

Begging, stealing and offering: food transfer in non-human primates

Gillian R. Brown<sup>1</sup>, Rosamunde E. A. Almond<sup>2</sup> and Yfke van Bergen<sup>2</sup>

<sup>1</sup>School of Psychology, University of St Andrews, St Andrews KY16 9JU, United Kingdom

<sup>2</sup>Sub-Department of Animal Behaviour, University of Cambridge, Madingley, Cambridge  
CB3 8AA, United Kingdom

*Correspondence to:*

Dr Gillian R. Brown,  
School of Psychology,  
University of St Andrews,  
St Andrews,  
Fife, KY16 9JU, U.K.  
[grb4@st-andrews.ac.uk](mailto:grb4@st-andrews.ac.uk)

- I. Introduction
- II. Adult-adult food transfer
- III. Food transfer to infants from parents and helpers
- IV. Does food transfer influence infant growth and/or survival?
- V. Functional explanations of infant food transfer
- VI. Information donation and ‘teaching’
- VII. Summary

## I. INTRODUCTION

The idea that eating and sharing meat played an important role in human evolution (Isaac, 1978) has led to considerable interest in reports of hunting and meat-sharing in chimpanzees (Standford, 1999). A detailed understanding of food-sharing behavior in chimpanzees and other non-human primates could arguably provide insights into the evolutionary history of food sharing in human beings. Although the role of meat-eating and meat-sharing in human evolution remains a highly debated issue (Stanford and Bunn, 2001), the pervasiveness of food transfer within contemporary human societies is beyond doubt (Gurven, 2004). What benefits might individuals obtain from allowing others to gain access to their food? Several evolutionary explanations have been suggested for the benefits of transferring food to other individuals, including kin selection, reciprocal altruism and costly signalling. While the literature on food transfer in human beings has been compiled and evaluated recently (Gurven, 2004), the latest similar review in non-human primates was published over a decade ago (Feistner and McGrew, 1989). Therefore, the aim of this review was to bring together recent theoretical and empirical work on food transfer in non-human primates (hereafter referred to as ‘primates’). While food transfer has also been found to occur in a broad range of species, including insects, birds, cetaceans, bats and other mammals (reviewed by Stevens and Gilby, 2004), such behaviour has been particularly well studied in primates.

Acquiring food captured or harvested by another individual has been described using several different terms, including ‘sharing’ (Feistner and McGrew, 1989), ‘scrounging’ (Barnard and Sibley, 1981), ‘kleptoparasitism’ (Brockmann and Barnard, 1979) and ‘tolerated theft’ (Blurton Jones, 1984; 1987). We use the term ‘food transfer’ to avoid implying either willingness or reluctance on the part of the possessor to relinquish the food item (additional terms are defined in **Table I**). The transfer of food from one individual to another raises interesting questions regarding the costs and benefits that might be involved in: 1) the decision of

the food-possessor to defend a food item or allow it to be taken, and 2) the decision of the food-receiver to obtain a food item from another individual rather than forage independently. As the interests of the food-possessor and food-receiver may not coincide, the behavior of both individuals must be considered. Here, we first describe transfers among adult primates and investigate whether patterns of food transfer may be explained in terms of trade or reciprocity, or whether alternative explanations provide a better fit to the data. Although adult-adult food transfer in primates has gained considerable attention, the most common form of food transfer in primates appears to occur between mothers and infants. We move on to describe the transfer of solid food to infant primates from parents and alloparents, reviewing the inter- and intra-specific evidence that food transfer reduces time to weaning, increases the infant's growth rate or increases the infant's chance of survival. The transfer of food to infants may ensure that infants: 1) receive nutrients during the critical transition to independent foraging (*nutritional hypotheses*), and/or 2) learn about diet breadth or food processing techniques (*informational hypotheses*). The evidence in favour of these hypotheses is discussed, with particular reference to whether adults or infants appear to be controlling patterns of food transfer. The key difference between this type of provisioning and, for example, the feeding of chicks at the nest, is that infants are able to locomote and have some control over which individuals they approach for food and the types of food for which they beg. The situations that we describe perhaps more closely match feeding patterns of fledgling birds. Finally, we investigate whether there is any evidence that adults actively use food transfer to direct offspring learning, and discuss potential directions for future research.

## II. ADULT-ADULT FOOD TRANSFER

Most interactions over food among adults are likely to be predicted by dominance relationships, with higher ranking individuals taking food items from lower ranking individuals or displacing them from feeding sites. For low-ranking individuals, relinquishing food could be the least costly strategy in terms of time, energy and risk of injury (Wrangham, 1975; Blurton Jones, 1986). However, the observation that adult male chimpanzees sometimes allow lower-ranking individuals to take a portion of their meat (Teleki, 1973; Takahata *et al.*, 1984) led to the suggestion that meat transfer involves trade, either for grooming, enhanced alliance partnerships or sexual interactions (Teleki, 1973; Nishida *et al.*, 1992).

In chimpanzee communities, adult males are generally the primary hunters of large prey, such as bush pigs or colobus monkeys (Takahata *et al.*, 1984; Boesch and Boesch, 1989; Boesch,

1994; Mitani and Watts, 1999). Following a hunt, large items are frequently broken up into several pieces, usually involving a large amount of aggressive competition for a piece (Teleki, 1973; Wrangham, 1975; Takahata *et al.*, 1984; Goodall, 1968; 1986). Grooming relationships and alliances during aggressive encounters tend to parallel food transfer relationships in both free-ranging and captive chimpanzee groups, leading to the hypothesis that food was being traded for social support (de Waal, 1989; 1997a; Nishida *et al.*, 1992; Mitani and Watts, 2001). For example, a study of free-ranging adult male chimpanzees found a significant association between the number of times that meat was transferred within a dyad and the number of times that these males engaged in coalitionary support (Mitani and Watts, 2001). Although such findings are consistent with the hypothesis that food is traded for social services, there remains the possibility that food transfer is simply more likely to occur within affiliative relationships, or between closely-ranked individuals, and are not causal in maintaining such relationships.

Female chimpanzees exhibiting a sexual swelling have been reported to have higher success at begging for meat from males than do other females (Teleki, 1973). Additionally, meat transfer has been seen to occur between a male and a female either just before, or soon after, a copulation has occurred, or during a consortship (Takahata *et al.*, 1984; Goodall, 1986; Nishida *et al.*, 1992), leading to the hypothesis that meat was being exchanged for sexual interactions. However, reports of meat-for-sex exchanges are relatively uncommon in the literature and account for only a small proportion of cases of food transfer. Also, recent studies have reported that male chimpanzees are not more likely to gain matings with females during cycles in which they transfer food compared to cycles in which they do not transfer food (Mitani and Watts, 2001), nor does food transfer appear to increase a male's chance of siring offspring with a particular female (Hemelrijk *et al.*, 1999). Therefore, there is currently no compelling evidence that male chimpanzees gain greater mating access, or significantly increase their chance of paternity, by transferring meat to females.

Food transfer has also been hypothesised to increase the likelihood that the recipient will provide food to the original possessor in the future. Whether food transfer involves reciprocal altruism has been specifically investigated in capuchins and tamarins. In captivity, capuchins have been observed to throw food, or push food through wire-mesh partition, into a cage containing other capuchins, and to pass food directly to a group-mate (de Waal *et al.*, 1993; Westergaard *et al.*, 1998; 1999). Experimental studies, in which pairs of female capuchins were separated by a wire mesh and provided with food at different times, indicated that rates of food exchange were similar in both directions within dyads (de Waal, 1997b; 2000). While the results of these experimental studies may be interpreted as evidence of a well developed system of

exchange or reciprocity, these patterns of food transfer may instead reflect affiliative relationships and tolerance of proximity (de Waal, 1997b). Most exchanges involved one individual picking up items that had been dropped by the other while sitting near the mesh, suggesting that excess food was available. When the food was of a preferred type, the capuchin with food sat further away from the mesh and appeared less willing to allow the other individual to obtain food items (de Waal, 2000). While data on capuchins may be explained most simply as cases of tolerated food taking, a recent study of captive tamarins suggests that these monkeys may have the ability to engage in reciprocal food transfer (Hauser *et al.*, 2003). However, another study of food transfer in captive groups of tamarins failed to find significant correlations between frequencies of food given and food received within dyads (Rapaport, 2001). Cheney and Seyfarth (1990) have postulated that reciprocity in primates is more likely to involve social interactions, such as grooming, than the exchange of material goods, such as food. The possibility of reciprocal food transfer in primates ensures that this will remain an interesting area for future research.

While most studies on food transfer among adult primates have focused on the role of trade or reciprocal altruism, the early idea that food transfer may result from the costs imposed by harassment, such that relinquishing food may be the least costly strategy in terms of time, energy or risk of injury (Wrangham, 1975; Blurton Jones, 1986), has been gaining renewed attention (Caraco and Brown, 1986; Stevens and Stephens, 2002). Stevens and Stephens (2002) produced a game theoretical model of food transfer, which predicted that transfer would be most likely to occur when harassment costs on the owner are high and when the owner cannot easily defend the food. Stevens (2004) went on to test predictions from this model in captive chimpanzees and spider monkeys, and confirmed that food-owners transferred food more frequently as begging intensity increased. If two individuals were to be repeatedly involved in bouts of harassment and transfer, the resulting pattern of food transfer could resemble reciprocal exchange (Brown, 2004; Stevens and Cushman, 2004). Thus, Stevens (2004) points out that, while harassment does not exclude the possibility that other factors may be involved in food transfer, harassment must either be ruled out, or statistically controlled for, before more complex explanations such as trade or reciprocity are invoked.

A number of additional theoretical perspectives may provide directions for further investigation of food transfer among adults. For example, producer-scrounger games (Giraldeau and Beauchamp, 1999; Giraldeau and Caraco, 2000) have already been used to investigate foraging behaviour in a small foraging group of capuchins (Di Bitetti and Janson, 2001). Ideal free distribution models could be used to investigate how the occurrence of food transfer

depends upon attributes of the food, such as handling time, and upon attributes of the competitors, such as competitor density and relative fighting ability (Hamilton, 2002). The predictions of these models could be tested experimentally by manipulating variables such as the feeding rate of individuals, the divisibility of the food resource, and the numbers of individuals present (Stevens and Stephens, 2002), providing considerable scope for future research. Additionally, researchers studying the distribution of food within human populations have investigated the possibility that food transfer may be a form of costly signalling that provides information about phenotypic quality or about an individual's willingness to cooperate (see Winterhalder, 1996; Gurven, 2004). The hypotheses and predictions formulated by these researchers may stimulate future lines of enquiry for those studying food transfer in non-human primates.

The remainder of this review concentrates on food transfer between older and younger individuals. Although in some cases older individuals take food items from younger animals, in most cases food is transferred in the opposite direction. Where food is transferred from an older to a younger individual, dominance relations, trade or reciprocity are unlikely to provide convincing explanations.

### III. FOOD TRANSFER TO INFANTS FROM PARENTS AND HELPERS

In mammals, infants may be most likely to obtain their first solid food items by taking a portion of the food that their mothers are eating. In primates, the most commonly reported occurrences of food transfer are from mothers to infants (Feistner and McGrew, 1989). Once infants are more mobile, they may move away from their mothers, approach other group members and beg for food. Importantly, this mobility results in infants having the opportunity to determine which foods they are most likely to receive by approaching individuals who are holding particular food items. In the following sections, we first review the evidence that food transfer influences infant growth or survival, and then discuss the two main sets of functional explanations for transfer of food to infants, the nutritional and informational hypotheses. However, first, the distribution of food transfer across primate species, and involvement of different age and sex categories in provisioning of infants, will be summarised.

The transfer of solid food to infants has been reported in 27 species of primate, both in captivity and in free-ranging populations (**Table II**). The data in Table II suggest that the occurrence of food transfer from adults to infants is not evenly distributed across primate groups (1 species of tarsier; 13 species of callitrichids; 8 other New World primates; 5 apes; no Old

World primates). One possible explanation for this pattern of data is that there has been a reporting bias in the literature. However, given the large amount of research that has been carried out on Old World primates, the lack of reporting suggests that transfer of food to infants from others is a genuinely rare occurrence. The most detailed studies of food transfer to infants have been carried out on callitrichid primates and chimpanzees. In callitrichids, which exhibit cooperative breeding systems in which twin offspring are reared communally, infants appear to be almost entirely provisioned by others when they begin to eat solid food, before gradually developing into independent feeders (e.g. Hoage, 1982; Feistner and Price, 1990; 2000; Ruiz-Miranda *et al.*, 1999). The high level of food transfer in callitrichids may be related to their cooperative breeding system. Alternatively, the breadth of diet or importance of extractive foraging in the diets of chimpanzees and some callitrichid species may potentially explain the high frequency with which infants obtain solid food items from others if food transfer plays a role in infants learning diet choices or food processing skills. Evidence described later suggests that the function of food transfer may differ between chimpanzees and callitrichids.

In callitrichid primates, mothers, fathers, and alloparents may be predicted to differ in the frequency with which they transfer food to infants. For example, as breeding females are able to become pregnant while suckling the previous set of offspring, fathers may be selected to provision offspring with solid food if this allows their mate to allocate resources to the next set of offspring, while mothers may play a lesser role in provisioning as they bear the metabolic costs of gestation and lactation (Feistner and Price, 1990). Both parents may be predicted to transfer food to infants more frequently than do alloparents. Only a small number of studies have reported the relative contributions of mothers, fathers and alloparents to offspring provisioning in callitrichids, with variable results and generally small sample sizes (**Table III**). Six out of the ten studies reported that fathers transfer food to offspring more frequently than do other group members (also see Washabaugh *et al.*, 2002), and the two studies with the largest samples reported that fathers transfer more food than do others (Roush and Snowdon, 2001) or that both parents transfer more food than do siblings (Price, 1992a). These limited data suggest that callitrichid fathers play a particularly important role in providing offspring with solid food.

Parents are expected to transfer solid food to offspring if this increases offspring growth, increases the chance of infant survival or precipitates weaning. However, it is less clear why individuals other than parents would allow infants to take their food. The proposed benefits to helpers include: 1) gaining experience in rearing offspring, so as to improve their chance of successfully breeding in the future, 2) increasing their chance of inheriting a breeding position by reducing the likelihood of being expelled from the group; 3) raising individuals that may serve as

future helpers once in a breeding position; 4) gaining inclusive fitness through caring for and improving the survival chances of relatives; 5) increasing the chances of being chosen as mating partner; and 6) increasing their own survival probability by increasing group size (reviewed by Emlen, 1991; Jennions and Macdonald, 1994; Snowdon, 1996; Tardif, 1997; Cockburn, 1998; Kokko *et al.*, 2001).

The costs and benefits of alloparental care may depend upon the age, sex and relatedness of the helper to the offspring. For example, helpers of the sex that remains in the natal group may be predicted to provide higher levels of care than the sex that disperses, as a result of being more closely related to infants or being more likely to benefit from an increase in future group size (Brotherton *et al.*, 2001). The predicted relationship between dispersal patterns and levels of alloparental care has been upheld in a number of studies on cooperatively-breeding mammals. For example, in species such as meerkats (*Suricata suricatta*) and red foxes (*Vulpes vulpes*) in which males generally disperse from their natal group to breed, females contribute more to rearing young than do males (Moehlman and Hofer, 1997; Brotherton *et al.*, 2001; Clutton-Brock *et al.*, 2001; 2002), while in other species, such as African wild dogs (*Lycaon pictus*), females disperse to breed and male helpers provide more care than do females (Malcolm and Marten, 1982). As yet, there are insufficient data on the provisioning levels of male and female non-parental helpers to test this relationship in callitrichid primates. Studies that investigate the extent to which different categories of carers contribute to the feeding of offspring need to control for the effects of individual differences in food acquisition (Clutton-Brock *et al.*, 2001); for example, in meerkats, the number of food items given by helpers to pups was found to be approximately linearly related to the number of items located (Clutton-Brock *et al.*, 2001).

#### IV. DOES FOOD TRANSFER INFLUENCE INFANT GROWTH AND/OR SURVIVAL?

Before investigating the manner in which infants might benefit by receiving food from others, it is important to assess whether infants do in fact obtain fitness benefits as a result of obtaining solid food from other group members. The transfer of food to infants could: 1) increase offspring growth rates, reduce the age of weaning or reduce the age of nutritional independency, and/or 2) increase offspring survival chances during the transition to complete nutritional independence (McGrew, 1975; Lefebvre, 1985; Feistner and McGrew, 1989; Price and Feistner, 1993; Fraga and Bard, 1997). By weaning infants at an earlier age, mothers may be able to begin the next reproductive event sooner (Ross and MacLarnon, 2000). Here we use inter- and intra-specific data to evaluate key predictions.

*Prediction 1: offspring that receive solid food from others have younger ages at weaning, higher growth rates, or younger ages at nutritional independency compared to offspring that obtain most of their solid food themselves*

In an early comparative study, Lefebvre (1985) found that weaning did not occur at an earlier age than expected in those species in which food transfer has been reported most frequently (i.e., lion tamarins and chimpanzees). However, more recent cross-species comparative analyses have indicated that, among anthropoid primates, alloparenting (based on the occurrence of carrying rather than food transfer) does correlate with relatively high infant growth rates, a young age at weaning (but at the same weight relative to the mother) and high reproductive rates (Mitani and Watts, 1997; Ross and MacLarnon, 2000). The relative importance of provisioning as an aspect of alloparental care is not known and there are currently insufficient data on the levels of food transfer across a broad range of primate species to test this hypothesis further. However, in callitrichid primates, the transfer of solid food to infants potentially played a vital role in the evolution of twinning and the ability of females to return to reproductive condition and conceive soon after giving birth (Garber and Leigh, 1997).

Cross-species comparisons are confounded by the possibility that food transfer may have evolved to compensate for otherwise slow growth rates or late weaning ages in particular species. A further complication is that an earlier age at weaning does not necessarily translate into a correspondingly early age at full nutritional independence. In species in which helpers provision offspring with solid food, the period of post-weaning care may in fact be longer than in other species, as a result of helpers feeding infants while parents initiate the next breeding attempt. In birds, cooperative breeding is associated with unusually long periods of offspring dependency (Langen, 2000). Therefore, the transfer of solid food to infants may reduce the time to weaning but may be offset by an increased age at full independence.

There is little evidence from within species to test whether those infants receiving food from others grow faster or are weaned earlier compared to other infants, or to test whether mothers that provide solid food to infants have shorter interbirth intervals than other mothers. Again, correlational data are problematic as there may be confounding factors; for example, high levels of food transfer may not correlate with infant growth rate if slow-growing infants obtain more food from others than do fast-growing infants.

*Prediction 2: infant survival is positively correlated with the amount of food received from others*

Although there are no empirical data with which to test directly the prediction that food transfer increases infant survival chances, it is possible to evaluate whether infants that have many helpers in their social group have a higher chance of survival than other infants. A number of studies of free-ranging callitrichids report that infant survival is positively correlated with the number of helpers in the group (moustached tamarins: Garber *et al.*, 1984; common marmosets: Koenig, 1995; cotton-top tamarins: Snowdon, 1996; lion tamarins: Bales *et al.*, 2000). Studies of captive cotton-top tamarins have shown that infants in large groups receive more food in total than those in smaller groups (Feistner and Price, 1990; Price, 1992b). The presence of helpers is also reported to significantly increase offspring survival in other mammalian species in which helpers provision offspring, including silverbacked and golden jackals (*Canis mesomelas* and *Canis aureus*: Moehlman and Hofer, 1997) and meerkats (Russell *et al.*, 2002). However, in contrast, no relationship between group size and infant survival has been found in other callitrichid populations (free-ranging lion tamarins: Baker *et al.*, 1993; Dietz and Baker, 1993; free-ranging pygmy marmosets: Heymann and Soini, 1999; captive cotton-top tamarins: Price and McGrew, 1990; captive common marmosets: Rothe and Darms, 1993). Unfortunately, correlations between group size and infant survival are generally confounded by other variables, such as territory quality, and provide no indication of the relative importance of food transfer compared to other aspects of care, such as defense against predators.

In summary, the presence of alloparents appears to correlate with relatively high infant growth rates and early age at weaning in primates, although food transfer may not necessarily correlate with an early age at nutritional independence. Also, there is some evidence that the presence of helpers increases the survival chances of infants during early life. However, the relative importance of food transfer in comparison to other aspects of alloparental care in accounting for these findings is currently unknown.

## V. FUNCTIONAL EXPLANATIONS OF INFANT FOOD TRANSFER

Two main sets of hypotheses have been put forward for the mechanisms by which infant growth or survival may be enhanced by food transfer (McGrew, 1975; Silk, 1978; Lefebvre, 1985; Price and Feistner, 1993; Rapaport, 1999; Ruiz-Miranda *et al.*, 1999). The transfer of food may: 1) provide nutrients to infants during the period of weaning when they are susceptible to food shortage or, more generally, while they develop as independent foragers – *nutritional hypotheses*, and 2) play a role in the acquisition of knowledge about diet choices and food processing skills – *informational hypotheses*. These sets of hypotheses are not necessarily

mutually exclusive. For example, by receiving a half-eaten insect, an infant primate may benefit by gaining important nutrients that it may not be able to obtain for itself, may learn that a particular insect species is edible and may gain the opportunity to practice essential food processing skills. Additionally, both sets of benefits may play a role but their relative importance may vary with infant age; for example, prior to weaning, food transfer may supplement infant nutrition, while after weaning it may play a role in increasing diet breadth (Rapaport, 1999). The two hypotheses can nonetheless be regarded as distinct in suggesting that the primary function of food transfer is the acquisition of nutritive or informational benefits, respectively, while any additional benefits are regarded as by-products of selection rather than traits directly favoured by selection. Predictions and evidence in favour of these two sets of hypotheses are discussed in the following sections, with distinctions being made between the relative roles of beggars and food possessors in determining patterns of food transfer.

At this point, it is important to remember that, as the transfer of food involves two individuals, there may be a number of circumstances under which conflicts of interest occur. A food possessor that is approached by a begging infant may not necessarily hand over a portion of their food, and may instead resist by moving away or turning the body away from the other individual or by exhibiting threat displays or physical aggression to the individual attempting to gain access to the food item. Food possessors may be less willing to transfer food if they have low energy levels, if there is little food currently available, if the item is highly preferred, or if it has taken substantial time or energy to obtain. Additionally, adults and offspring may be in conflict over the amount of investment provided to offspring (Trivers, 1974). In the following sections, separate predictions are made regarding the behaviour of the infant and the food possessor, as evidence in favour of the prediction for one individual does not necessarily mean that the prediction for the other individual is also supported.

#### A) *Nutritional hypotheses*

Food transfer may simply provide infants with additional nutrients during the period of weaning or during a more extended transition to independent foraging. Observational data suggest that food transfer are not evenly distributed between food types. Below, we compare patterns of begging and food transfer to the prediction that food items that are nutritionally rich, or that infants are unable to obtain for themselves, are more likely to be transferred than other items, and the prediction that rates of food transfer will be highest during the period of weaning or the transition to independent foraging.

*Prediction 3a: infants beg for food items that are nutritionally rich, or that they are unable to obtain for themselves, more than for other items*

*Prediction 3b: adults transfer food items that are nutritionally rich, or that infants are unable to obtain for themselves, more than other items*

Observational studies of free-ranging primates suggest that large insects and large plant items that infants find difficult to process are the items most frequently solicited by infants (buffy-headed marmosets: Ferrari, 1987; black-mantle tamarins: Izawa, 1978; moustached tamarins: Heymann, 1996; golden lion tamarins: Ruiz-Miranda *et al.*, 1999; yellow-handed titi monkeys: Starin, 1978; lar gibbon: Nettelbeck, 1998; chimpanzees: Assersohn and Whiten, 1999; Corp and Byrne, 2002). For instance, free-ranging infant chimpanzees solicit those foods that are both nutritionally rich and difficult for infants to obtain by themselves, such as nuts and fruits that require processing, more frequently than expected by chance given the amount of time that mothers were feeding on these different food types (Silk, 1978; Hiraiwa-Hasegawa, 1990a; Nishida and Turner, 1996). Such items appear to require manual dexterity, strength or skills not yet acquired by the infants. Chimpanzee infants do not differ in rates of begging for high-quality and low-quality food (Nishida and Turner, 1996), suggesting that the important variable for infants is whether they are able to obtain specific food resources themselves. The amount of food acquired by transfer was greatest for those food types that infants were not observed to obtain independently (defined as difficult-to-process items), although the success begging was similar for these foods and items that infants were able to acquire by themselves (Silk, 1978; Hiraiwa-Hasegawa, 1990a; Nishida and Turner, 1996). At least in chimpanzees, infants appear to be responsible for the observed patterns of food transfer.

These data suggest that food transfer may provide infants with an opportunity to gain nutrients, particularly protein, that they would not otherwise be able to obtain. However, the data are also consistent with the hypothesis that infant begging allows them to practice food-processing skills. Additionally, food items such as insects, large fruits and nuts may be relatively rare and therefore novel to some youngsters, supporting the suggestion that infants gain information about diet breadth through provisioning. Studies in captivity, in which particular characteristics of food items, such as novelty, rarity and difficulty in processing, can be varied independently, will allow the relative importance of these characteristics to be unravelled.

*Prediction 4a: rates of infant begging will be highest during the period of weaning*

*Prediction 4b: rates of food transfer from adults will be highest during the period of weaning*

If food transfer provides infants with nutritional benefits, begging may be predicted to peak during the weaning period if infants are most susceptible to nutritional deficits during this transition to independent foraging, while if food transfer provides infants with informational benefits, no such peak is necessarily expected. In both cases, begging is predicted to decline as infants become better able to forage for themselves, although the time course may depend upon the food items involved, with difficult-to-process items continuing to be transferred to offspring until a later age. In fact, surprisingly little is known about the development of independent feeding in primates (Nicolson, 1986; Feistner and Price, 2000). However, in captive callitrichid primates, both begging and provisioning peak around the time of weaning (10-14 weeks), while food items such as large insects continue to be transferred until a later age (Hoage, 1982; Feistner and Price, 1990; 2000; Price and Feistner, 2001). Begging success appears to remain relatively constant during the transition to independent feeding (Feistner and Price, 2000; Price and Feistner, 2001), suggesting that adults respond directly to the begging levels of infants. The prediction therefore appears to be upheld in callitrichids, suggesting that provisioning may play an important role in the successful transition of infants through weaning in these species.

In free-ranging chimpanzees, no peak in food transfer occurs at the age of weaning (around 4 years: Ross and Jones, 1999), and most instances of food begging and transfer occur prior to weaning (Silk, 1978; Hiraiwa-Hasegawa, 1990a; Nishida and Turner, 1996). Begging success rates appear to be similar for offspring of all ages (Hiraiwa-Hasegawa, 1990a; Nishida and Turner, 1996). An exception to this time course is the transfer of nuts from mother to infant chimpanzees, which peaks around four years of infant age and continues to around eight years (Boesch and Boesch-Achermann, 2000).. The lack of a peak in begging and provisioning around the age of weaning suggests that the main function of food transfer in chimpanzees may be informational rather than nutritional, and highlights the possibility that the role of food transfer differs between species.

#### *B) Informational hypotheses*

Here, we assess the evidence that young primates acquire information about dietary choice or food-processing skills by obtaining food from other individuals.

##### *i) Learning food preferences*

Rather than simply acquiring nutrients, young primates may acquire food preferences through exposure to food obtained from other group members, and food transfer may provide a supplemental source of information that is used in addition to that acquired by an infant during

its own exploration (Schessler and Nash, 1977). Social learning may be an important means by which primates incorporate new foods into their diets, as it is for many other animal species (Zentall and Galef, 1988; Heyes and Galef, 1996; Galef and Giraldeau, 2001; Galef *et al.*, 2001). If food transfer allows infants to learn about diet choices, a number of predictions follow.

*Prediction 5a: infants beg more for food items that are novel than for food items that are familiar to them*

*Prediction 5b: adults are more likely to transfer food items that are novel to infants than ones that are familiar to them*

Studies of captive callitrichid primates have reported that infants are relatively unwilling to take novel food items from food bowls themselves compared to familiar items (Price and Feistner, 1993) and exhibit higher levels of begging for novel than for familiar food items (Brown *et al.*, submitted). In contrast, older immature callitrichids are willing to eat novel food items in the absence of experienced conspecifics (Vitale and Queyras, 1997; Queyras *et al.*, 2000). These data suggest that infant callitrichids preferentially obtain novel food items from social group members, while older immatures perhaps rely on their own experiences with novel foods or acquire food preferences through observational learning. A recent study has reported that, when family groups of captive common marmosets were provided with either novel or familiar food, levels of begging by infants were higher with novel than with familiar food (Brown *et al.*, 2004). These data support the hypothesis that infant marmosets actively attempt to obtain information about diet by soliciting food from adults. Two earlier studies did not find higher levels of begging with novel food (Price and Feistner, 1993; Rapaport, 1999), although the age differences in subjects used may explain the different patterns of results see Brown *et al.*, 2004). Few data are available to test these predictions in chimpanzees, although one study suggests that the amount of time spent by infants feeding on items transferred from the mother is greater for novel than for familiar foods (Hiraiwa-Hasegawa, 1990b). The study by Brown *et al.* (2004) also reported that adults exhibited higher levels of refusals with novel than with familiar food, and begging success with novel foods was lower than with familiar, leading to similar levels of food transfer during tests with novel and familiar food. These data do not support the suggestion that adults are actively involved in facilitating learning about diet in infants. Similarly, Price and Feister (1993) reported that refusals occurred more frequently, and begging success was lower, in tests with novel than with familiar food. In contrast, Rapaport's (1999) study reported that frequencies of transfer per food item were higher in tests with novel than with familiar food, which would suggest that adults did alter their behaviour in a manner that would

facilitates learning in immatures. The contradictory findings of these studies indicate that further data are required, and highlight the potential influence of offspring age on patterns of begging and food transfer.

*Prediction 6a: the variety of items that are begged for will decline with age and begging will decrease as diet is learned*

*Prediction 6a: the variety of items that are transferred will decline with age and provisioning will decrease as diet is learned*

While frequencies of food transfer generally decrease as infants grow older, there are currently insufficient data to assess whether the variety of food items begged for and transferred declines with age, or whether begging and transfer decrease specifically in line with increasing offspring diet breadth. Observational data from field and captive settings are required that monitor the range of items that are begged for and transferred over time, and that relate patterns of begging and provisioning to the knowledge levels of particular youngsters.

*Prediction 7: offspring provisioning influences future dietary choices*

Despite the relatively large number of studies on social influences on feeding, there is little direct evidence that obtaining food from others during early life influences subsequent dietary choices in mammals (Fragaszy and Visalberghi, 1996; Galef and Giraldeau, 2001), apart from one study on brown rats (*Rattus norvegicus*: Galef *et al.*, 2001). Social influences on diet choice may involve processes other than food transfer, including the use of olfactory and visual cues. For instance, young free-ranging baboons sniff adults' muzzles while they are eating (King, 1991; 1999) and may gain olfactory cues about diet through this behaviour, in a similar manner to rodents (Galef, 1996). Also, in captive cotton-top tamarins, individuals emit alarm calls and exhibit head shaking, frothing at the mouth and mouth rubbing when they encounter noxious foods, which appears to deter other animals from approaching the food (Snowdon, 2001; Snowdon and Boe, 2003). However, one recent study has experimentally investigated whether infants acquire a dietary preference as a result of food transfer. This study found that infant common marmosets given a choice between food that had been transferred from group members and food that had been experienced independently exhibited a strong preference for the food that had been obtained from others (Almond *et al.*, submitted). These data, together with the data presented by Brown *et al.* (submitted), strongly suggest that infant common marmosets actively seek and obtain information about diet via food transfer.

### *ii) Learning food processing skills*

Social learning has been hypothesised to result in the transmission of complex food processing techniques within groups of primates, including the transmission of traditional food processing techniques that differ between communities (Whiten *et al.*, 1999; Fraga and Perry, 2003). A number of recent studies of chimpanzees have presented data supporting the suggestion that social interactions are important in the transmission of specific tool-using techniques, particularly interactions between mothers and offspring (Biro *et al.*, 2003; Hirata and Celli, 2003; Lonsdorf *et al.*, 2004). When mothers are processing food items, the transfer of food to infants could potentially facilitate the transmission of information about processing techniques (Russon, 2003; Caldwell and Whiten, 2003). Where there is the potential to obtain a food reward, infants may be particularly likely to attend to the processing techniques of their mothers and learn by observation, compared to situations where no food reward is available. Alternatively, by obtaining half-processed items, infants may have the opportunity to learn specific techniques for themselves, as has been reported in young black rats (*Rattus rattus*: Terkel, 1996). An important recent study on common marmosets has shown that scrounging a food reward increases the probability that a naïve individual will learn a novel foraging task that is being carried out by a trained demonstrator (Caldwell and Whiten, 2003). Scrounging food items that have been harvested by others has also been shown to increase the probability that foraging behaviour will be learned in adult black-capped chickadees (*Parus atricapillus*: Sherry and Galef, 1984) and Florida scrub jays (*Aphelocoma coerulescens*: Midford *et al.*, 2000), but has been reported to hinder such learning, for example in pigeons (*Columba livia*: Giraldeau and Lefebvre, 1987). If food transfer involves learning about food processing skills, the following predictions can be made.

*Prediction 8a: infants beg more for food items that they are unable to process than for items that they can process themselves*

*Prediction 8b: adults transfer food items that infants cannot process themselves at a higher rate than food items that infants can process themselves*

Earlier, we discussed whether begging and food transfer are more likely to involve food items that infants find difficult to process, and suggested that the data could be interpreted as supporting either nutritional or informational hypotheses. The key distinction between these hypotheses is whether food transfer results in infant learning. Adults may actively encourage learning of food processing techniques by preferentially transferring items that are difficult for infants to process. However, studies of free-ranging chimpanzee infants reported that begging

success is not greater with difficult-to-process compared to easy-to-process foods (Silk, 1978; Nishida and Turner, 1996). In fact, when chimpanzee infants are very young, mothers are less likely to respond to infant begging by relinquishing difficult-to-process food compared to easy-to-process food (Silk, 1978; Hiraiwa-Hasegawa, 1990a; Byrne, 1999; Corp and Byrne, 2002). Mothers may be unwilling to transfer unprocessed food items that could be harmful to infants.

*Prediction 9a: rates of infant begging will be related to the skill level of that individual and will decrease as skills are learned*

*Prediction 9b: rates of food transfer will be related to the skill level of that individual and will decrease as skills are learned*

With difficult-to-process foods, the amount of food obtained via transfer from their mothers decreases in line with an increase in the amount of these food items that youngsters obtain by themselves (Boesch and Boesch-Achermann, 2000; Corp and Byrne, 2002). However, whether infant begging decreases with age, strength or foraging ability is not known. Difficult-to-process food items may continue to be obtained via transfer until a later age because youngsters lack the physical strength or dentition to open these items, rather than because they lack a particular skill that requires time to learn. Future studies may ascertain whether levels of begging are related to the skill levels of individual youngsters. Studies in captivity would be particularly useful as skill levels could be manipulated independently of physical strength and dental development. There is currently no evidence that primate mothers are more willing to transfer food depending upon the skill level of the infant. Captive adult capuchin monkeys did not differ in their willingness to hand over nuts to infants that were either able or unable to open nuts by themselves (Fragaszy *et al.*, 1997).

*Prediction 10: individuals that have had the opportunity to obtain food from other individuals acquire processing skills at a younger age than individuals without this opportunity and acquire skills similar to those of their demonstrators*

While researchers have postulated that infants may learn processing skills through the transfer of food items from others, at present there is no direct evidence that food transfer influences the subsequent processing abilities of youngsters or reduces the age at which skills are learned. In species in which different food processing techniques exist across study sites (Whiten *et al.*, 1999; Fragaszy and Perry, 2003), there is currently little direct evidence that infants socially learn the technical variants exhibited by their social group members (Galef, 2003). The role of food transfer could be assessed in captivity by manipulating the amount of food

transferred and recording the development of food processing abilities, or in the field by determining the correlation between these variables. Whether the learning of processing skills is differentially influenced by the transfer of unprocessed, semi-processed or processed food items also deserves further investigation.

## VI. INFORMATION DONATION AND ‘TEACHING’

Adults may direct the learning of dietary choices and processing skills in younger individuals in a number of ways. One method would be to prevent infants from eating certain foods by removing food items from the hands or mouths of infants, by giving vocalisations when infants attempt to eat particular items, or by threatening infants when they approach specific food sources. This would be an example of ‘coaching’ (Caro and Hauser, 1992). There are a number of descriptive accounts, particularly among apes, in which adult primates have apparently prevented younger individuals from eating certain food items (e.g. Goodall, 1973; Flettemeyer, 1978; Nishida *et al.*, 1983; Boinski and Fraga, 1989; Hiraiwa-Hasegawa, 1990b). However, researchers generally agree that there is a distinct absence of evidence that adults prevent youngsters from ingesting food items that adults have learned to avoid (King, 1994; Fraga and Visalberghi, 1996; Galef and Giraldeau, 2001; Snowdon, 2001).

Rather than preventing youngsters from eating certain foods, adults might actively encourage them to eat other food types. Adults in several species of callitrichid primate have been reported to ‘offer’ food to offspring by holding a food item in an outstretched hand and emitting a vocalization that is similar to the one used during begging and appears to result in an infant approaching and taking the food item (e.g. Moody and Menzel, 1976; Brown and Mack, 1978; Hoage, 1982; Ferrari, 1987; Feistner and Price, 1990; 1991). A number of primate species have been reported to give ‘food calls’ on locating a patch of food (including spider monkeys: Chapman and Lefebvre, 1990; macaques: Dittus, 1984; Hauser and Marler, 1993a; 1993b; chimpanzees: Wrangham, 1975; Hauser and Wrangham, 1987), which may benefit the caller by, for example, attracting the caller’s relatives, reducing predation risk, or enhancing social status (Wrangham, 1975; Hauser and Marler, 1993b; Hauser, 1996; Evans and Evans, 1999). Therefore, the fact that adults give food calls does not necessarily imply that coaching or teaching is occurring. However, adults could potentially enhance infant learning by giving food calls preferentially with food items that are novel to infants or that infants are not yet able to process themselves (Maestripieri and Call, 1996; King, 1999; Snowdon, 2001).

For food calling to infants to be seen as a form of ‘teaching’ (Caro and Hauser, 1992), it would need to be shown that 1) adults produce more calls when infants are present than when they are absent (controlling for any effects of group size), 2) adults transfer food at a higher rate after calling than when holding food and not calling, 3) adults are sensitive to the state of the infant such that they give more calls for foods that are novel rather than familiar to infants, or for foods that infants do not have the skills to process for themselves rather than for other food items, and 4) the subsequent diet choices or food processing skills of infants are influenced by these interactions. Recent studies of captive cotton-top tamarins have revealed 1) that rates of food calling while eating are higher for adults with offspring than for adults without offspring (Roush and Snowdon, 2000) and 2) that attempts by infants to take food from adults are more successful when the adult vocalizes (Roush and Snowdon, 2001). Points 3) and 4) have yet to be tested. Current data suggest that calls are given when individuals are aroused and when competition for food is greatest, and that calls provide a signal of arousal that results in attraction of offspring to food sources that are preferred or rapidly consumed (Elowson *et al.*, 1991; Benz *et al.*, 1992; Caine *et al.*, 1995; Roush and Snowdon, 2000). However, there is currently insufficient evidence that food calling functions to transmit information to offspring or that it directs learning in offspring. In summary, while diet choice and food handling techniques may be passed from one generation to another via social learning processes, there is debate over whether adult primates provide active guidance to their offspring in a manner congruent with coaching or teaching (Caro and Hauser, 1992; Russon, 1997).

## VII. SUMMARY

The main aim of this review was to collate data on food transfer in primates and to compare these data to predictions that stem from various functional explanations of food transfer. First, the data on adult-adult food transfer were summarised. In adults, although patterns of food transfer can often be predicted by dominance relationships, with dominant individuals obtaining food from subordinates, the data indicate that not all food transfer follows this pattern. Researchers have suggested that food transfer may therefore involve trade for other commodities, including grooming, social support or sexual access, although these hypotheses are not strongly supported by the available data. Also, while studies of chimpanzees, capuchins and tamarins have indicated that frequencies of food transfer between individuals are often correlated within dyads, such patterns do not necessarily indicate that reciprocity had occurred. Analysing the costs and benefits of defending a food item may reveal that the costs of harassment provides

sufficient explanation for a notable proportion of food transfer events. A number of theoretical perspectives may prove useful in future investigations of food transfer among adults.

Patterns of food transfer from older to younger individuals were then reviewed. Infants obtain food from older individuals in a number of primate species, in particular the callitrichid primates. Quantifying the relative contributions of individuals of different age and sex categories to offspring provisioning will potentially increase our understanding of parental and alloparental care in cooperatively breeding species. The current data on callitrichids and chimpanzees highlight the possibility that both nutritional and informational benefits may be gained by infants. In callitrichids, food transfer peaks around the age of weaning and is most likely to involve novel or difficult-to-process items, with recent evidence suggesting that infants learn dietary preferences via food transfer. In chimpanzees, most food transfer occurs prior to weaning and involve items that are difficult for infants to process by themselves. Recent studies suggest that interactions between mothers and infants may result in the transmission of tool-using skills. Obtaining a food reward during such interactions may enhance any social learning processes that are taking place. Whether adults actively direct the dietary choices or food processing techniques of youngsters remains controversial. We hope to have shown that this area of research has undergone recent key developments and presents considerable scope for further empirical investigation both in primates and in other animal species.

### Acknowledgements

This research was funded by the MRC (GRB and REAA) and the BBSRC (YvB). We thank Richard Byrne, Christine Caldwell, Jeff Galef, Rebecca Kilner, Kevin Laland, Tim Roper, Joan Silk, Peter Slater, Charles Snowdon and an anonymous referee for comments on the manuscript.

### References

- Almond, R. E. A., van Bergen, Y. and Brown, G. R. (Submitted). Social influences on dietary preferences in infant common marmosets (*Callithrix jacchus*).
- Assersohn, C. and Whiten, A. (1999). Food sharing between mother and infant chimpanzees in the wild: beggars can be choosers. *Folia Primatol.* **70**, 226-227.
- Baker, A. J., Dietz, J. M. and Kleiman, D. G. (1993). Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Anim. Behav.* **46**, 1091-1103.

- Bales, K., Dietz, J., Baker, A., Miller, K. and Tardif, S. D. (2000). Effects of allocare-givers on fitness of infants and parents in Callitrichid primates. *Folia Primatol.* **71**, 27-38.
- Barnard, C. J. and Sibly, R. M. (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim. Behav.* **29**, 543-550.
- Beck, B. B., Kleiman, D. G., Dietz, J. M., Castro, I., Carvalho, C., Martins, A. and Rettberg-Beck, B. (1991). Losses and reproduction in reintroduced golden lion tamarins *Leontopithecus rosalia*. *Dodo* **27**, 50-61.
- Benz, J. J., Leger, D. W. and French, J. A. (1992). Relationship between food preferences and food-elicited vocalisations in golden lion tamarins (*Leontopithecus rosalia*). *J. Comp. Psychol.* **106**, 142-149.
- Bethell, E., Whiten, A., Muhamuza, G. and Kakura, J. (2000). Active plant sharing by wild chimpanzees. *Primate Report* **56**: 67-71.
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C. and Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim. Cogn.* **6**, 213-223.
- Blurton Jones, N. G. (1984). A selfish origin for human food sharing: tolerated theft. *Ethol. Sociobiol.* **5**, 1-3.
- Blurton Jones, N. G. (1986). Fitness returns from resources and the outcome of contests: some implications for primatology and anthropology. In "Primate Ontogeny, Cognition and Social Behaviour" (J. G. Else and P. C. Lee, Eds), pp. 393-406. C.U.P., Cambridge.
- Blurton Jones, N. G. (1987). Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Soc. Science Info.* **26**, 31-54.
- Boesch, C. (1991). Teaching among wild chimpanzees. *Anim. Behav.* **41**, 531-532.
- Boesch, C. (1994). Hunting strategies of Gombe and Taï chimpanzees. In "Chimpanzee Cultures" (R. W. Wrangham, W. C. McGrew, F. B. M. de Waal and P. G. Heltne, Eds), pp. 77-91. Harvard University Press, Harvard.
- Boesch, C. and Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *Am. J. Phys. Anthropol.* **78**, 547-573.
- Boesch, C. and Boesch-Achermann, H. (2000). "The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution" Oxford University Press, Oxford.
- Boinski, S. and Fraga, D. M. (1989). The ontogeny of foraging in squirrel monkeys, *Saimiri oerstedii*. *Anim. Behav.* **37**, 415-428.
- Brockmann, H. J. and Barnard, C. J. (1979). Kleptoparasitism in birds. *Anim. Behav.* **27**, 487-514.
- Brotherton, P. N. M., Clutton-Brock, T. H., O'Riain, M. J., Gaynor, D., Sharpe, L., Kansky, R. and McIlrath, G. M. (2001). Offspring food allocation by parents and helpers in a cooperative mammal. *Behav. Ecol.* **12**, 590-599.
- Brown, G. R. (2004). Tolerated scrounging in non-human primates. *Behav. Brain Sci.* **27**, 562-563.

- Brown, G. R., Almond, R. E. A. and Bates, N. (2005). Adult-infant food transfer in common marmosets: an experimental study. *American Journal of Primatology* **65**, 301-312.
- Brown, K. and Mack, D. S. (1978). Food sharing among captive *Leontopithecus rosalia*. *Folia Primatol.* **29**, 268-290.
- Byrne, R. W. (1999). Cognition in great ape ecology: skill-learning ability opens up foraging opportunities. In "Mammalian Social Learning: Comparative and Ecological Perspectives" (H. O. Box and K. R. Gibson, Eds), pp. 333-350. Cambridge University Press, Cambridge.
- Caine, N. G., Addington, R. L. and Windfelder, T. L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Anim. Behav.* **50**, 53-60.
- Caldwell, C. and Whiten, A. (2003). Scrounging facilitates social learning in common marmosets, *Callithrix jacchus*. *Anim. Behav.* **65**: 1085-1092.
- Caraco, T. and Brown, J. L. (1986). A game between communal breeders: when is food-sharing stable? *J. Theor. Biol.* **118**, 379-393.
- Caro, T. M. and Hauser, M. D. (1992). Is there teaching in nonhuman animals? *Q. Rev. Biol.* **67**, 151-174.
- Carpenter, C. R. (1965). The howlers of Barro Colorado island. In "Primate Behavior: Field Studies of Monkeys and Apes" (I. DeVore, Ed), pp. 250-291. Holt, Rinehart and Winston, New York.
- Cebul, M. S. and Epple, G. (1984). Father-offspring relationships in laboratory families of saddle-back tamarins (*Saguinus fuscicollis*). In "Primate Paternalism" (D. M. Taub, Ed), pp. 1-19. Van Nostrand Reinhold Company, New York.
- Chalmers, N. R. and Locke-Haydon, J. (1984). Correlations among measures of playfulness and skillfulness in captive common marmosets (*Callithrix jacchus jacchus*). *Devel. Psychobiol.* **17**, 191-208.
- Chapman, C. A. and Lefebvre, L. (1990). Manipulating foraging group size: spider monkey food calls at fruiting trees. *Anim. Behav.* **39**, 891-896.
- Cheney, D. L. and Seyfarth, R. M. (1990). "How Monkeys See the World: Inside the Mind of Another Species." University of Chicago Press, Chicago.
- Clutton-Brock, T. H., Brotherton, P. N. M., O'Riain, M. J., Griffin, A. S., Gaynor, D., Kansky, R., Sharpe, L. and McIlrath, G. M. (2001). Contributions to cooperative rearing in meerkats. *Anim. Behav.* **61**, 705-710.
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Young, A. J., Balmforth, Z. and McIlrath, G. M. (2002). Evolution and development of sex differences in cooperative behavior in meerkats. *Science* **297**, 253-256.
- Coates, A. and Poole, T. B. (1983). The behaviour of the callitrichid monkey, *Saguinus labiatus labiatus*, in the laboratory. *Int. J. Primatol.* **4**, 339-371.
- Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. *Ann. Rev. Ecol. System.* **29**, 141-177.
- Corp, N. and Byrne, R. W. (2002). The ontogeny of manual skill in wild chimpanzees: evidence from feeding on the fruit of *Saba florida*. *Behaviour* **139**, 137-168.

- Dare, R. (1974). Food-sharing in free-ranging *Ateles geoffroyi* (red spider monkeys). *Lab. Primate Newsletter* **13**, 19-21.
- Di Bitetti, M. S. and Janson, C. H. (2001). Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. *Anim. Behav.* **62**, 47-56.
- Dietz, J. M. and Baker, A. J. (1993). Polygyny and female reproductive success in golden lion tamarins, *Leontopithecus rosalia*. *Anim. Behav.* **46**, 1067-1078.
- Dittus, W. P. J. (1984). Toque macaque food calls: semantic communication concerning food distribution in the environment. *Anim. Behav.* **32**, 470-477.
- Drapier, M. and Thierry, B. (2002). Social transmission of feeding techniques in tonkean macaques. *Int. J. Primatol.* **23**, 105-122.
- Elowson, A. M., Tannenbaum, P. L. and Snowdon, C. T. (1991). Food-associated calls correlate with food preferences in cotton-top tamarins. *Anim. Behav.* **42**, 931-937.
- Emlen, S. T. (1991). Evolution of cooperative breeding in birds and mammals. In "Behavioural Ecology: an Evolutionary Approach 3<sup>rd</sup> Edition" (J. R. Krebs and N. B. Davies, Eds), pp. 301-337. Blackwell Scientific Publishing, Oxford.
- Evans, C. S. and Evans, L. (1999). Chicken food calls are functionally referential. *Anim. Behav.* **58**, 307-319.
- Feistner, A. T. C. and Chamove, A. S. (1986). High motivation towards food increases food-sharing in cotton-top tamarins. *Devel. Psychobiol.* **19**, 439-452.
- Feistner, A. T. C. and McGrew, W. C. (1989). Food-sharing in primates: a critical review. In "Perspectives in Primate Biology, Vol. 3" (P. K. Seth and S. Seth, Eds), pp. 21-36. Today and Tomorrow's Printers and Publishers, New Delhi.
- Feistner, A. T. C. and Price, E. C. (1990). Food-sharing in cotton-top tamarins (*Saguinus oedipus*). *Folia Primatol.* **54**, 34-45.
- Feistner, A. T. C. and Price, E. C. (1991). Food offering in New World primates: two species added. *Folia Primatol.* **57**, 165-168.
- Feistner, A. T. C. and Price, E. C. (2000). Food sharing in black lion tamarins (*Leontopithecus chrysopygus*). *Am. J. Primatol.* **52**, 47-54.
- Ferrari, S. F. (1987). Food transfers in a wild marmoset group. *Folia Primatol.* **48**, 203-206.
- Ferrari, S. F. (1992). The care of infants in a wild marmoset (*Callithrix flaviceps*) group. *Am. J. Primatol.* **26**, 109-118.
- Flettemeyer, J. R. (1978). Communication about potentially harmful foods in free-ranging chacma baboons, *Papio ursinus*. *Primates* **19**, 223-226.
- Fragaszy, D. M. and Bard, K. (1997). Comparison of development and life history in *Pan* and *Cebus*. *Int. J. Primatology* **18**, 683-701.
- Fragaszy, D. M., Feuerstein, J. M. and Mitra, D. (1997). Transfers of food from adults to infants in tufted capuchins (*Cebus apella*). *J. Comp. Psychol.* **111**, 194-200.

- Fragaszy, D. M. and Perry, S. (2003). "The Biology of Traditions: Models and Evidence." University of Chicago Press, Chicago.
- Fragaszy, D. M and Visalberghi, E. (1996). Social learning in monkeys: primate "primacy" reconsidered. In "Social Learning in Animals: the Roots of Culture" (C. M. Heyes and B. G. Galef, Eds), pp. 65-84. Academic Press, San Diego.
- Galef, B. G. (1996). Social enhancement of food preferences in Norway rats: a brief review. In "Social Learning in Animals: the Roots of Culture" (C. M. Heyes and B. G. Galef, Eds), pp. 49-64. Academic Press, San Diego.
- Galef, B. G. (2003). Social learning: promotor or inhibitor of innovation? In "Animal Innovation" (S. M. Reader and K. N. Laland, Eds). O.U.P., Oxford. Pp. 137-152.
- Galef, B. G. and Giraldeau, L. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim. Behav.* **61**, 3-15.
- Galef, B. G., Marczinski, C. A., Murray, K. A. and Whiskin, E. E. (2001). Food stealing by young Norway rats. *J. Comp. Psychol.* **115**, 16-21.
- Garber, P. A. and Leigh, S. R. (1997). Ontogenetic variation in small-bodied New World primates: implications for patterns of reproduction and infant care. *Folia Primatol.* **68**, 1-22.
- Garber, P. A., Moya, L. and Malaga, C. (1984). A preliminary field study of the moustached tamarin monkey (*Saguinus mystax*) in northeastern Peru: questions concerned with the evolution of a communal breeding system. *Folia Primatol.* **42**, 17-32.
- Giraldeau, L.-A. and Beauchamp, G. (1999). Food exploitation: searching for the optimal joining policy. *Trends Ecol. Evol.* **14**, 102-106.
- Giraldeau, L.-A. and Caraco, T. (2000). "Social Foraging Theory." Princeton University Press, Princeton.
- Giraldeau, L.-A. and Lefebvre, L. (1987). Scrounging prevents cultural transmission of food-finding behaviour in pigeons. *Anim. Behav.* **35**, 387-394.
- Goldizen, A. W. (1989). Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus fuscicollis*). *Behav. Ecol. Sociobiol.* **24**, 79-89.
- Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream reserve. *Anim. Behav. Monographs* **1**, 161-311.
- Goodall, J. (1986). "The Chimpanzees of Gombe: Patterns of Behavior." Harvard University Press, Harvard.
- Gursky, S. (2000). Allocare in a nocturnal primate: data on the spectral tarsier, *Tarsius spectrum*. *Folia Primatol.* **71**, 39-54.
- Gurven, M. (2004). To give and not to give: the behavioral ecology of human food transfers. *Behav. Brain Sci.* **27**, 543-583.
- Hamilton, I. M. (2002). Kleptoparasitism and the distribution of unequal competitors. *Behav. Ecol.* **13**, 260-267.
- Hauser, M. D. (1996). "The Evolution of Communication." MIT Press, Cambridge MA.

- Hauser, M. D., Chen, M. K., Chen, F. and Chuang, E. (2003). Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proc. R. Soc. Lond. B* **270**, 2363-2370.
- Hauser, M. D. and Marler, P. (1993a). Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. *Behav. Ecol.* **4**, 194-205.
- Hauser, M. D. and Marler, P. (1993b). Food-associated calls in rhesus macaques (*Macaca mulatta*): II. Costs and benefits of call production and suppression. *Behav. Ecol.* **4**, 206-212.
- Hauser, M. D. and Wrangham, R. W. (1987). Manipulation of food calls in captive chimpanzees. *Folia Primatol.* **48**, 207-210.
- Hemelrijk, C. K., Meier, C. and Martin, R. D. (1999). 'Friendship' for fitness in chimpanzees? *Anim. Behav.* **58**, 1223-1229.
- Heyes, C. M. and Galef, B. G. (1996). "Social Learning in Animals: the Roots of Culture." Academic Press, San Diego.
- Heymann, E. W. (1996). Social behavior of wild moustached tamarins, *Saguinus mystax*, at the Estación Biológica Quebrada Blanco, Peruvian Amazonia. *Am. J. Primatol.* **38**, 101-113.
- Heymann, E. W. and Soini, P. (1999). Offspring number in pygmy marmosets, *Cebuella pygmaea*, in relation to group size and the number of adult males. *Behav. Ecol. Sociobiol.* **46**, 400-404.
- Hiraiwa-Hasegawa, M. (1990a). Role of food sharing between mother and infant in the ontogeny of feeding behavior. In "The Chimpanzees of the Mahale Mountain: Sexual and Life History Strategies" (T. Nishida, Ed), pp. 267-275. University of Tokyo Press, Tokyo.
- Hiraiwa-Hasegawa, M. (1990b). A note on the ontogeny of feeding. In "The Chimpanzees of the Mahale Mountain: Sexual and Life History Strategies" (T. Nishida, Ed), pp. 277-283. University of Tokyo Press, Tokyo.
- Hirata, S. and Celli, M. L. (2003). Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. *Anim. Cogn.* **6**, 235-244.
- Hoage, R. J. (1982). Social and physical maturation in captive lion tamarins, *Leontopithecus rosalia rosalia* (Primates: Callitrichidae). *Smithsonian Contrib. Zool.* **354**, 1-56.
- Isaac, G. (1978). The food-sharing behavior of protohuman hominids. *Scientific American* **238**, 90-108.
- Izawa, K. (1978). A field study of the ecology and behavior of the black-mantle tamarin (*Saguinus nigricollis*). *Primates* **19**, 241-274.
- Jennions, M. D. and Macdonald, D. W. (1994). Cooperative breeding in mammals. *Trends Ecol. Evol.* **9**, 89-93.
- Jurke, M. H. and Pryce, C. R. (1994). Parental and infant behaviour during early periods of infant care in Goeldi's monkey, *Callimico goeldii*. *Anim. Behav.* **48**, 1095-1112.
- King, B. J. (1991). Social information transfer in monkeys, apes, and hominids. *Yrbk Phys. Anthropol.* **34**, 97-115.

- King, B. J. 1994. "The Information Continuum: Evolution of Social Information Transfer in Monkeys, Apes, and Hominids." School of American Research Press, New Mexico.
- King, B. J. (1999). New directions in the study of primate learning. In "Mammalian Social Learning: Comparative and Ecological Perspectives" (H. O. Box and K. R. Gibson, Eds), pp. 17-32. Cambridge University Press. Cambridge.
- Koenig, A. (1995). Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *Am. J. Primatol.* **35**, 311-317.
- Kokko, H., Johnstone, R. A. and Clutton-Brock, T. H. (2001). The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond. B* **268**, 187-196.
- Kuroda, S. (1984). Interactions over food among pygmy chimpanzees. In "The Pygmy Chimpanzee: Evolutionary Biology and Behavior" (R. L. Susman, Ed), pp. 301-324. Plenum Press, New York.
- Langen, T. A. (2000). Prolonged offspring dependence and cooperative breeding in birds. *Behav. Ecol.* **11**, 367-377.
- Lefebvre, L. (1985). Parent-offspring food sharing: a statistical test of the early weaning hypothesis. *J. Human Evol.* **14**, 255-261.
- Lonsdorf, E. V., Eberly, L. E. and Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature* **428**, 715-716.
- Maestripieri, D. and Call, J. (1996). Mother-infant communication in primates. *Adv. Study Behav.* **25**, 613-642.
- Maestripieri, D., Ross, S. K. and Megna, N. L. (2002). Mother-infant interactions in western lowlands gorillas (*Gorilla gorilla gorilla*): spatial relationships, communication, and opportunities for social learning. *J. Comp. Psychol.* **116**, 219-227.
- Malcolm, J. R. and Marten, K. (1982). Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behav. Ecol. Sociobiol.* **10**, 1-13.
- McGrew, W. C. (1975). Patterns of plant food sharing by wild chimpanzees. In "Contemporary Primatology; Proc. 5<sup>th</sup> Int. Congr. Primat., Nagoya" (S. Kondo, M. Kawai, and A. Ehara, Eds), pp. 304-309.
- Midford, P. E., Hailman, J. P. and Woolfenden, G. E. (2000). Social learning of a novel foraging patch in families of free-living Florida scrub jays. *Anim. Behav.* **59**, 1199-1207.
- Mitani, J. C. and Watts, D. (1997). The evolution of non-maternal caretaking among anthropoid primates: do helpers help? *Behav. Ecol. Sociobiol.* **40**, 213-220.
- Mitani, J. C. and Watts, D. P. (1999). Demographic influences on the hunting behavior of chimpanzees. *Am. J. Phys. Anthropol.* **109**, 439-454.
- Mitani, J. C. and Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Anim. Behav.* **61**, 915-924.

- Moehlman, P. D. and Hofer, H. (1997). Cooperative breeding, reproductive suppression, and body mass in canids. In "Cooperative Breeding in Mammals" (N. G. Solomon and J. A. French, Eds), pp. 76-128. Cambridge University Press, Cambridge.
- Moody, M. I. and Menzel, E. W. (1976). Vocalizations and their behavioral contexts in the tamarin *Saguinus fuscicollis*. *Folia Primatol.* **25**, 73-94.
- Nettelbeck, A. R. (1998). Observations on food sharing in wild lar gibbons (*Hylobates lar*). *Folia Primatol.* **69**, 386-391.
- Nicolson, N. A. (1986). Infants, mothers, and other females. In "Primate Societies" (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Strusaker, Eds), pp. 330-342. Chicago: University of Chicago Press.
- Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y. and Uehara, S. (1992). Meat-sharing as a coalition strategy by an alpha male chimpanzee? In "Topics in Primatology, Volume 1: Human Origins" (T. Nishida, W. C. McGrew, P. Marler, M. Pickford and F. B. M. de Waal, Eds), pp. 159-174. University of Tokyo Press, Tokyo.
- Nishida, T. and Turner, L. A. (1996). Food transfer between mother and infant chimpanzees of the Mahale Mountains National Park, Tanzania. *Int. J. Primatol.* **17**, 947-968.
- Nishida, T., Wrangham, R. W., Goodall, J. and Uehara, S. (1983). Local differences in plant-feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park, Tanzania. *J. Human Evol.* **12**, 467-480.
- Perry, S. and Rose, L. (1994). Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capuchinus*. *Primates* **35**, 409-415.
- Price, E. C. (1992a). Contributions to infant care in captive cotton-top tamarins (*Saguinus oedipus*): the influence of age, sex, and reproductive status. *Int. J. Primatol.* **13**, 125-141.
- Price, E. C. (1992b). The benefit of helpers: effects of group and litter size on infant care in tamarins (*Saguinus oedipus*). *Am. J. Primatol.* **26**, 179-190.
- Price, E. C. and Feistner, A. T. C. (1993). Food sharing in lion tamarins: tests of three hypotheses. *Am. J. Primatol.* **31**, 211-221.
- Price, E. C. and Feistner, A. T. C. (2001). Food sharing in pied bare-faced tamarins (*Saguinus bicolor bicolor*): development and individual differences. *Int. J. Primatol.* **22**, 231-2241.
- Queyras, A., Scolavino, M., Puopolo, M. and Vitale, A. (2000). Social influence on induced food preference in common marmosets (*Callithrix jacchus*). *Folia Primatol.* **71**, 367-374.
- Rapaport, L. G. (1999). Provisioning of young in golden lion tamarins (Callitrichidae, *Leontopithecus rosalia*): a test of the information hypothesis. *Ethology* **105**, 619-636.
- Rapaport, L. G. (2001). Food transfer among adult lion tamarins: mutualism, reciprocity or one-sided relationships? *Int. J. Primatol.* **22**, 611-629.

- Rose, L. M. (2001). Meat and the early human diet: Insights from neotropical primate studies. In “Meat-Eating and Human Evolution” (C. B. Stanford and H. T. Bunn, Eds), pp. 141-159. Oxford University Press, Oxford.
- Ross, C. and Jones, K. E. (1999). Socioecology and the evolution of primate reproductive rates. In “Comparative Primate Socioecology” (P. C. Lee, Ed), pp. 73-110. Cambridge University Press, Cambridge.
- Ross, C. and MacLarnon, A. (2000). The evolution of non-maternal care in anthropoid primates: a test of the hypotheses. *Folia Primatol.* **71**, 93-113.
- Rothe, H. and Darms, K. (1993). The social organisation of marmosets: a critical evaluation of recent concepts. In “Marmosets and Tamarins; Systematics, Behaviour, and Ecology” (A. B. Rylands, Ed), Pp. 11-77. Oxford University Press, Oxford.
- Roush, R. S. and Snowdon, C. T. (2000). Quality, quantity, distribution and audience effects on food calling in cotton-top tamarins. *Ethology* **106**, 673-690.
- Roush, R. S. and Snowdon, C. T. (2001). Food transfer and development of feeding behavior and food-associated vocalizations in cotton-top tamarins. *Ethology* **107**, 415-429.
- Ruiz-Miranda, C. R., Kleiman, D. G., Dietz, J. M., Moraes, E., Grativil, A. D., Baker, A. J. and Beck, B. B. (1999). Food transfers in wild and reintroduced golden lion tamarins, *Leontopithecus rosalia*. *Am. J. Primatol.* **48**, 305-320.
- Russell, A. F., Clutton-Brock, T. H., Brotherton, P. N. M., Sharpe, L. L., McIlrath, G. M., Dalerum, F. D., Cameron, E. Z. and Barnard, J. A. (2002). Factors affecting pup growth and survival in co-operatively breeding meerkats *Suricata suricatta*. *J. Anim. Ecol.* **71**, 700-709.
- Russon, A. E. (1997). Exploiting the expertise of other. In “Machiavellian Intelligence II, Extensions and Evaluations” (A. Whiten and R. W. Byrne, Eds), pp. 174-206. Cambridge University Press, Cambridge.
- Russon, A. E. (2003). Developmental perspectives on great ape traditions. In “The Biology of Traditions: Models and Evidence” (D. Fragaszy and S. Perry, Eds), Cambridge University Press, Cambridge.
- Schessler, T. and Nash, L. T. (1977). Food sharing among captive gibbons (*Hylobates lar*). *Primates* **18**, 677-689.
- Sherry, D. F. and Galef, B. G. (1984). Cultural transmission without imitation: milk bottle opening by birds. *Anim. Behav.* **32**, 937-938.
- Silk, J. B. (1978). Patterns of food sharing among mother and infant chimpanzees at Gombe National Park, Tanzania. *Folia Primatol.* **29**, 129-141.
- Silk, J. B. (1979). Feeding, foraging, and food sharing behavior of immature chimpanzees. *Folia Primatol.* **31**, 123-142.
- Snowdon, C. T. (1996). Infant care in cooperatively breeding species. *Adv. Study Behav.* **25**, 643-689.
- Snowdon, C. T. (2001). Social processes in communication and cognition in callitrichid monkeys: a review. *Animal Cogn.* **4**, 247-257.

- Snowdon, C. T. and Boe, C. Y. (2003). Social communication about unpalatable foods in tamarins. *J. Comp. Psychol.* **117**: 142-148.
- Stanford, C. B. (1999). "The Hunting Apes: Meat Eating and the Origins of Human Behavior." Princeton University Press, Princeton, New Jersey.
- Stanford, C. B. and Bunn, H. T. (Eds.) (2001). "Meat-eating and Human Evolution." Oxford University Press, Oxford.
- Starin, E. D. (1978). Food transfer by wild titi monkeys (*Callicebus torquatus torquatus*). *Folia Primatol.* **30**, 145-151.
- Stevens, J. R. (2004). The selfish nature of generosity: harassment and food sharing in primates. *Proc. R. Soc. Lond. B* **271**, 451-456.
- Stevens, J. R. and Cushman, F. A. (2004). Cognitive constraints on reciprocity and tolerated scrounging. *Behav. Brain Sci.* **27**, 569-570.
- Stevens, J. R. and Gilby, I. C. (2004). A conceptual framework for nonkin food sharing: timing and currency of benefits. *Anim. Behav.* **67**, 603-614.
- Stevens, J. R. and Stephens, D. W. (2002). Food sharing: a model of manipulation by harassment. *Behav. Ecol.* **13**, 393-400.
- Stevenson, M. F. and Poole, T. B. (1976). An ethogram of the common marmoset (*Callithrix jacchus jacchus*): general behavioural repertoire. *Anim. Behav.* **24**, 428-451.
- Takahata, Y., Hasegawa, T. and Nishida, T. (1984). Chimpanzee predation in the Mahale mountains from August 1979 to May 1982. *Int. J. Primatol.* **5**, 213-233.
- Tardif, S. D. (1997). The bioenergetics of parental behavior and the evolution of alloparental care in marmosets and tamarins. In "Cooperative Breeding in Mammals" (N. G. Solomon and J. A. French, Eds), pp. 11-33. Cambridge University Press, Cambridge.
- Teleki, G. (1973). "The Predatory Behavior of Wild Chimpanzees." Bucknell University Press, Lewisburg.
- Terkel, J. (1996). Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). In "Social Learning in Animals: the Roots of Culture" (C. M. Heyes and B. G. Galef, Eds), pp. 17-47. Academic Press, San Diego.
- Trivers, R. L. (1974). Parent-offspring conflict. *Am. Zool.* **14**, 249-264.
- Utami, S. S. and van Hooff, J. A. R. A. M. (1997). Meat-eating by adult female Sumatran orangutans (*Pongo pygmaeus abelii*). *Am. J. Primatol.* **43**, 159-165.
- Vitale, A. and Queyras, A. (1997). The response to novel foods in common marmoset (*Callithrix jacchus*): the effects of different social contexts. *Ethology* **103**, 395-403.
- de Waal, F. B. M. (1989). Food sharing and reciprocal obligations among chimpanzees. *J. Human Evol.* **18**, 433-459.
- de Waal, F. B. M. (1997a). The chimpanzee's service economy: food for grooming. *Evol. Human Behav.* **18**, 375-386.

- de Waal, F. B. M. (1997b). Food transfers through mesh in brown capuchins. *J. Comp. Psychol.* **111**, 370-378.
- de Waal, F. B. M. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Anim. Behav.* **60**, 253-261.
- de Waal, F. B. M., Luttrell, L. M. and Canfield, M. E. (1993). Preliminary data on voluntary food sharing in brown capuchin monkeys. *Am. J. Primatol.* **29**, 73-78.
- Washabaugh, K. F., Snowdon, C. T. and Ziegler, T. E. (2002). Variations in care for cottontop tamarin, *Saguinus oedipus*, infants as a function of parental experience and group size. *Anim. Behav.* **63**, 1163-1174.
- Westergaard, G. C., Haynie, M. K., Lundquist, A. L. and Suomi, S. J. (1999). Carrying, sharing, and hand preference in tufted capuchins (*Cebus apella*). *Int. J. Primatol.* **20**, 153-162.
- Westergaard, G. C., Kuhn, H. E., Babitz, M. A. and Suomi, S. J. (1998). Aimed throwing as a means of food transfer between tufted capuchins (*Cebus apella*). *Int. J. Primat.* **19**, 123-131.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. and Boesch, C. (1999). Cultures in chimpanzees. *Nature* **399**, 682-685.
- Winterhalder, B. (1996). Social foraging and the behavioral ecology of intragroup resource transfers. *Evol. Anthropol.* **5**, 46-57.
- Wolters, H. J. (1978). Some aspects of role taking behaviour in captive family groups of the cotton-top tamarin (*Saguinus oedipus oedipus*). In "Biology and Behaviour of Marmosets" (H. Rothe, H. Wolters and J. P. Hearn, Eds), pp. 259-278. Eigenverlag, Göttingen, Germany.
- Wrangham, R. W. (1975). "The behavioural ecology of chimpanzees in Gombe National Park, Tanzania." Unpublished Ph.D. thesis; University of Cambridge.
- Wright, P. C. (1984). Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In "Female Primates: Studies by Women Primatologists" (M. F. Small, Ed), pp 59-75. Alan Liss, New York.
- Yamagiwa, J. (1992). Functional analysis of social staring behavior in an all-male group of mountain gorillas. *Primates* **33**, 523-544.
- Zentall, T. R. and Galef, B. G. (1988). "Social Learning: Psychological and Biological Perspectives." Lawrence Erlbaum Associates, New Jersey.

**Table I** Definitions of behaviour patterns observed during food transfer events.

Term	Definition	Exemplars:
Interest	An individual looks at, touches or sniffs a food item that is in the possession of another individual	de Waal <i>et al.</i> , 1993; Perry & Rose, 1994; Wrangham, 1975
Beg	An individual exhibits specific posture (eg extended upturned hand) or specific vocalisation while showing interest	Feistner & Price, 1990; Goodall, 1968
Attempted transfer	An individual attempts to take a portion of a food item	Brown <i>et al.</i> , 2004
Transfer / provision	Any situation in which part or all of the food item changes possession from one individual to another	Brown & Mack, 1978; Blurton Jones, 1987
Displacement	An individual moves into the feeding position vacated by another individual	Yamagiwa, 1992; Nishida & Turner, 1996
Resist	An individual attempts to prevent transfer by moving or turning away, or by vocal or physical aggression or threat	Brown and Mack, 1978; Goodall, 1986
Steal	Food transfer occurs despite resistance by the possessor	Hoage, 1982; Ruiz-Miranda <i>et al.</i> , 1999
Offer	A food possessor passes food to another individual or adopts a specific posture and/or vocalises	Brown & Mack, 1978; Goodall, 1968; Hoage, 1982; Feistner & Chamove, 1986
Retrieve	An individual takes food that another individual has dropped on the ground or placed there	Boesch & Boesch, 1989

**Table II** Species in which infants or juveniles have been reported to obtain food via transfer from older group members. C = captive; FR = free-ranging.

Species	Habitat	References
Spectral tarsier, <i>Tarsius spectrum</i>	FR	Gursky, 2000
Bare-ear marmoset, <i>Callithrix argentata</i>	C	Feistner & Price, 1991
Buffy-headed marmoset, <i>Callithrix flaviceps</i>	FR	Ferrari, 1987; 1992
Geoffroy's marmoset, <i>Callithrix geoffroyi</i>	C	Feistner & Price, 1991
Common marmoset, <i>Callithrix jacchus</i>	C	Brown <i>et al.</i> , 2004; Chalmers & Locke-Haydon, 1984; Feistner & Price, 1991; Vitale & Quayras, 1997
Pied bare-faced tamarin, <i>Saguinus bicolor</i>	C	Price & Feistner, 2001
Saddle-back tamarin, <i>Saguinus fuscicollis</i>	C	Cebul & Epple, 1984;
	FR	Goldizen, 1989
Red-bellied tamarins, <i>Saguinus labiatus</i>	C	Coates & Poole, 1983; Cebul & Epple, 1984; Feistner & Price, 1991
Moustached tamarin, <i>Saguinus mystax</i>	FR	Heymann, 1996
Black-mantle tamarin, <i>Saguinus nigricollis</i>	FR	Izawa, 1978
Cotton-top tamarin, <i>Saguinus oedipus</i>	C	Feistner & Chamove, 1986; Feistner & Price, 1990; 1991; Roush & Snowdon, 2001
Black lion tamarin, <i>Leio. chrysopygus</i>	C	Feistner & Price, 2000
Golden lion tamarin, <i>Leontopithecus rosalia</i>	C	Brown & Mack, 1978; Hoage, 1982; Price & Feistner, 1993; Rapaport, 1999
	FR	Ruiz-Miranda <i>et al.</i> , 1999
Pygmy marmoset, <i>Cebuella pygmaea</i>	C	Feistner & Price, 1991
Goeldi's monkey, <i>Callimico goeldii</i>	C	Jurke & Pryce, 1994; Feistner & Price, 1991
Dusky titi monkey, <i>Callicebus moloch</i>	FR	Wright, 1984
Yellow-handed titi, <i>Callicebus torquatus</i>	FR	Starin, 1978
Owl monkey, <i>Aotus trivirgatus</i>	C	Wright, 1984
Tufted capuchin, <i>Cebus apella</i>	C	Fragszy <i>et al.</i> , 1997
White-faced capuchin, <i>Cebus capucinus</i>	FR	Rose, 2001
Howler monkey, <i>Alouatta palliata</i>	FR	Carpenter, 1965
Spider monkey, <i>Ateles geoffroyi</i>	FR	Dare, 1974
White handed gibbons, <i>Hylobates lar</i>	C	Schessler & Nash, 1977
	FR	Nettelbeck, 1998
Orangutan, <i>Pongo pygmaeus</i>	FR	Russon, 2003; Utami & van Hooff, 1997;
Gorilla, <i>Gorilla gorilla</i>	C	Maestripieri <i>et al.</i> , 2002
Bonobo, <i>Pan paniscus</i>	FR	Kuroda, 1984

Chimpanzee, <i>Pan troglodytes</i>	C	Silk, 1979
	FR	Goodall, 1968; 1986; Silk, 1978; Nishida & Turner, 1996; Boesch & Boesch-Achermann, 2000

**Table III** The relative contributions of mothers, fathers and alloparents to provisioning infants with food (N = total number of provisioners in each class of individuals in study, listed in the same order as under relative contribution)

Species	Relative contribution	N	References
Spectral tarsier, <i>Tarsius spectrum</i>	mothers > subadult female > males	6,1,7	Gursky, 2000
Common marmoset, <i>Callithrix jacchus</i>	fathers = mothers > siblings	4,4,5	Vitale & Queyras, 1997
Pied bare-faced tamarin, <i>Saguinus bicolor</i>	fathers > mothers	3,3,	Price & Feistner, 2001
Saddle-back tamarin, <i>Saguinus fuscicollis</i>	siblings > mothers > fathers	3,5,5	Cebul & Epple, 1984
Cotton-top tamarin, <i>Saguinus oedipus</i>	fathers > mothers	6,6	Wolters, 1978
	parents > siblings	16,46	Price, 1992a
	fathers > others	5,17	Roush & Snowdon, 2001
Owl monkey, <i>Aotus trivirgatus</i>	father > mother	1,1	Wright, 1984
Dusky titi monkey, <i>Callicebus moloch</i>	father > mother	1,1	Wright, 1984
Yellow-handed titi monkey, <i>C. torquatus</i>	father > sibling > mother	1,1,1	Starin, 1978