts. As a result, a part of the food was directly transferred to an infant through mother's offering in 14% (14/103) of the trials. This pattern of sharing, which was classified as mother-initiated sharing, was observed in 10 trials for A–A, 2 trials for C–C, and 2 trials for P–P.

Palatability of shared food

To investigate the value of each shared food, we compared the palatability of transferred food parts in all incidents of food sharing between the two patterns of

sharing (Table 5). In total, 34 incidents of infant-initiated sharing and 15 incidents of mother-initiated sharing were observed in the three mother–infant pairs.

Through infant-initiated sharing, infants took palatable food items that their mothers ate in 94% (32/34) of the incidents. In other words, infants (Ayumu and Pal) took unpalatable parts of food only twice through infant-initiated sharing. In one of these two incidents, Ayumu took a seed of a peach at 14 months of age. In the other incident, Pal took skin of a mandarin at 12 months of age.

In contrast, through mother-initiated sharing, what infants took was restricted to unpalatable food items in all of the 15 incidents. In other words, the food parts the mother offered to her infant were restricted to unpalatable parts of foods. Thus, there was a clear and significant difference in palatability of shared food parts between the two patterns of sharing in all three mother–infant pairs (Fisher's exact probability test; $P < 0.001$, two tailed).

Familiarity with shared food

Familiarity with food items is assumed to be an important factor affecting the behavior of both infants and mothers, thus the occurrence of food sharing. To compare the occurrence of food sharing between familiar and novel foods, we investigated the frequency of trials with either pattern of food sharing for familiar and novel foods. When we compared the frequency of trials in which infant-initiated sharing occurred (Table 6), there was no significant difference between familiar foods and novel foods in any of the mother–infant pairs (Fisher's exact probability test; $P = 0.33$ for A–A, $P = 1$ for C–C, $P = 0.45$ for P–P, two tailed). As to mother-initiated sharing (Table 5), the frequency of trials with this pattern of sharing did not differ between familiar foods and novel foods in A–A (Fisher's exact probability test; $P = 1$, two tailed). In the other two pairs, mother-initiated sharing occurred in just two trials each, and only with novel foods.

However, we found that one of the infants, Ayumu, attempted to take novel foods in the possession of his mother significantly more often than familiar ones (Fisher's exact probability test; $P < 0.01$, two tailed). This was not merely because he had more opportunity to do so for novel foods than for familiar foods. The trial length did not differ statistically between familiar (mean = 110, SD = 44) and novel foods (mean = 172, SD = 144, Mann–Whitney U -test; $P = 0.08$), nor between the trials with Ayumu's attempts (mean = 150, SD = 116) and without them (mean = 106, SD = 50, Mann–Whitney U -test; $P = 0.09$).

The frequency of trials in which mothers offered food did not differ between familiar and novel foods in A–A (Fisher's exact probability test; $P = 1$, two tailed). Chloe offered a part of her food in two trials only for novel foods, and Pan did so in two trials for novel foods and in

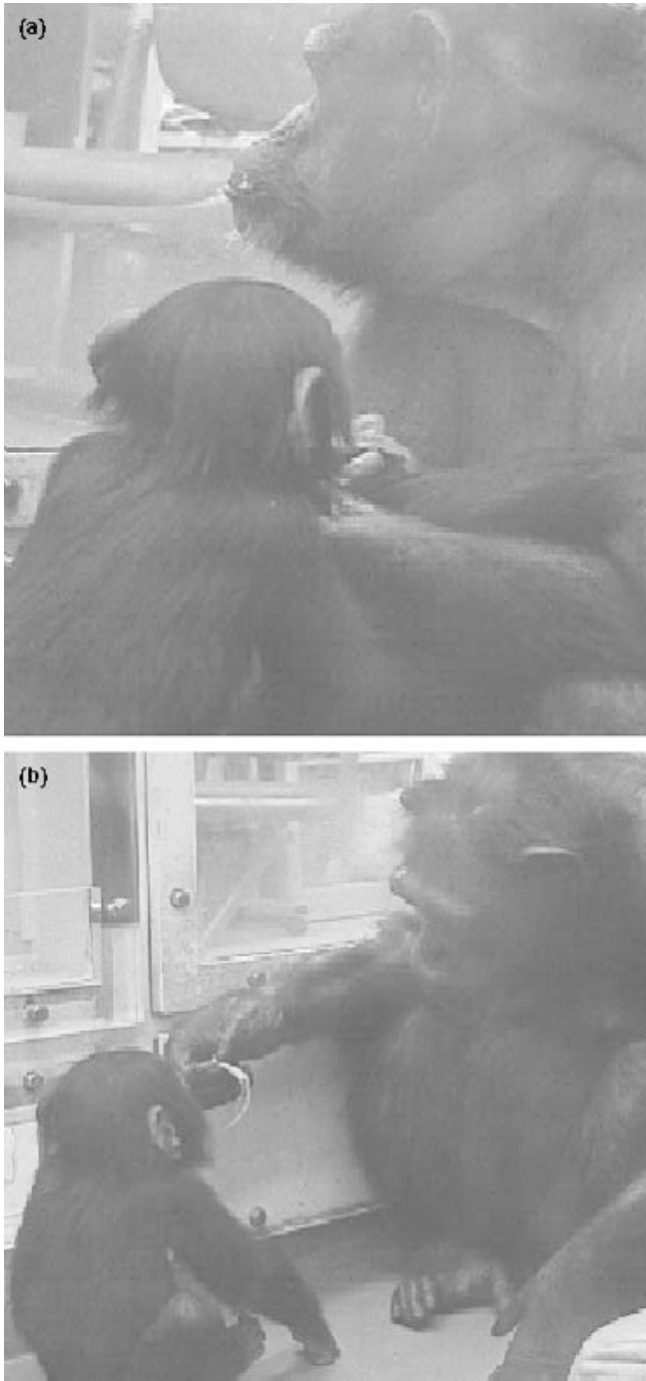


Fig. 1a, b Outcome of a trial with Ai–Ayumu pair. **a** The infant (Ayumu) approached the green pepper held by his mother (Ai), extended his hand, pulled it toward his mouth, upon which infant-initiated sharing occurred. **b** Ai offered a skin of fig to Ayumu after she chewed it, upon which mother-initiated sharing occurred

one trial for familiar foods. Two infants, Ayumu and Pal, ignored the offered part of foods in two trials only for familiar foods. In one of those two trials, Ayumu ignored a persimmon seed when he was 17 months old. In another trial, Pal ignored a calyx of strawberry when she was 18 months old. Cleo never ignored the offered parts of foods.

To investigate the developmental changes, we divided the data into the first half (~14 months of age) and the second half (15 months of age~) of the study. We found no statistical differences between the first and second phases in the frequency of trials with infant-initiated sharing, mother-initiated sharing, infant's attempts, mother's offering, and mother's rejection (two-tailed Fisher's exact probability test; $P = 0.10, 0.73, 1, 0.50, 0.17$, respectively, for A–A; $P = 1, 0.10, 0.14, 0.10, 1$, respectively, for C–C; and $P = 0.11, 0.53, 0.69, 1, 0.60$, respectively, for P–P).

However, one infant behavior, ignoring offered food, was observed only in the second phase in two infants. The infants ignored the offered food in only one trial in the whole study period, when they were 17 and 18 months old, respectively (see section on “Familiarity of shared food” for details).

The other two infant behaviors, showing a grin- or grimace-like facial expression and whimper vocalization (see Table 3), were also observed only in the second phase. Two of the three infants, Ayumu and Pal, first showed facial expressions, Ayumu when 17 months old and Pal when 15 months old. They first vocalized whimper when Ayumu was 23 months old and Pal was 17 months old. Cleo neither showed the facial expression nor vocalized during this study period. Ayumu showed the facial expression in 1 of 56 test trials, for persimmon, and he vocalized in 1 trial, for grapefruit. Pal showed the facial expression in 2 of 29 test trials, for hime-apple and banana. Accompanying the facial expression, she also vocalized in a trial for banana, and it was the only trial in which her vocalization was noted. In both trials with Pal's facial expression, either infant-initiated or mother-initiated sharing occurred. In both trials with Ayumu's facial expression or vocalization, food sharing did not occur. In a trial with Ayumu's facial expression, however, he ignored the offered food (persimmon seed) even though his mother offered it.

Discussion

In this study, two patterns of food sharing were recognized according to the interaction patterns leading to them. Both infant-initiated and mother-initiated sharing were observed in all three mother–infant pairs. In contrast, mothers have been rarely observed to offer foods voluntarily to their infants in wild chimpanzees (e.g., Nishida and Turner 1996). This might be partly because of restrictions in observational conditions. The conditions in this study enabled us to see all of the events at extremely close proximity. Though mother-initiated sharing was observed in a small number of instances compared to infant-initiated sharing in the present study, as well, it was revealed that infant-initiated and mother-initiated sharing differed significantly from each other in the characteristics of the food parts transferred.

Table 4 Distribution of trials by behavior and by the two patterns of sharing across mother–infant pairs. The values in *parentheses* represent the number of test trials for each mother–infant pair

Outcome of trials	Mother–infant			Total (<i>n</i> = 103)
	Ai–Ayumu (<i>n</i> = 56)	Chloe–Cleo (<i>n</i> = 18)	Pan–Pal (<i>n</i> = 29)	
Infant attempts to take food	35	11	18	64
Mother leaves	6	1	7	14
Mother rejects	29	10	11	50
Repetition of attempt	19	8	6	33
Mother leaves	4	0	3	7
Mother offers	11	2	3	16
Infant receives	10	2	2	14
Infant ignores	1	0	1	2
Infant-initiated sharing	12	2	10	24
Mother-initiated sharing	10	2	2	14

Table 5 The number of incidents in which either palatable or unpalatable food parts were directly transferred from a mother to her infant through infant- or mother-initiated sharing

Pattern of food sharing	Palatability	Mother–infant pair			Total
		Ai–Ayumu	Chloe–Cleo	Pan–Pal	
Infant-initiated sharing	Palatable	17	2	13	32
	Unpalatable	1	0	1	2
	Total	18	2	14	34
Mother-initiated sharing	Palatable	0	0	0	0
	Unpalatable	11	2	2	15
	Total	11	2	2	15

Table 6 Distribution of trials (as percentage) by behavior and by food-sharing pattern across mother–infant pairs according to whether the food was familiar or novel. Values in *parentheses* represent the actual numbers of trials used to calculate the percentages

Behavior/pattern of food sharing	Ai–Ayumu			Chloe–Cleo			Pan–Pal		
	Familiar	Novel	Significance	Familiar	Novel	Significance	Familiar	Novel	Significance
Infant attempts	49 (17/35)	86 (18/21)	*	63 (5/8)	60 (6/10)	NS	59 (10/17)	67 (8/12)	NS
Mother rejects	94 (16/17)	72 (13/18)	NS	100 (5/5)	83 (5/6)	NS	70 (7/10)	50 (4/8)	NS
Mother offers	20 (7/35)	19 (4/21)	NS	0 (0/8)	20 (2/10)	NS	6 (1/17)	17 (2/12)	NS
Infant ignores	14 (1/7)	0 (0/4)	NS	0 (0/0)	0 (0/2)	NS	100 (1/1)	0 (0/2)	NS
Infant-initiated sharing	17 (6/35)	29 (6/21)	NS	12 (1/8)	10 (1/10)	NS	41 (7/17)	25 (3/12)	NS
Mother-initiated sharing	17 (6/35)	19 (4/21)	NS	0 (0/8)	20 (2/10)	NS	0 (0/17)	17 (2/12)	NS

* $P < 0.01$; NS no significance (Fisher's exact probability test, two tailed)

Through infant-initiated sharing, the infant was able to take the same food part as that eaten by the mother. In contrast, through mother-initiated sharing, the infant had the opportunity to take only what the mother did not eat. Such offered food parts were assumed to be meaningless for the infant in the sense of nutrition and taste, because these were often offered after the mother had eaten all of the palatable parts of them. Only the attempts of infants resulted in their taking the same food part as their mothers were eating. While the results were not consistent in all three mother–infant pairs, one infant, Ayumu, tried to take novel food items in more trials than familiar ones. He did not do this merely because he had more opportunities to do so for novel foods than for familiar ones. The trial lengths

did not differ between novel and familiar foods, or between the trials in which he showed attempts and those in which he did not. Furthermore, two of the three infants ignored the offered food parts only for familiar foods in the second half of study period. The infants seemed to discriminate familiar from novel food items and responded accordingly by seeking novel items more frequently. From a field study comparing the frequency of infant-initiated sharing of familiar versus novel foods, Hiraiwa-Hasegawa (1990a) reported that novel foods were shared more often than familiar foods between chimpanzee mothers and infants (0–5 years old). In the chimpanzee, infants, rather than mothers, might be responsible for initiating and experiencing the diversity of adult foods and for gathering

information about them. This has also been noted for baboons (King 1994).

Mothers rejected their infants in 72% of trials when the infant attempted to take the mother's food. The mothers never offered palatable parts of their foods on their own initiative. Chimpanzee mothers seemed to be reluctant to give nutritious foods to their infants during this study period in which the infants were less than 2 years old. What purpose, then, does mother-initiated sharing serve? One of the possibilities is that it serves merely to distract the infant from the mother so that she can eat in peace. However, the mothers often offered food parts to their infants after they finished eating the food. For example, one mother, Ai, ate all the palatable parts of a grape by herself and then offered a grape stalk to her infant. It is unlikely that mother-initiated sharing is merely a means to keep the infant from interfering with the mother while she eats. The other possibility is that any part of food offered by the mother helps an infant to become familiar with that food item and facilitates the acceptance of it. Although mother-initiated sharing occurred in a few trials in two of the three mother–infant pairs (C–C and P–P), it was observed only for novel foods in those pairs. It is possible that unpalatable food parts offered by the mothers helped infants to become familiar with those novel foods. As another possibility, we propose that any of a mother's offerings work to maintain an infant's motivation to take adult foods actively. A mother's offering of unpalatable food parts may maintain an infant's interest in its mother's food, especially in novel ones, and enhances the infant's attitude toward learning about the diversity of the mother's foods.

The infants' behavioral repertoires in the context of their mothers' eating of food increased with their development. They showed the grin- or grimace-like facial expression and vocalized whimper in the second phase of the present study (15–21 months of age on average). These behaviors were recognized as kinds of infants' begging for food in previous studies (McGrew 1975; Nishida and Turner 1996). In two of four trials with these begging behaviors, food sharing occurred. The grin- or grimace-like facial expression and whimper vocalization have often been observed once the infants pass 2 years of age in the same experimental situation (A. Ueno and T. Matsuzawa, unpublished data). With the increase of an infant's behavioral repertoire, the interaction between mother and infant is expected to become more complex. The patterns of food sharing may also become more complicated with the infant's development.

In sum, in the present study, three features of infant-initiated sharing during the first 2 years of life in the chimpanzee were clearly shown: (1) almost all of the food parts that an infant took were palatable parts of the mother's food; (2) at least one of three infants attempted to take the mother's foods more often for novel foods than for familiar ones; and (3) even though rejected repeatedly by their mothers, the infants continued to

attempt to take the mother's food, and such repeated attempts led to success. Chimpanzee infants might learn about a diversity of foods and expand their food repertoire based on their own initiatives. On the other hand, mother-initiated sharing had the following three features: (1) all of the food parts transferred to an infant were unpalatable parts of the mother's food; (2) the frequency of a mother's offering of unpalatable food parts did not differ between familiar and novel foods; and (3) mothers continued to offer parts of foods throughout this study period. Mother-initiated sharing might have a complementary role to infant-initiated sharing, facilitating the interactions between mother and infant and enhancing the infant's motivation to gather the information about the mother's foods. Food sharing between chimpanzee mother and infant has been reported to occur frequently until around 3–4 years of age (Hiraiwa-Hasegawa 1990b; Nishida and Turner 1996). The present study shows that two patterns of food sharing, infant-initiated and mother-initiated sharing, had already emerged in infants less than 2 years old. The infants just started to beg for the mothers' foods with a grin- or grimace-like facial expression and whimper vocalization around at 2 years of age. Based on the two patterns of food sharing observed in this study, it is possible that mother and infant may develop more complex patterns of food sharing.

Acknowledgements This research was funded by Grants-in-Aid for Scientific Research from the MEXT (no. 12002009 to T. Matsuzawa, no. 10COE2005 to O. Takenaka, and 21COE program A14 to Kyoto University). We thank M. Tomonaga, M. Tanaka, and all the colleagues who participated in the research project on behavioral and cognitive development of infant chimpanzees for their support of this research. We also thank A. Mori, M.A. Huffman, and H. Sugiura for their valuable advice. Thanks are also due to N. Maeda and K. Kumazaki for their daily care, and to A. Kato, J. Suzuki, S. Goto, C. Hashimoto, and K. Matsubayashi for their veterinary treatment of chimpanzees.

References

- Goodall J (1986) *The chimpanzees of Gombe: patterns of behavior*. Harvard University Press, Cambridge, Mass.
- Hiraiwa-Hasegawa M (1990a) A note on the ontogeny of feeding. In: Nishida T (ed) *The chimpanzees of Mahale mountains*. Tokyo University Press, Tokyo, pp 279–283
- Hiraiwa-Hasegawa M (1990b) Role of food sharing between mother and infant in the ontogeny of feeding behavior. In: Nishida T (ed) *The chimpanzees of Mahale mountains*. Tokyo University Press, Tokyo, pp 267–275
- King BJ (1994) The information continuum—evolution of social information transfer in monkeys, apes, and hominids. School of American Research Press, Santa Fe, N.M.
- Lefebvre L (1985) Parent–offspring food sharing: a statistical test of the early weaning hypothesis. *J Hum Evol* 14:255–261
- Matsuzawa T (2003) The Ai project: historical and ecological contexts. *Anim Cogn* 6:199–211
- McGrew WC (1975) Patterns of plant food sharing by wild chimpanzees. In: Kondo S, Kawai M, Ehara A (eds) *Contemporary primatology*. Karger, New York, pp 304–309
- Nishida T, Turner L (1996) Food transfer between mother and infant chimpanzees of the Mahale mountains national park, Tanzania. *Int J Primatol* 17:947–968

- Nissen H, Crawford M (1936) A preliminary study of food-sharing behavior in young chimpanzees. *J Comp Psychol* 22:383–419
- Plooij FX (1984) The behavioral development of free-living chimpanzee babies and infants. Ablex, Norwood, N.J.
- Silk JB (1978) Patterns of food sharing among mother and infant chimpanzee at Gombe National Park, Tanzania. *Folia Primatol* 29:129–141
- Silk JB (1979) Feeding, foraging, and food sharing behavior of immature chimpanzees. *Folia Primatol* 31:123–142
- Ueno A, Matsuzawa M (2003) Mother–infant interactions over foods and food sharing. In: Tomonaga M, Tanaka M, Matsuzawa T (eds) *Cognitive and behavioral development in chimpanzees—a comparative approach* (in Japanese). Kyoto University Press, Tokyo, pp 243–247