RESEARCH ARTICLE

Food Transfers to Young and Mates in Wild Owl Monkeys (*Aotus azarai*)

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Accounts of food sharing within natural populations of mammals have focused on transfers to offspring or transfers of food items that are difficult to obtain (such as meat). Five groups of socially monogamous owl monkeys (*Aotus azarai azarai*) in Formosa, Argentina were observed during 107 hr to determine the pattern of food sharing under natural conditions. There were a total of 42 social interactions involving food with food being transferred on eight occasions. Adult males transferred food to young more often than did adult females. All types of food that were readily obtained and eaten by all age/sex classes were transferred to young. Adult females also transferred food to their mates. This type of food sharing is very rare among animals and may have social benefits specific to monogamous mammals with paternal care. Am. J. Primatol. 70:211–221, 2008. © 2007 Wiley-Liss, Inc.

INTRODUCTION

Food sharing, a transfer of a defensible food item from one food-motivated individual to another [Feistner & McGrew, 1989], is an affiliative social behavior that, when food is limited, imposes an immediate energetic cost of reduced potential caloric intake. Food sharing has evolved despite this cost, suggesting that there are compensatory fitness advantages to food donors. For the most common form of food sharing, between mothers and offspring, this advantage is clear. Because infants that receive food have greater chances of survival, females can increase their own fitness by sharing food with their offspring. In general, mothers transfer food to offspring when it is difficult for infants to obtain the food independently [in golden lion tamarins, *Leontopithecus rosalia*, Price & Feistner. 1993; in capuchins, *Cebus apella*, Fragaszy et al., 1997], and when the food is rare, of high quality, or requires considerable strength, experience, or fine motor skills to obtain or possess (e.g. meat, insects, hard-shelled fruits in chimpanzees, *Pan troglodytes* [Silk, 1979]; in cotton-top tamarins, *Saguinus oedipus oedipus,* [Feistner & Chamove, 1986]). In addition to ensuring adequate infant nutrition, provisioning young may also offer the recipients valuable information regarding foraging techniques and/or the palatability of particular foods [Rapaport, 2006].

Food sharing from adult males to young is expected to arise when males have relatively high levels of paternal certainty [Trivers, 1972] and/or when caregiving by males represents a form of courtship behavior used by females in selecting mates or breeding with males [Price, 1990, 1991]. Although paternal care does not always coexist with paternal certainty [van Schaik and Paul, 1996; Wright, 1990], there can be substantial fitness benefits for adult males to invest in infant care [Garber, 1997]. Males who invest in paternal care may also reduce the energetic burden that lactation poses on their mates and, therefore, allow their mates to become pregnant again sooner [Brown & Mack, 1978; Holekamp & Smale, 1990; Lappan, 2006]. Interbirth intervals would subsequently be reduced, increasing male fitness. Food sharing by adult males has been described for several socially monogamous species (titi monkeys, *Callicebus torquatus torquatus* [Starin, 1978]; beavers, *Castor canadensis* [Buech, 1995]; white-handed gibbons, *Hylobates lar* [Nettelbeck, 1998] wolves, *Canis lupis* [Mech et al., 1999]; owl monkeys, *Aotus* spp. [Wolovich et al., 2006]), and for cooperatively rearing

species (*Leontopithecus rosalia* [Brown & Mack, 1978]; *Callithrix flaviceps* [Ferrari, 1992]; *Saguinus mystax* [Heymann, 1996; Huck et al., 2004]; *Saguinus oedipus oedipus* [Roush & Snowdon, 2001]).

Food sharing between adults is even more rare than between males and young [Feistner & McGrew, 1989]. Possible benefits of males sharing food with females include indirect contributions to the care of offspring that those males are likely to have sired, increased mating opportunities, and/or increased fecundity of their mates. For example, courtship feeding in birds provides females with extra nutrients resulting in an increased number of eggs produced [common terns, *Sterna hirundo*, Gonzalez-Solis et al., 2001; Nisbet, 1973, 1977; red-billed gulls, *Larus novaehollandiae scopulinus*, Tasker & Mills, 1981]. In insects, males that offer nuptial gifts to females obtain more copulations and fertilize more eggs than other males [bushcrickets, *Anabrus simplex*, Gwynne, 1984; katydids, *Requena verticalis*, Gwynne, 1986; fireflies, *Ellychia corrusca*, *Photinus ignitus*, Rooney & Lewis, 2002], whereas females that consume a nuptial gift produce larger eggs and a larger clutch size than females that do not [Gwynne, 1984]. Food sharing may serve an additional function in species that form social bonds between mates: adults may use food transfers to convey information about or to strengthen those bonds [Brown & Mack, 1978; Lack, 1940; Ruiz-Miranda et al., 1999; Wilson, 1976].

Owl monkeys (*Aotus* spp.) are socially monogamous primates with extensive male care of offspring [Rotundo et al., 2002; Wright, 1984]. Infants begin eating solid food around 4 weeks of age [Rotundo et al., 2005; Wolovich & Evans, 2004], but are not weaned until after 5 months of age [Dixson & Fleming, 1981] and may continue to nurse until they are 8 months of age [Rotundo et al., 2005]. Individuals disperse from their natal group when they are between 2 and 4 years of age [Fernandez-Duque, 2007] and reach a reproductive position in a group a couple of years later.

Although there is conclusive evidence that captive owl monkeys transfer food from adults to offspring and between adults [Wolovich et al., 2006; Wright, 1984], patterns of food sharing in wild owl monkeys under a natural regime of food availability have not been examined. Wild owl monkeys in Argentina (*Aotus azarai*) share food with infants [Rotundo et al., 2005], but details of these food transfers have not been described. More importantly, it is unknown whether food transfers occur between mates. This study aimed to describe the patterns of food transfer in a wild population of owl monkeys with respect to age and sex as well as the type of food transferred.

METHODS

Study Site and Subjects

The study site is located within Estancia Guaycolec, a 25,000 ha cattle ranch in Formosa Province, Argentina. An undisturbed portion of the ranch contains semi-deciduous gallery forest that is continuous along the Riacho Pilagá river where the studied population of owl monkeys (*A. azarai azarai*) is located [Fernandez-Duque et al., 2001]. This region of Argentina is highly seasonal in rainfall, temperature, and photoperiod [Fernandez-Duque et al., 2002].

Five habituated social groups were systematically observed between June and September 2005 (Table I). These are the months when most copulations take place and when conceptions are most likely to occur because births are concentrated in October and November [Fernandez-Duque et al., 2002]. The adults had been sexed and marked with unique patterns of shaved hair on their tails, and one adult in each social group had been fitted with a Telonics MOD-080 radio collar (Telonics Inc., Mesa, AZ) [Fernandez-Duque & Rotundo, 2003] making all adults identifiable. The remaining individuals were distinguishable by size or by uniquely patterned beaded collars. Young individuals were defined as individuals within groups that were not reproducing adults. The sexes of the young were unknown. The male in Group D500 entered the group between March and May 2004 and was unlikely to be the father of the young born in October 2003.

TABLE I. Compositions of Study Groups

Group name	Adult male	Time observed (hours)	Adult female	Time observed (hours)	Age of young (months)
C0	Cesar	3.7	Celina	3.7	N/A
D100	Durazno	5.5	Duquesa	4.6	6.5
D500	Dido	7.6	Dinamita	8.3	20
E350	Erico	7.5	Eva	8.1	18.5
F1200	Dardo	7.0	Fumata	6.7	9

Sampling effort is listed for each adult and represents the total time spent in-view. When the groups had young present, the age of the young is reported. N/A, no young present.

General Protocol

Owl monkeys at Estancia Guaycolec are active during both day and night. Much of this daytime activity occurs during morning and evening twilight [Fernandez-Duque, 2003; Fernandez-Duque & Eckert, 2006]. The monkeys were observed during the twilight hours and during the morning and afternoon activity bouts that typically occur during the cold winter months [Fernandez-Duque, 2003; Fernandez-Duque & Eckert, 2006; Wright, 1985]. No observations were made at night because even with the aid of night vision binoculars it is extremely difficult to accurately identify individuals and to monitor details of social behavior. All research complied with protocols approved by the Animal Care and Use Committees of the San Diego Zoo and the University of Pennsylvania and adhered to the legal requirements of Argentina.

Two observers located a group before sunrise using a two-element antenna and a TR-4 receiver (Telonics Inc., Mesa, AZ). Once the group was located, the individuals were observed until they went to sleep mid-morning. Both observers remained with the monkeys until they awoke a few hours later. Observations then resumed during the subsequent activity bout that lasted between 20 min and 1 hr. Another group was located during the late afternoon before the monkeys started their dusk activity bout. Observations were made from the time the monkeys became active until sunset for approximately 1–1.5 hr. Observation periods lasted 20 min or until it was too dark to see the animal's behavior. The observation schedule was designed by systematically rotating observations among the five groups, alternating morning and afternoon observations for each group.

Behavioral Observations

One observer monitored the adult male, whereas the other observer simultaneously monitored the adult female. The observers alternated focal subjects with each 20-min observation period. Instantaneous sampling with 1-min intervals was used to record behavioral state (resting, moving, social, or feeding) and to collect data on the amount of time feeding on different food types. When a monkey was manipulating, holding, or chewing plant material it was scored as feeding, and the type of food (flowers, fruit, new leaves, mature leaves, or unknown) was recorded.

A food interaction was scored every time when two monkeys were within arms' reach of each other and at least one monkey had a food item and the other monkey's face was oriented toward the food and that monkey moved its face or hand toward the food item. For each food interaction, the identities of the possessor and potential recipient, the identity of the individual that approached, and the presence or absence of a beg, investigate, resistance, and transfer were noted. The possessor was defined as the individual holding food in its mouth or hand, and the potential recipient as the individual not holding food in its mouth or hand at the beginning of an interaction. Interactions in which the possessor approached the potential recipient were referred to as possessor-initiated interactions, whereas interactions in which the potential recipient approached the possessor were referred to as recipient-initiated interactions. Resistance was defined as the possessor turning away from, moving its hand with food away from, or moving its entire body away from the potential recipient. A transfer was defined as the movement of food from the hand or mouth of the possessor to the hand or mouth of the recipient. Investigating was defined as the potential recipient moving a closed mouth toward the food item held by the possessor, whereas begging was defined as the potential recipient reaching its hand or open mouth toward the food item. The time, general type of food involved, and identity of the source plant were recorded.

Each observer recorded the amount of time their focal individual was "in-view" and "out-of-view" using a stopwatch. Time "out-of-view" was noted when the monkey was hidden behind dense foliage or had moved beyond the observer's sight.

Sampling

There were a total of 189 observation periods of males and 189 of females during 107 hr of data collection across 70 days (Table I). The monkeys were in-view 65% of the time (mean individual time in-view; $n = 10$ monkeys, range 61–71%), and there were no marked sex differences for time in-view (medians: males = 66%, females = 65%). All rates reported were calculated using the total time in-view for each individual.

Statistical Analyses

All statistical tests were performed using Systat version 11 and all reported P-values are two-tailed. The proportion of sampling points in which the monkeys were feeding was calculated by dividing the number of points when they were observed feeding by the total number of points in-view for each observation period. A mean proportion of sampling points in-view spent feeding was then calculated for each individual.

For each young, rates of food interactions, begs, and transfers were calculated using the total numbers of each variable and the total time in-view (for the adult male and female) for that social group. The proportion of begs with resistance and the proportion of begs that resulted in transfer were calculated for each young using the total number of begs for each individual. The proportion of begs resisted and the proportion of begs that resulted in transfer were

calculated for each food type using the total number of food interactions for all individuals combined. In the four social groups that included young, patterns of food transfers were examined among the various age and sex classes (adult male, adult female, and young) using log-likelihood ratio statistics [*G*-test; Sokal & Rohlf, 1995]. If the social groups were found to be homogenous, pooled observed frequencies were compared with the expected frequencies that were generated from the total number of individuals in each age and sex class (four adult males, four adult females, four young). A binomial test was used to compare the number of food interactions between adult males and young, and those of adult females and young to determine if the observed pattern differed from the expectation that males and females would be equally likely to interact with young. A binomial test was also used to compare the number of investigations by males and females of their mate's food to determine if the observed pattern differed from the expected that males and females equally investigate one another's food.

To determine the proportion of time spent feeding on different food types, the total number of sampling points that the adult male and female were feeding on each food type were summed for each group then divided by the total number of sampling points that the group was observed feeding. The proportion of sampling points that the monkeys were feeding for each food type was then multiplied by the total number of food interactions observed in that group generating an expected number of food interactions for each food type. The observed pattern of food interactions was compared with the generated expected pattern using log-likelihood ratio statistics to determine if the monkeys interacted with some food types more or less often than expected had they interacted with each food type indiscriminately.

Interobserver Reliability

Because food transfers in nature are relatively infrequent, interobserver reliability was assessed before the onset of the study observing owl monkeys (*Aotus nancymaae*) in captivity at the DuMond Conservancy for Primates and Tropical Forests, Inc. [for description of housing and basic methods, see Wolovich et al., 2006]. Five pairs of adult monkeys were observed feeding on 38 different occasions (January–April 2005). The observers followed the same definitions and methodology for recording food interactions as described above. The observers had 97% agreement on the number of food interactions (117/121), 100% agreement on the identities of the possessor and potential recipient, 97% agreement on whether a potential recipient investigated or begged for food (113/117), 88% agreement on the presence of resistance during the observed begs (29/33), and

100% agreement on whether a beg resulted in transfer (33/33).

RESULTS

The owl monkeys were feeding during approximately half of the sampling points when they were in-view (median = 0.45, *n* = 10 individuals). Groups did not vary in the proportion of sampling points spent feeding (*H* = 8.3, df = 4, *P* = .081). Twenty-four investigations and twenty-one begs were observed in the five groups. All age/sex classes were observed to be possessors and potential recipients during these 45 food interactions (Fig. 1).

Food Interactions With Young

Twenty-three food interactions with adults as possessors and young as potential recipients occurred in three of the social groups that contained young: 17 occurred between adult males and young, whereas only six were between adult females and young (Fig. 1). This observed frequency of males as possessors is higher than the expected frequency generated if males and females were equally likely to be possessors (*N* = 23, χ^2 = 6, *P* = .017, binomial test). Adult males and females appear equally likely to resist the begging attempts of young, but the sample sizes were too small to test for statistical significance because of the complete lack of any begs to one female. In three social groups with adult–young food interactions (D100, F1200, and E350), the patterns of food sharing are identical; young investigated and begged for food more often from males than from females (Table II). In the fourth social group (D500), food interactions with an adult as the possessor and the young as the potential recipient were not observed, but there was one food interaction with the young as the possessor and the adult female as the potential recipient (Fig. 1).

General patterns in the identities of possessors and potential recipients are evident. The frequencies of males, females, and young as possessors during food interactions are independent of social group (*G* = 6.8, *n* = 44, df = 6, *P* = 0.342). Because the groups are homogenous, data were pooled. A *G*-test using the pooled data indicates that young are less often possessors during food interactions than would be expected if there was an equal chance of each individual being a possessor (*G* = 22.1, *n* = 44, df = 2, *P* < .001). The frequencies of males, females, and young as potential recipients during food interactions vary among social groups (*G* = 18.3, *n* = 44, df = 6, *P* = .005). Because the pattern of food interactions appeared different in D500, and because its adult male was most likely the stepfather of the young, the analysis was run again excluding the data from D500. The frequencies of males, females, and young as potential recipients during food interactions are independent of the remaining three social
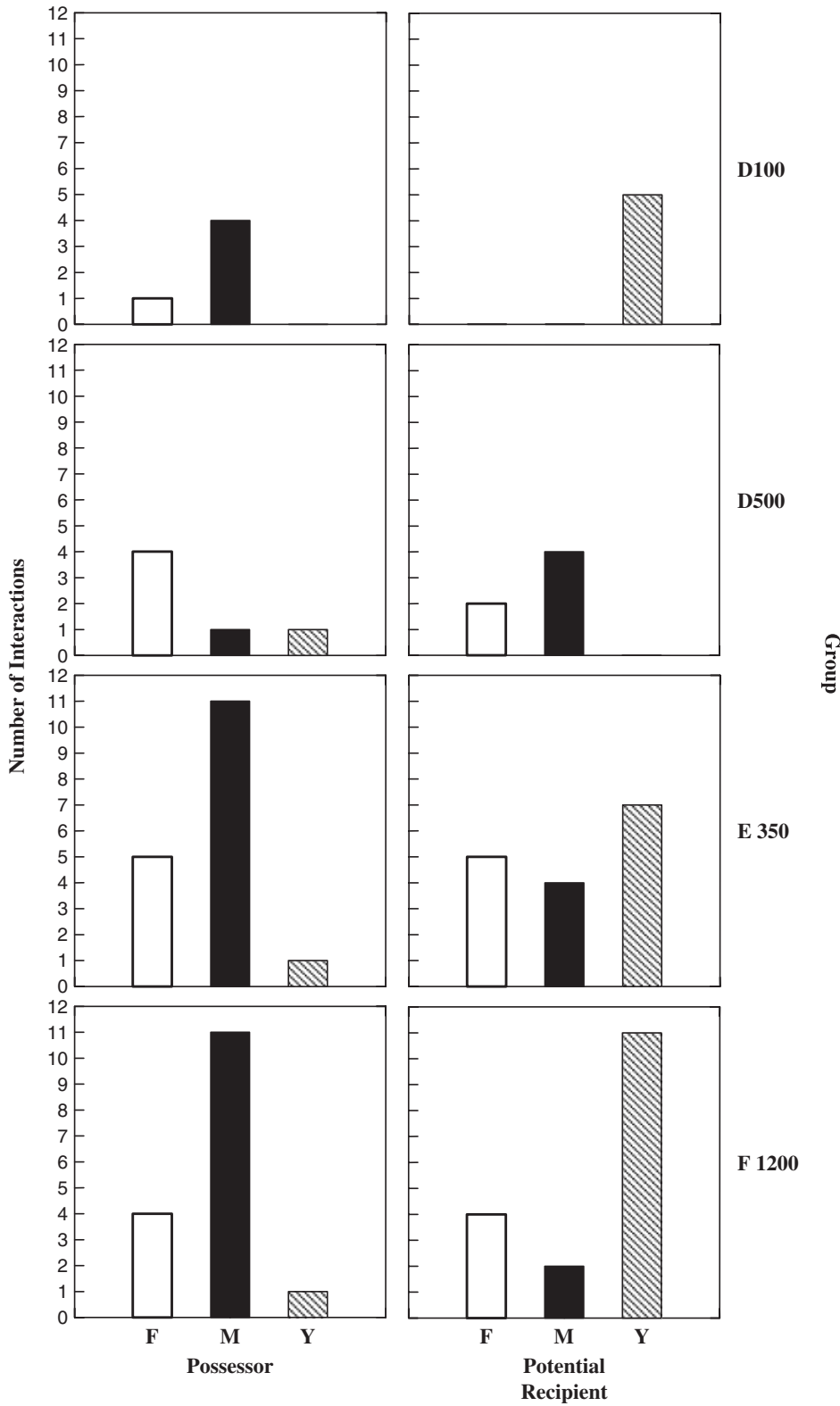
Fig. 1. The distribution of possessors and potential recipients during food interactions within each of the four social groups that included young. F, adult female; M, adult male; Y, young.

groups ($G = 7.2$, $n = 38$, df $= 4$, $P = .127$). These data were pooled for further analyses because the three social groups are homogeneous. A *G*-test using the

pooled data indicates that young are more often potential recipients and males are less often potential recipients during food interactions than would be

TABLE II. Food Interactions Between Adults and Young

Social group	Investigations/hour Male	Investigations/hour Female	Begs/hour Male	Begs/hour Female	Transfers/hour Male	Transfers/hour Female	Proportion of begs resulting in transfer Male	Proportion of begs resulting in transfer Female	Proportion of begs with resistance Male	Proportion of begs with resistance Female
D100	0.45	0.00	0.45	0.22	0.22	0.00	0.50	0.00	0.00	0.00
D500	0.00	0.00	0.00	0.00	0.00	0.00	N/A	N/A	N/A	N/A
E350	0.39	0.12	0.39	0.00	0.13	0.00	0.33	N/A	0.67	N/A
F1200	0.27	0.14	0.68	0.41	0.41	0.14	0.60	0.33	0.40	0.67

Values represent rates and proportions for the four social groups of monkeys that contained young.
N/A, not applicable because no begs were observed.

expected if there was an equal chance of each individual being a potential recipient ($G = 34.2$, $n = 38$, df $= 2$, $P < .001$).

Food Interactions With Mates

There were food interactions between mates in four groups. Both adult males and females were possessors of food during these food interactions and most food interactions were recipient-initiated (18/19). Females investigated food held by their mates significantly more than males did ($N = 13$, $\chi^2 = 3$, $P = .046$, binomial test).

Males and females begged their mates for food on six occasions. Four of the six begs were made by males, once in D500 and three times in E350. Two of the four begs resulted in transfer of food from females to their mates. On both occasions, the female transferred G*uazuma ulmifolia* fruit to her mate. Females were observed begging their mates for food only twice (in E350 and F1200), neither of which resulted in a transfer.

Foods Involved in Food Interactions

The monkeys in all five groups fed on flowers, fruit, and new and mature leaves. Monkeys were not observed feeding on insects, but it remains possible that some of the unknown food items were actually insects. Mature leaves may have contained leaf miners or insect galls that the monkeys were eating, but this possibility was neither confirmed nor rejected. Although the groups do not vary in the proportion of time spent feeding on each food type ($\chi^2 = 7.32$, df $= 3$, $P = .062$), some groups primarily fed on fruit, whereas others fed mainly on leaves (Table III). There was no particular food type involved in food interactions. When comparing the observed number of food interactions for each food type to the expected number of food interactions for each social group, only one social group differs significantly from the expected pattern (Table IV). F1200 interacted less often than expected with fruit and more often than expected with leaves.

TABLE III. Proportion of Total Sampling Points Spent Foraging on Different Food Items

Group	Proportion of sampling points spent foraging Flowers	Fruit	Leaves	Unknown
C0	.11	.01	.47	.41
D100	.11	.08	.49	.33
D500	.01	.38	.43	.18
E350	.03	.40	.39	.18
F1200	.06	.67	.14	.13

All age/sex classes investigated and begged for leaves and fruits. Males and young investigated flowers, but females did not. Including only those food interactions in which plant species could be identified (eight species), the monkeys most often begged for *G. ulmifolia* fruit and most often investigated new leaves and fruit of *Ficus guaranitica* (Moraceae, Table V). The two youngest individuals were the only potential recipients that investigated or begged for mature leaves (four occasions). Males, females, and young investigated or begged for leaves that appeared new (relatively small and light in coloration).

DISCUSSION

Adult female and male owl monkeys transferred food to young, whereas only females transferred food to their partners. Food interactions never occurred following intense (repeated or vocal) begging, nor did they involve food items that appeared difficult for any of the individuals to obtain independently. The nature of food sharing among wild owl monkeys, therefore, does not seem to conform to the patterns observed in other species, in which food sharing occurs mainly from the mother to the offspring, or when the food item is difficult to obtain [Feistner & Chamove, 1986; Feistner & McGrew, 1989; Fragaszy et al., 1997; Price & Feistner, 1993]. Food sharing in wild owl monkeys differed from that of wild

callitrichids [*Leontopithecus rosalia*, Rapaport, 2006; Ruiz-Miranda et al., 1999; *Callimico goeldii*, Porter, 2001] in that food transfers were rare and not a result of stereotyped ''offering'' behavior [c.f. Feistner & McGrew, 1989].

Owl monkeys shared all types of food independent of their relative abundance in the diet and of the age/sex class of the participants. Although chimpanzees and capuchins seem to share food that is difficult to obtain, such as meat [Mitani & Watts, 2001; Rose, 1997], owl monkeys shared food that was easily accessible by all age/sex classes. Because each food item transferred was small and potentially consumable within seconds, the possessor should have been able to avoid beggars long enough to ingest the food and prevent a transfer. The fact that both high-quality (fruit) and low-quality (mature leaves) food items were transferred suggests that food sharing offers the recipients benefits in addition to nutritional gains. In the following sections, these findings are discussed in greater detail and some plausible functions of food sharing in socially monogamous primates are suggested.

Food Interactions With Young

The pattern of food transfers to young in wild owl monkeys differs from that reported for wild callitrichids. In moustached tamarins (*S. mystax*), the breeding females transfer more food to young than do other group members [Heymann, 1996; Huck et al., 2004] and in buffy-headed marmosets (*C. flaviceps*), adult females shared food as often as adult males [Ferrari, 1992]. On the contrary, adult male owl monkeys shared food with young almost three times as frequently as did adult females. Although the number of food interactions was relatively small (17 vs. six), food interactions were observed in three different social groups indicating that they may be widespread. Sex differences in food sharing with young are even more evident when the pattern of actual food transfers is examined. An adult female transferred food to young only once, whereas adult males transferred food to young on five occasions. Rates of begging and food transfers were highest among the youngest juveniles (6.5–9 months). If food

TABLE IV. Observed and Expected Number of Food Interactions Involving Various Food Types for Each Group

Group	Food	Number of food interactions		G-statistic	P
		Observed	Expected		
C0	Flowers	0	0.22	3.02	>.10
	Fruit	0	0.12		
	Leaves	2	0.94		
	Unknown	0	0.78		
D100	Flowers	1	0.53	5.22	>.10
	Fruit	0	0.39		
	Leaves	4	2.44		
	Unknown	0	1.64		
D500	Flowers	0	0.05	2.46	>.10
	Fruit	3	1.89		
	Leaves	2	2.16		
	Unknown	0	0.79		
E350	Flowers	2	0.38	3.75	>.10
	Fruit	5	6.42		
	Leaves	6	6.27		
	Unknown	3	2.91		
F1200	Flowers	2	0.95	18.36	<.001
	Fruit	4	11.34		
	Leaves	9	2.33		
	Unknown	2	2.33		

Expected values were generated by multiplying the total number of food interactions for each group by the proportion of time that the group spent feeding on each food type (Table II). Log-likelihood ratio statistics were used for comparisons. α = .05.

TABLE V. Number and Type of Food Interactions Involving Each Food Item and Plant Species

Species	Food type	No. of investigates	No. of begs	No. of begs resisted	No. of begs resulting in transfer
Ficus guaranitica (Moraceae)	FR, NL	5	2	1	0
Ficus luschnathiana (Moraceae)	NL	1	1	1	0
Gleditsia amorphoides (Fabaceae)	NL	1	0	—	—
Guazuma ulmifolia (Sterculiaceae)	FR	3	4	2	2
Myrcianthes pungens (Myrtaceae)	ML	0	2	0	2
Paullinia pinnata (Sapindaceae)	NL	2	1	1	0
Tabebuia ipe (Bignoniaceae)	FL	3	0	—	—
Terminalia triflora (Combretaceae)	FL	1	1	0	1
Unknown	NL, UK	8	10	3	3

Values represent totals from all five groups.
FR, fruit; FL, flowers; NL, new leaves; ML, mature leaves; UK, unknown.

sharing helps offspring to learn which foods are edible or if it occurs most often when individuals have the most difficulty in obtaining food, these patterns of food sharing may be even more pronounced when infants are being weaned (5–8 months) [Rotundo et al., 2005]. Owl monkeys have high growth rates during their weaning periods, and such high growth rates may be related to the food they receive from their fathers [Garber & Leigh, 1997]. Captive and wild juveniles also share food with young infants [Rotundo et al., 2005; Wolovich et al., 2006].

The young sought out adult males more frequently than their mothers when begging for or investigating food, providing behavioral evidence for what seems to be a special relationship between adult males and young in Azara's owl monkeys. Infant owl monkeys spend significantly more time on males than on their mothers after the first week of life, and after nursing they are more likely to return to the male than to remain with the mother [Rotundo et al., 2005]. The infant–male relationship in owl monkeys appears similar to that described for monogamous titi monkeys, in which the male is the primary attachment figure for the infant [Hoffman et al., 1995; Mendoza & Mason, 1986]. In contrast, in cotton-top tamarins (Saguinus oedipus), which are cooperatively reared, the primary attachment figures are both the adult males and older brothers that carry them and transfer food to them [Kostan & Snowdon, 2002]. An understanding of the differences in food sharing with young in socially monogamous owl monkeys and that in cooperatively rearing callitrichids add to our knowledge of social and reproductive traits that distinguish these taxa of new world primates [Garber, 1994].

The prediction that males in socially monogamous species will be more likely to provide care to young because of higher paternity certainty [Trivers, 1972] still needs to be adequately tested with male–infant genetic data. Although a male in socially monogamous species is likely to monopolize his mate and monitor her activities better than a male living in a large multi-male multi-female group [Birkhead & Moller, 1992], extra-pair copulations and fertilizations can occur [Fietz, 2003; Mason, 1966; Reichard, 1995]. Paternity certainty can be further reduced in socially monogamous taxa where groups suffer periodic and frequent replacements of the reproducing adults. The replacement of adults in socially monogamous primates has now been reported among white-handed gibbons [Hylobates lar, Brockelman & Reichard, 1998; Palombit, 1994], siamangs [H. syndactylus, Palombit, 1994], saki monkeys [Pithecia aequatorialis, Di Fiore et al., 2007], and owl monkeys [Fernandez-Duque, 2007]. Incoming males may care for young by play with them, aiding in territorial defense [Brockelman & Reichard, 1998], and by carrying them [Fernandez-Duque et al., in press]. It remains unknown whether these males actually conceived the young by extra-pair copulations or are in some other way genetically related to the young. Palombit [1994] suggests that the variability of paternal care among groups of hylobatids may be a reflection of stepfathers not caring for young as much as biological fathers. In our study, only one male did not share food with the juvenile in his group (D500) and this male was not the resident male at the time of the juvenile's conception. It is possible that this represents an example of a male limiting care for young he did not sire, or it may simply reflect a reduction in food transfers to an older juvenile.

Food Interactions With Mates

There were two observed instances of female owl monkeys sharing food with their mates. Females have rarely been observed to give up food to other adults in nature [bonobos, Pan paniscus, White, 1994; vampire bats, Desmodus rotundus, DeNault & McFarlane, 1995]. Such behavior is especially interesting because females suffer the costs of gestation and lactation, and the selective advantages to giving up energetic resources to individuals other than offspring are not immediately obvious.

One possibility is that food may be transferred between mates with the expectation that the offer will be reciprocated in the future with food or another commodity such as grooming. Reciprocity has been proposed as a mechanism that maintains the occurrence of food transfers between adults in vampire bats [Wilkinson, 1984], capuchins, Cebus apella [deWaal, 2000], and chimpanzees [deWaal, 1997]. Female golden lion tamarins transfer food to males when males carry infants [Brown & Mack, 1978]. On the basis of an estimated gestation period of approximately 4 months [Hunter et al., 1979], the females that transferred food to their mates in our study were pregnant at the time of the transfers because they gave birth in mid-September and mid-December. These transfers, therefore, may have functioned as an incentive for the males to remain with the females and help with future parental care.

Another possibility is that the females simply responded to the begging harassment of males who could not acquire food [Stevens & Stephens, 2002]. This scenario seems unlikely because the males foraged for the same type of fruits as the females and did not seem to have any difficulty obtaining fruit. The type of fruit transferred (G. ulmifolia) is eaten by owl monkeys only when it is still green and immature, before it darkens and hardens with maturity. In the study area, all of the monitored G. ulmifolia trees fruit synchronously and sometimes possess both immature and mature fruits within the same tree [Fernandez-Duque, unpublished data]. During the winter, immature green G. ulmifolia fruits are relatively rare and may be difficult for the monkeys to locate because owl monkeys do not have

trichromatic vision [Jacobs et al., 1996; Levenson et al., 2007]. Food interactions may occur when one individual possesses a green fruit that another individual could not locate, thus making the food item more desirable. Because this study took place entirely during the winter months when fruit and insects are least abundant [Fernandez-Duque et al., 2002], the rates of food sharing may be lower than during the summer months if the monkeys are less likely to relinquish food that is more difficult to obtain. In contrast, food sharing to offspring may be more frequent during times of food scarcity to ensure adequate infant nutrition. Future studies should, therefore, consider the effect of food availability on food sharing.

Social Bonding

Owl monkeys are likely to benefit by forming a close relationship with their mates. Males and females that retain this relationship ensure the availability of a potential mate. In birds, mating with the same partner from year to year allows for a more accurate assessment of the mate's age than if a bird switches mates, ensures a good breeding site, and eliminates the time and energy otherwise spent searching for a mate [Rowley, 1983]. Those benefits, as well as others such as joint territorial defense [Bartlett, 2007; Sommer & Reichard, 2000], may encourage owl monkeys to maintain pair-bonds.

Owl monkeys may share food with their mates to strengthen social bonds. This hypothesis has been suggested for other species that form bonds between mates such as golden lion tamarins [Wilson, 1976] and monogamous birds [Lack, 1940] and has also been extended to chimpanzees [Slocombe & Newton-Fisher, 2005] and man [Homo sapiens, Lovejoy, 1981]. Most socially monogamous species perform duets, sleep in close proximity, and engage in other species-typical affiliative behaviors (such as allo-grooming) that are suggested to strengthen pair-bonds [Kleimann, 1977]. Although owl monkeys huddle together while sleeping [Moynihan, 1964], they do not duet and rarely allogroom [Moynihan, 1964; Wolovich & Evans, 2007]; therefore, food sharing may fulfill a pair-bonding function.

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