# RESEARCH ARTICLE

## Begging for Information: Mother–Offspring Food Sharing Among Wild Bornean Orangutans

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Transfer of solid food from mothers or other adults to dependent offspring is commonly observed in various primate species and both nutritional and informational benefits have been proposed to explain the function of such food sharing. Predictions from these hypotheses are tested using observational data on wild orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, Central Borneo, Indonesia. In 1,145 hr of focal observation and 458 recorded food interactions between four pairs of females with offspring it was found that virtually all transfers were initiated by the offspring and that younger infants solicited food more often and did so for a greater variety of items than older offspring. All offspring primarily solicited food that was difficult to process, i.e., inaccessible to them. Furthermore, the amount of food solicitation was negatively correlated with ecological competence. Hence food sharing seemed to be related to an offspring's skill level, as suggested by the informational hypothesis. In contrast, offspring did not solicit high-quality items more than low-quality items and food sharing did not peak around the age of weaning, as predicted by the nutritional hypothesis. Mothers were usually passively tolerant, allowing offspring to take food but hardly ever provisioned. Parent–offspring conflict concerning food sharing was only observed well after weaning. Thus, by taking food directly from the mother, young orangutans were able to obtain information about the affordances and nutritional value of food items that were otherwise out of their reach and could familiarize themselves with the mother's diet. In species such as orangutans or other apes, characterized by a broad diet that requires extractive foraging, informational food transfer may be vital for an immature to acquire complex feeding skills and adult diet. Am. J. Primatol. 70:533–541, 2008.     © 2008 Wiley-Liss, Inc.

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## INTRODUCTION

Food sharing and provisioning from parents or other caretakers to offspring occur in many mammals, especially social carnivores [Courchamp et al., 2002; Doolan & Macdonald, 1999; Mech et al., 1999]. The *nutritional hypothesis* suggests that by providing infants with additional nutrients, the transfer of solid food can increase growth rates and reduce the age of weaning. Among primates, food sharing with offspring may serve an additional function: transfer of information [Brown et al., 2004; Feistner & McGrew, 1989; King, 1991]. According to the *informational hypothesis,* obtaining food from older individuals may allow offspring to acquire information about dietary choices or food-processing skills and thus support learning [Brown et al., 2004]. The two hypotheses are of course not mutually exclusive. For example, by obtaining a highly nutritious and difficult-to-process food item, an immature may gain both important nutrients to complement its diet, as well as information about which part of the item is eaten and how it is processed. In addition to information or nutrient transfer, patterns of food sharing may also reflect conflict about rates of investment by food possessors [Brown et al., 2004] as predicted by *parent–offspring conflict theory* [Trivers, 1974].

Until now, most quantitative analyses on mother–offspring food sharing in primates have been conducted on callithrichids and chimpanzees, despite extensive long-term studies on other primates [Brown et al., 2004]. Food sharing in callithrichids and chimpanzees, however, may serve

different functions. In the cooperatively breeding callithrichids, infants appear to be almost entirely provisioned by parents and helpers when they begin to eat solid food; food transfer peaks around the age of weaning and involves mostly difficult-to-process foods [Feistner & Price, 1990, 2000; Rapaport & Ruiz-Miranda, 2002; Ruiz-Miranda et al., 1999]. Thus, food transfer is controlled by adults and by regularly obtaining food from multiple group members; callithrichid infants may both learn dietary preferences and increase their growth rates.

In chimpanzees, most food transfer occurs before weaning and also involves mostly difficult-to-process items [Hiraiwa-Hasegawa, 1990; Nishida & Turner, 1996; Silk, 1978]. Nishida and Turner [1996] showed that by the age of weaning, rates of solicitation were low and focused on a few items that remained difficult for the immatures to process. This study also found that it was primarily the offspring who controlled patterns of food sharing, whereas mothers merely reacted to their infants' solicitation. More recently, the same pattern was shown in a captive setting [Ueno & Matsuzawa, 2004]. Thus, food sharing in chimpanzees seems to be mainly related to learning about food and tends to be initiated by infants.

So far, little is known for apes other than chimpanzees [bonobos: Hashimoto & Furuichi, 2002; gorillas: Nowell & Fletcher, 2006]. Here we present the first quantitative observational study of food transfer between wild orangutan mothers and offspring, and use this data set to examine the function of such food sharing. Orangutans are well suited for such a study because of their semi-solitary lifestyle and long dependent period as well as their broad diet, which involves many hard and/or difficult-to-process food items [Galdikas, 1988; van Adrichem et al., 2006; van Noordwijk & van Schaik, 2005; Vogel et al., in press; Wich et al., 2004]. Being the only social model and caretaker for their offspring, mothers should be highly tolerant toward them and immatures could benefit from their presence to provide both information and nutrition before they reach feeding independence.

### Hypotheses and Predictions

Brown et al. [2004] present a set of predictions for patterns of food sharing. Here we list the ones testable with our data set. The *nutritional hypothesis* yields the following relevant predictions:

(1) Rates of food transfer are highest during the period of weaning to facilitate the latter.
(2) Offspring solicit more food items that are nutritionally rich and/or that they are unable to obtain for themselves compared with other items.

The *informational hypothesis* predicts that the rates of solicitation are related to the offspring's skill level, and thus:

(3) Solicitation rates should correlate negatively with (a) age and/or (b) ecological competence as immatures become more skilled in foraging.
(4) The variety of solicited food items should decline with (a) age and/or (b) ecological competence as more about the diet has been learned.
(5) Immatures solicit more food items that they are unable to process independently, regardless of their nutritional value.
(6) Immatures solicit rare food items more than common ones because rare food items are more likely to be unfamiliar to them.

*Parent–offspring conflict theory* [Trivers, 1974] predicts that:

(7) Mothers become less willing to share as offspring grow older.
(8) Mothers are less willing to share (a) high quality and/or (b) difficult-to-process items as these are more costly for them to give away.
(9) Mothers should terminate investment when they become pregnant again, and thus resist food solicitations by the weaned immatures.

We test all these predictions with a quantitative data set on orangutans. The results largely support the informational hypothesis, which may be typical for apes in general.

## MATERIALS AND METHODS

### Study Site, Period and Subjects

This study was conducted at the Tuanan field station (2°09′S, 114°26′E) in the Mawas Reserve, Central Kalimantan, Indonesia. The research area was approximately 725 ha and orangutan density was 4.25 individuals/km$^2$ [van Schaik et al., 2005]. The habitat consisted of lowland peat-swamp forest that has been subject to selective logging before the onset of continuous research in 2003. Detailed observations on food interactions were made from March to September 2005 and the main subjects were the four resident females with offspring (see Table I). Estimated ages ranged from 2 to almost 6 years and the oldest offspring was last seen nursing just before the start of this study. Age estimates were based on body size and locomotor competence on first encounter in 2003 [van Noordwijk & van Schaik, 2005].

Total focal observation time for all mother–offspring pairs was 1,145 hr. Because females were followed in the same period, sometimes on the same days, ecological factors such as food availability were similar for all subjects. Because one female, Sumi,

**TABLE I. Subjects, Estimated (est.) Time of Offspring Births, Total Focal Observation Time (Obs-*t*) in Hours and Number of Food-Related Interactions (inter.), Mean Sharing (Shar.) Rates and Percentage of Items Solicited**

| Female | Offspring, sex | Est. birth | Obs-*t*; inter. | Shar. rate±SD | % items sol. |
|---|---|---|---|---|---|
| Jinak | Jerry (JER), m | I[a] 2003 | 339; *145* | 8.84±9.1 | 45.8 (59[b]) |
| Sumi | Susi (SUS), f | II 2002 | 236; *184* | 15.21±9.1 | 47.4 (38) |
| Mindy | Milo (MIL), f | II 2001 | 345; *92* | 4.74±5.3 | 23.7 (59) |
| Kerry | Kondor (KON), f | II 1999 | 225; *37* | 3.11±3.9 | 12.2 (49) |

[a]I = 1st half of the year, II = 2nd half of the year.
[b]Number of items eaten by the mother.

occasionally foraged in a disturbed open habitat on plant species not available in the forest, 18.4 hr of her feeding time was not considered.

## Sampling Methods and Definitions

The animals were followed from the morning to the night nest for a maximum of 10 days in a row. The activities of both females and offspring were recorded with scan sampling every 2 min [Martin & Bateson, 1993]. All occurrences of social interactions between mother and offspring were described in the field and later labeled for analysis by A. J. Whenever the focal animals ate, the food species and the part eaten were recorded and the feeding technique was described [see also van Schaik, 1999, or www.aim.uzh.ch/orangutannetwork.html]. Observers were students from the Universitas Nasional Jakarta and the Universities of Utrecht and Zurich as well as trained local assistants. On every follow-up at least two observers were present and continuous dialogue and comparison of descriptions between them ensured completeness and agreement of the recordings.

The following operational definitions were employed:

*Feeding bout*: A continuous period of feeding within a feeding patch.

*Offspring-selected feeding*: The percentage of feeding bouts in which the offspring started to feed *before* the mother did in the same patch or fed altogether alone.

*Food items*: Different plant parts—fruits, flowers, mature leaves, young leaves, pith, inner bark (including phloem and cambium) and vegetative plant parts—of the same species were classified as different food items. Because of identification difficulty and similar feeding techniques, all species of figs, termites, and ants were lumped as one food item, respectively.

*Difficult and easy food*: Following Silk [1978], food items were divided into difficult (D) and easy food (E). D foods are defined per individual as those items that an immature was never observed to procure and/or process independently or that it tried to process but failed, such as those that require (a) strength to open or (b) dexterous manipulation to extract their edible portions efficiently. In contrast, E foods are any items that an immature had no difficulty in eating such as leaves and soft-shelled fruits.

*High- and low-quality food*: Following Nishida and Turner [1996], we classified food with high average caloric value or high average protein content, i.e., fruits, flowers and insects, as high-quality food, whereas leaves, pith, inner bark or other plant parts were classified as low-quality food [cf. Knott, 1998; McConkey et al., 2003].

*Food solicitation*: Any attempt by an immature to obtain food from its mother: reaching with its hand to her mouth or to the food in her possession, or holding her head and placing its mouth on hers. If this resulted in transfer of the food, or part of it, the solicitation was considered successful. If the immature stopped its attempt without getting a food part and started another activity the solicitation was considered over and unsuccessful. Begging by waiting with extended hand for the other to give was relatively rare. Instead, offspring usually took food out of their mother's hand or mouth without waiting for a reaction, comparable to a *relaxed claim* [*sensu* de Waal, 1989].

*Food sharing*: The transfer of a defendable food item from one food-motivated individual to another [Feistner & McGrew, 1989]. *Active sharing* (i.e., the mother giving food to a begging immature rather than allowing it to take) was recorded as well as *active resistance* (i.e., the mother turning her head or hand away, not letting go of a food item or even pushing away the offspring's hand). Transfers not classified as *active sharing* may be called *relaxed claims* [de Waal, 1989]. When both mother and offspring fed from the same large item, this was called *co-feeding*. Food transfers initiated by the mother by giving or bringing food to her offspring were called *offering*.

*Solicitation-, sharing- and success rates*: Following Nishida and Turner [1996] we defined solicitation and sharing rates as the percentage of maternal feeding bouts in which solicitation or sharing, respectively, occurred at least once. Furthermore, we measured rates of *solicitation* and *sharing per hour* of maternal feeding time. Because results were the same, only values of the bout rates are given.

*Success rates* were calculated as the percentage of single solicitation incidents in which food was transferred.

## Analyses

For between-subject comparisons of age-related differences we calculated mean rates for each off-spring using complete nest-to-nest follow days as unit of sampling. Because the hypotheses were directional (increase or decrease with age), one-tailed probabilities are reported. For within-subject comparisons of transfer of food items of different characteristics (high–low, difficult–easy) the unit of sampling was the food item, i.e., for each food item eaten by a female we calculated rates of solicitation, sharing, etc. by its her own offspring. This procedure takes into account individual variation in preferences among the offspring and, thus, in responses to the food items eaten by the mother. All statistical tests were non-parametric. Analyses were done using SPSS 14.0 with exact testing to avoid incorrect *P* values for small sample sizes. [Mundry & Fischer, 1998; Siegel & Castellan, 1988].

This research complied with protocols approved by the Indonesian Institute of Sciences (LIPI Research Permit No.: 1068/SU/KS/2005) and adhered to the legal requirements of Indonesia.

## RESULTS
### General Patterns of Food Transfer

Immatures co-fed from an item procured by the mother on 33 occasions, in most cases from pieces of termite-containing wood, large enough to accommodate two feeders. As the mother made this food available to the offspring, co-feeding was counted as a food solicitation, but because it was not taken from the mother, it was not counted as a transfer and thus co-feeding was not considered for success rates. The offspring tried to take food from the mother on 418 occasions, in 28 of which it was unclear whether food was transferred. From the remaining 390 observations, 344 (88.2%) resulted in food being transferred, i.e., were successful. Only 20 (5.1%) of all solicitations were actively resisted and only 8 (2.1%) of all transfers were active sharing. Hence, the vast majority of food transfers were relaxed claims. On only one occasion did a mother offer food to her offspring who did not take it. Five times, a mother took away food from her infant, always eating it herself afterwards. Thus, immatures generally controlled patterns of food transfer, whereas mothers were passive but tolerant, allowing high success rates.

The number of different items eaten by the females is given in Table I. A complete list of food items and rates of solicitation, sharing, etc. is available on request. For none of the subjects there were a significant relationship between food difficulty and quality, i.e., difficult-to-process food items were not more likely to be high-quality items, etc. ($\chi^2$: JER $\chi^2 = 1.73$, $df = 1$, $P = 0.19$; SUS $\chi^2 = 2.24$, $df = 1$, $P = 0.14$; MIL $\chi^2 = 0.31$, $df = 1$, $P = 0.58$; KON $\chi^2 = 0.21$, $df = 1$, $P = 0.65$).

### Nutritional Benefits

(Prediction 1): The nutritional hypothesis predicts food transfer to peak around weaning. To test this, rates of solicitation and sharing were compared between subjects. Mean sharing rates and estimated ages are given in Table I, mean solicitation rates in Figure 1. Approximate age of weaning was 5 years for KON, who had the lowest rates of food transfer. Over all subjects, there was a high *negative* correlation between estimated age and solicitation as well as sharing rates, albeit not significant (Spearman's $r_s = -0.8$, $n = 4$, $P = 0.18$). Thus, food transfer did not peak around the age of weaning.

(Prediction 2): The nutritional hypothesis predicts that offspring should solicit high-quality food more than low-quality food to get important nutrients. Yet, solicitation rates did not differ for high (H) and low (L) quality items for any of the subjects (Mann–Whitney *U* test: JER $n_1 = 44$ (H), $n_2 = 15$ (L), $z = 0.23$, $P = 0.83$; SUS $n_1 = 25$, $n_2 = 13$, $z = 0.35$, $P = 0.74$; MIL $n_1 = 43$, $n_2 = 16$, $z = 0.61$, $P = 0.58$; KON $n_1 = 37$, $n_2 = 12$, $z = 1.47$, $P = 0.28$). Items that offspring were unable to obtain independently, i.e., difficult food (D) should also be solicited more than easy food (E). Indeed, a significant difference was found for all four offspring (JER $n_1 = 20$ (D), $n_2 = 38$ (E), $z = 4.84$, $P < 0.0001$; SUS $n_1 = 15$, $n_2 = 22$, $z = 2.77$, $P < 0.01$; MIL $n_1 = 18$, $n_2 = 41$, $z = 3.01$, $P < 0.01$; KON $n_1 = 9$, $n_2 = 39$, $z = 2.21$, $P < 0.05$). Thus, immatures preferentially solicited difficult-to-process food but not nutritionally rich food.

In sum, prediction (1) was not supported and prediction (2) only in part. Thus, there were possible nutritional benefits of food transfer in providing access to otherwise unobtainable food parts, yet transfer did not focus on high-quality foods and the frequency was unrelated to weaning.

### Informational Benefits

(Prediction 3): Young, inexperienced offspring should solicit more food to gather information about items unfamiliar to them. (a) As shown above, in (1), there was a high negative correlation between estimated age and solicitation, as well as sharing rates, albeit not significant owing to the small sample size. However, as two subjects were very close in age and estimated ages are only a crude measure of an individual's skill-level, we looked for correlations with ecological competence: Orangutan mothers and their offspring forage as a pair and often feed in the
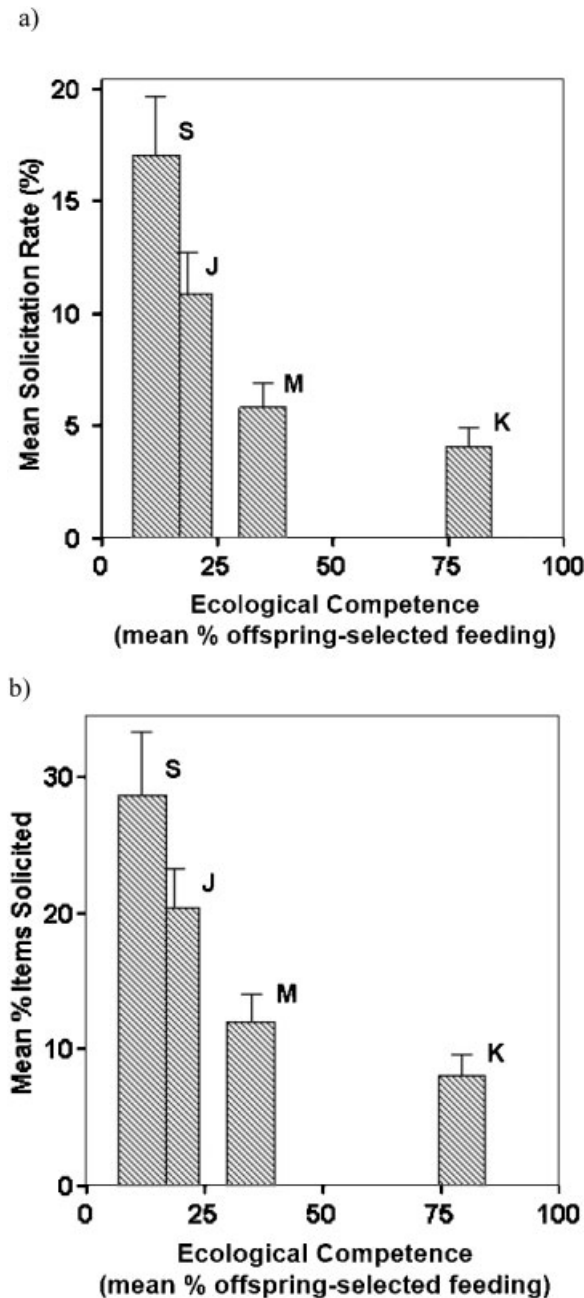
a)



b)



Fig. 1. Mean solicitation rates (a) and mean variety of solicited food items (b) are shown as a function of ecological competence for all subjects. Both correlations were significant ($P = 0.05$). Solicitation rates are percentage of maternal feeding bouts in which solicitation occurred. Variety of solicited food items is the percentage of items eaten by the mother that were solicited by the respective offspring. Ecological competence was measured in percentage of an offspring's feeding bouts in which it started to feed before the mother or altogether alone. Error bars represent one standard error of the mean. Names of the subjects are abbreviated by the first letter.

same patch, with inexperienced offspring following the mother [Jaeggi et al., in preparation.]. The amount of *offspring-selected feeding* was used as a measure of ecological competence as the offspring

recognized a food patch, showing food knowledge and food selection competence. (b) Mean solicitation and sharing rates were negatively correlated with the mean amount of offspring-selected feeding (Spearman: $r_s = -1.0$, $n = 4$, $P = 0.05$). This relation is shown in Fig. 1A) for solicitation rates. Hence, ecologically more competent offspring solicited less food from the mother.

(Prediction 4): The variety of solicited food items were predicted to decline with age as more of the diet has been learned. This variety is given in Table I as a percentage of items eaten by a female that were solicited by the respective offspring. There was significant variation in these percentages among the four subjects ($\chi^2$ test: $\chi^2 = 19.99$, $df = 3$, $P < 0.001$). (a) Pair-wise comparisons showed no significant difference between the two youngest offspring, who are close in age, as they each solicited a wider variety of items than each of the older ones. A trend for a further decrease was found between the two older subjects (JER/SUS: $\chi^2 = 0.02$, $df = 1$, $P = 0.89$; JER/MIL: $\chi^2 = 6.32$, $df = 1$, $P = 0.012$; JER/KON: $\chi^2 = 16.81$, $df = 1$, $P < 0.0001$; SUS/MIL: $\chi^2 = 5.84$, $df = 1$, $P = 0.016$, SUS/KON: $\chi^2 = 15.6$, $df = 1$, $P < 0.0001$; MIL/KON: $\chi^2 = 3.23$, $df = 1$, $P = 0.072$). Thus, the younger immatures solicited a wider variety of items eaten by their mother. As the variety of solicited items should decrease with experience and food knowledge, we also looked for correlations with ecological competence as defined above. (b) The variety of solicited items declined significantly with increased offspring-selected feeding (Spearman: $r_s = -1.0$, $n = 4$, $P = 0.05$). This is given in Figure 1B as mean percentages per follow-up day. Thus older, ecologically more competent offspring solicited fewer different food items.

(Prediction 5): As shown above, in (2), food items that offspring were unable to obtain independently were solicited more than easily obtained ones, regardless of nutritional value. Figure 2 shows mean solicitation rates for difficult and easy foods for all four subjects.

(Prediction 6): Offspring should solicit food items rarely eaten by the mother more often, because these are more likely to be novel for them. Thus, an offspring's solicitation rate should correlate negatively with the number of maternal feeding bouts on a particular item. However, no negative correlation was found for any of the subjects. On the contrary, some significant positive correlations were found (JER Spearman's $r_s = 0.377$, $P < 0.01$, $n = 59$ food items; SUS $r_s = 0.202$, $P = 0.225$, $n = 38$; MIL $r_s = 0.286$, $P < 0.05$, $n = 59$; KON $r_s = 0.161$, $P = 0.269$, $n = 49$).

In sum, predictions (3), (4) and (5) have been supported whereas prediction (6) was not supported. There were possible informational benefits of food transfer, especially for young, inexperienced offspring by acquiring items that they were not (yet)
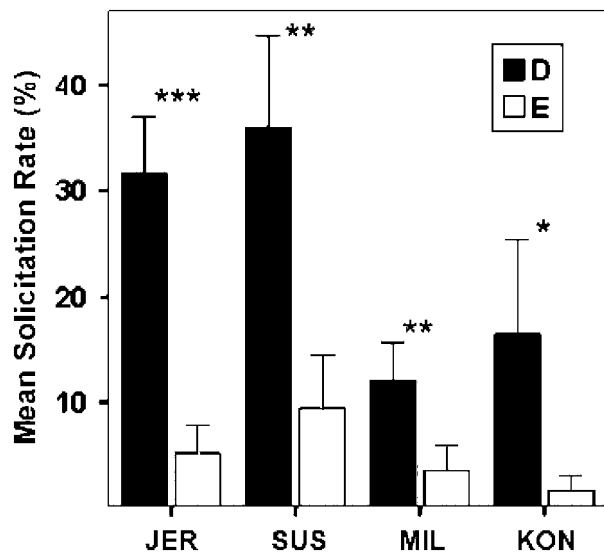
Fig. 2. Mean solicitation rates (+SE) for difficult-to-process (D) and easy (E) food items for the four subjects. M–W $U$ test: *$p < 0.05$; **$p < 0.01$; ***$p < 0.0001$.

able to process independently. Thus, rates of food transfer seemed to be related to an individual's skill level.

### Parent–Offspring Conflict

(Prediction 7): Parent–offspring conflict could result in lower success rates for older offspring. Yet, there was no significant correlation between solicitation success and age ($r_s = -0.4$, $n = 4$, $P = 0.325$).

(Prediction 8): To assess whether mothers selectively shared some foods more than others, success rates were compared for food items of different characteristics that were solicited by offspring. Because the overall success was relatively high (see above, only 46/390 solicitations were unsuccessful) all food items of interest were lumped by category (H/L, D/E) to provide better resolution. Depending on the sample size, within-subject $\chi^2$ tests with Yates correction or Fisher's exact probability tests were used. (a) *High-quality food*: Nutritiously rich food may be preferred by mothers and thus less readily released. However, for none of the subjects a difference in success rate for high-quality (H) or low-quality (L) food could be found (JER: H 81/105, L 16/20 successful, $\chi^2 = 0$, $df = 1$, $P = 1$; SUS: H 122/140, L 9/12, $\chi^2 = 0.54$, $P = 0.46$; MIL: H 67/74, L 3/3, Fisher's $P = 1$; KON never solicited low-quality food). (b) *Difficult food*: Difficult-to-process food may require considerable investment before ingestion, even for adults. Despite these potential costs for mothers, two subjects had significantly more success when soliciting difficult food and there was a clear trend for another subject (JER: D 85/102, E 12/23, $\chi^2 = 8.77$, $df = 1$, $P = 0.0031$; SUS: D 120/138, E 11/14, $\chi^2 = 0.21$, $P = 0.65$; MIL: D 66/71, E 4/6, Fisher's

$P = 0.09$; KON: D 20/21, E 2/5, Fisher's $P = 0.014$). Thus, prediction (8) was not supported. On the contrary, success rates were even higher for difficult-to-process food.

(Prediction 9): This prediction about termination of investment could be tested on only one mother–offspring pair. Agonistic interactions: In September 2005 Kerry showed swollen genitalia indicative of a new pregnancy [Rijksen, 1978]. She displaced KON from feeding patches on six occasions and they engaged in three severe physical fights. Thus, there was a significant increase in days with aggressive behavior (Fisher's exact probability $P < 0.05$). Time spent in close proximity ($< 2$ m) decreased from 43% in early 2005 to 18.5% in late 2005 and 12.4% in early 2006. Patterns of food transfer: Active resistance to the offspring's solicitation increased significantly from 3.6% in March–September 2005 to 45.5% in October 2005–May 2006 (Fisher's $P < 0.01$); hence, solicitation success dropped significantly, from 100 to 72.7% (Fisher's $P < 0.01$). Thus, there was increased aggression and increased resistance to food solicitations between one pregnant mother and her weaned offspring leading to increased distance and lower solicitation success, which supports prediction (9).

In sum, contrary to predictions (7) and (8), all mothers supported their offspring by readily sharing high-quality and difficult food items, thus responding to their offspring's solicitation. Conflict over rates of investment in one mother–offspring pair started as the female was pregnant with a new offspring, supporting prediction (9). This suggests that sharing food is in the interest of both mother and offspring, at least up to a new pregnancy.

### DISCUSSION

The younger, inexperienced immatures in this study solicited food more often and did so for a greater variety of food items than older offspring, and all immatures mainly solicited items that they had difficulty processing. Furthermore, this difference seemed to be related to ecological competence: offspring that were more competent in finding their own food solicited less from the mother. Thus, solicitation rates and variety of solicited items seemed related to the offspring's skill level, as predicted by the informational hypothesis. Predictions of the nutritional hypothesis were not supported. Orangutans did not solicit highly nutritious items more than low-quality ones, food transfer did not peak around the age of weaning and was almost always initiated by the offspring. Thus, food transfer in orangutans does not seem to be related to weaning, contrasting provisioning patterns found in cooperatively breeding callithrichids [Brown et al., 2004]. Of course infants also gain nutritional benefits from food transfers, especially by acquiring difficult-

to-process food. This may explain high solicitation rates for items that are both difficult –to process and high quality. However, many transfers involved only small amounts of food that was often pre-masticated (typically seeds stripped of most pulp) and thus probably retained little nutritional value. Similarly, captive chimpanzee mothers seem to transfer mostly unpalatable food parts to their offspring [Ueno & Matsuzawa, 2004]. Transferred food was at no time the main source of nutrition for immatures, thus food transfer is unlikely to increase growth rates as in callithrichids [Brown et al., 2004].

The predictions flowing from parent–offspring conflict theory on rate of investment were not supported. Offspring age did not affect success rates of food solicitation (prediction 7), and mothers were not less willing to share difficult-to-process or high-quality food (8). On the contrary, immatures achieved even higher success rates when soliciting difficult food. This may be either because the immatures were more persistent when soliciting such food, which could not be measured, or because the mothers more readily allowed transfer. This latter point raises the intriguing possibility that mothers were aware of their offspring's processing abilities and tended to share accordingly. Similar cognitive abilities may be at work when mothers support their offspring's locomotion by selectively bridging tree gaps with their bodies [van Schaik, 2004]. In sum, conflict over food sharing was not observed until well after weaning, probably because mothers also benefit from transferring food to their offspring. However, conflict over termination of investment (prediction 9) was observed in one mother–offspring pair. Increased resistance to food solicitations coincided with higher aggression toward the offspring, leading to an increase in distance. Possibly, these were the first indications of the necessity for this newly pregnant female to segregate with her offspring to be able to care for a new one [van Adrichem et al., 2006; van Noordwijk & van Schaik, 2005]. Thus, although no conflict was observed over rates of investment, conflict over the timing of termination of food sharing was, fitting patterns reported from other primates [Maestripieri, 2002].

Owing to the small number of subjects in this study, any suggested age effect has to be interpreted with caution, because it may also reflect idiosyncratic differences between individuals. However, because of similarities to the age pattern observed among chimpanzees [Hiraiwa-Hasegawa, 1990; Nishida & Turner, 1996; Silk, 1978] and qualitative data from other orangutan sites [Suaq Balimbing: van Noordwijk & van Schaik, 2005; Ketambe: van Noordwijk et al., in press] we feel confident in saying that food transfer is related to an individual's skill level and thus declines with age. Additional qualitative observations at Tuanan support this interpretation: An

offspring born on February 10, 2006, was seen taking food out of its mother's mouth as early as 6 weeks after birth, long before it was first seen feeding on solid food. All four main subjects have been observed taking food from their mothers ever since their habituation in 2003. Most recently, the oldest immature was never seen soliciting food from her mother, although often feeding in the same patch, in 26 full days spent in association between December 2006 and June 2007. Thus, food transfers start early in life and cease some time after weaning although immatures may remain loosely associated with their mothers.

Overall, food transfer among orangutan mothers and their offspring resembled patterns observed in gorillas [Nowell & Fletcher, 2006] and chimpanzees [Hiraiwa-Hasegawa, 1990; Nishida & Turner, 1996; Silk, 1978]. The parallels with chimpanzees are particularly striking: Both rates of solicitation and sharing and their age trajectories were similar, as were the characteristics of shared food items. Peaking early in the dependent period, the amount of food transfer then decreases up to weaning age when food solicitation is rare and focuses on a few food items that remain difficult for the offspring. In both species the prediction that rare foods are transferred more was not upheld, possibly because increased food interest may only be detectable on first encounter with an unfamiliar item, which could not be fully covered with the applied sampling schedule. Finally, as in orangutans, higher rates of displacement were followed by increased distance between mothers and older, weaned offspring [Nishida & Turner, 1996].

Generally, the diets of great apes are characterized by a substantial amount of food obtained through extractive foraging [Byrne, 1997; Parker & Gibson, 1977], and it takes years for offspring to acquire all processing skills [Boesch & Boesch-Achermann, 2000; Jaeggi et al., in preparation; Matsuzawa et al., 2001; van Noordwijk et al., in press; van Noordwijk & van Schaik, 2005]. Arguably, food transfer aids and promotes learning by providing information about food affordances and by creating incentives for immatures to acquire the necessary processing skills [Boesch & Boesch-Achermann, 2000; Brown et al., 2004; King, 1991; Rapaport and Brown, in press; Russon, 2006]. Our findings that ecologically less-competent immatures solicit more food support this notion. Hence, mothers as food possessors also benefit from transferring food toward inexperienced offspring as a form of parental investment. Informational food sharing and high levels of social tolerance are, thus, expected to occur in great apes and other species which extensively use extractive foraging, such as aye-ayes [Erickson, 1991] or capuchins [Rosenberger, 1992]. Recent studies on mother–offspring food transfer in these species seem to confirm this hypothesis

[Boinski et al., 2003; Fragaszy & Visalberghi, 2004; Krakauer & van Schaik, 2005; Rapaport & Brown, in press].

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