RESEARCH ARTICLE

Social Patterns of Food Sharing in Monogamous Owl Monkeys

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Captive owl monkeys (*Aotus nancymaae*, *A. azarai*) share food frequently within both families and pairs. In this study food sharing was observed in seven mated pairs and four families (i.e., four mated pairs and their offspring). Patterns of food sharing were examined with respect to age class, sex, and the presence or absence of dependent offspring. Within families, most food transfers were from adult males to developing offspring. Adult males and females transferred food to their mates in caged pairs as well as in family units. Food interactions between adults are as likely to result in food transfers as those between adults and offspring. This pattern of food sharing between mates in a monogamous species may serve both nutritional and social functions that differ from those in polygamous species. Am. J. Primatol. 68:663–674, 2006. © 2006 Wiley-Liss, Inc.

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INTRODUCTION

   Relinquishing food to other individuals incurs a greater immediate cost to the donor compared to most other affiliative social behaviors. When food is transferred from a donor to a recipient, the donor's potential energetic intake is reduced and its energetic cost of acquiring the food is not recouped. There are, however, several possible fitness advantages to be gained by food donors. Offspring survival may be enhanced by the additional nutrition, and indeed most food transfers occur from adults to their developing young [Feistner & McGrew, 1989]. In primates (e.g., chimpanzees (*Pan troglodytes*) [Silk, 1979], capuchins (*Cebus apella*) [Fragaszy et al., 1997], and golden lion tamarins (*Leontopithecus rosalia*) [Price & Feistner, 1993]), most food sharing occurs when infants have difficulty obtaining food, thus ensuring that the infants receive adequate nutrition.

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Food sharing between adults can enhance reproductive success by increasing fecundity. In insects that practice nuptial feeding, males that offer nuptial gifts to females obtain more copulations and are more likely to fertilize eggs [Gwynne, 1984, 1986; Rooney & Lewis, 2002]. Courtship feeding in birds provides females with added nutrition for egg production and results in an increased number of eggs produced in a breeding season [Nisbet, 1973, 1977; Tasker & Mills, 1981; Gonzalez-Solis et al., 2001].

Research on food sharing between adult mammals has focused on species that live in large multimale, multifemale groups. Vampire bats (*Desmodus rotundus*) frequently experience shortages of blood and can starve within 48–72 hr of food deprivation [McNab, 1973]. If a bat fails to feed, it can prevent starvation by receiving regurgitated blood from a bat that has successfully fed. Blood is preferentially regurgitated for individuals that previously donated a blood meal, thereby establishing a network of reciprocal sharers [Wilkinson, 1984; DeNault & McFarlane, 1995]. Male chimpanzees that share food with one another also help each other during dominance struggles [Mitani & Watts, 2001]. Male bonobos (*Pan paniscus*) share food with females, and those males may receive more mating opportunities than males that do not share food with females [Hohmann & Fruth, 1996]. Adult capuchins (*C. apella*) transfer food to other adults, both in the wild [Rose, 1997] and in captivity [de Waal, 1997; Westergaard & Suomi, 1997]. Reciprocity [DeNault & McFarlane, 1995; de Waal, 2000] and reductions in harassment [Stevens, 2002] have been proposed as benefits that favor the evolution of food sharing in species that live in large groups.

Food sharing between adults may serve a nutritional function. Gestation and lactation are costly reproductive states for female mammals [Thompson, 1992]. To help offset these costs, female guinea pigs (*Cavia porcellus*) increase their consumption of food by spending more time foraging [Kunkele, 2000]. Pregnant and lactating females may also receive food from other individuals, increasing energy intake while avoiding the time and energy expenditure of increased foraging. Fathers would benefit from transferring food to lactating females by providing indirect provisioning to their offspring. Food transfers from males to pregnant or lactating females could increase the nutrient content of the female's milk. Infants that receive more nutritious milk may have higher survival rates and may also be weaned earlier, thereby reducing interbirth intervals [Brown & Mack, 1978] and enhancing lifetime reproductive success. These advantages to both males and females are most evident in monogamous species with a high level of paternity assurance.

Many monogamous species require biparental care of offspring, and there is often a high frequency of affiliative behaviors, such as grooming, that may strengthen the social bond [Kleimann, 1977]. Sharing food with a mate may be another behavior that strengthens the pair-bond in monogamous species [Wilson, 1976].

There is some support for both nutritional and social functions of food sharing in captive golden lion tamarins (*Leontopithecus rosalia*). Golden lion tamarins live in groups that contain only a single breeding female and one or several adult males. Food is transferred between the adults [Brown & Mack, 1978; Rapaport, 1997]. It is transferred from males to females following parturition, suggesting that it may play a role in increasing the females' nutrition. Prior to a female's first conception, however, food is transferred from females to males, suggesting that food sharing in captive golden lion tamarins serves additional functions [Brown & Mack, 1978].

The owl monkey (*Aotus* spp.) is a monogamous New World primate that lives in social groups consisting of one adult male, one adult female, and one or two dependent young [Wright, 1985]. Owl monkeys exhibit biparental care, with males helping to transport and groom infants [Rotundo et al., 2002, 2005; Wright, 1984]. Details of owl monkey social behavior are largely unknown because they are nocturnal and arboreal [Moynihan, 1964; Wright, 1985], making it difficult to study them in the field. Food sharing in captivity has not been systematically examined, and has been observed in only one *Aotus* group [Wright, 1984]. Rotundo et al. [2005] report several occasions of adults sharing food with infants in *A. azarai* in the wild, but details regarding this behavior remain unknown.

This study was undertaken to determine the social patterns of food transfer in the socially monogamous owl monkey with respect to the presence or absence of dependent offspring.

The frequency of food transfers between adults, and the direction in which food is transferred, may differ between monogamous and polygamous species because individuals in monogamous groups benefit by cooperating rather than competing for food resources [McGrew & Feistner, 1992]. Food sharing models that are based on harassment [Stevens, 2002] or depend on reciprocal exchanges [de Waal, 2000] may not necessarily apply to monogamous species in which males have a high certainty of paternity and biparental care is necessary for offspring survival. If a function of food sharing is to increase the nutritional intake of infants, then food transfers are expected to be frequent when offspring are present, and the majority of the food is expected to be transferred to juveniles and infants. Adult males are expected to transfer most of the food before infants are weaned because males provide a high degree of the parental care, and, unlike females, they are not energetically burdened with lactation.

If food transfers between adults play a nutritional role, then males would be expected to transfer food to females when unweaned infants are present. Lactating females would benefit more from the increased energy supplied through food transfers than nonlactating females. Females would not be expected to transfer food to males unless food transfers serve a social function. If food sharing serves a function in social bonding, both males and females would be expected to transfer food to their mates because both sexes derive benefits from the pair-bond.

MATERIALS AND METHODS

Subjects

Captive owl monkeys housed in the naturally forested area of the DuMond Conservancy for Primates and Tropical Forests, Inc. (Miami, FL) were observed between September 2001 and June 2002. Pairs of owl monkeys consisting of one adult male and one adult female are maintained in cylindrical wire-mesh enclosures (2.4 m diameter × 2.4 m high). Families of owl monkeys (pairs of adults with offspring) are housed in 3 m × 3 m cylindrical wire-mesh enclosures. Each enclosure contains a nest box and a variety of perches and platforms. The enclosures are visually separated from one another by dense foliage, but vocalizations from conspecifics in nearby enclosures can be heard.

Eleven groups of owl monkeys were observed. These consisted of seven pairs without offspring (all *A. nancymaae*; pregnancy status was not completely known because the spontaneous abortion rate is high) and four families (three pairs with one juvenile, one with two juveniles, and all four with suckling infant). Three of

the families consisted of *A. nancymaae* individuals, while the fourth family was comprised of an *A. azarai boliviensis* adult female, an *A. nancymaae* male, and two hybrid offspring. Offspring were classified as infants until they reached 6 months of age, a typical age for weaning [Dixson & Fleming, 1981], and then as juveniles until they were removed from their natal family at 24–30 months of age.

General Procedures

Observations began at dusk or within 2 hr afterwards, the period when the monkeys were normally fed and are known to be most active [Wright, 1985]. Flashlights with lenses covered by red cellophane were used to aid in observing behaviors and identifying individuals. Owl monkeys are least sensitive to light in the red spectrum [Ogden, 1994]. The subjects were observed for at least 10 preliminary observation periods during the 2 weeks prior to the onset of data collection. After that time, the subjects no longer vocalized when they faced the observers or otherwise oriented their faces toward the observers, and were thus considered to be habituated.

Food Presentation

For the food interaction trials, the monkeys were presented with one of two food treatments: a regular open feeding dish or a semi-closed feeding container. Their regular feeding dishes were 6 cm × 2.5 cm × 15 cm plastic bowls. For these trials, the dishes contained the same items, and hence the same nutritional value, that the monkeys are normally fed (three types of monkey chow (LabDiet®), and a fruit and vegetable mix). Inedible fruit skins and stems were removed prior to presentation, so all food items were of types normally consumed in their entirety. The dishes were attached to the inside wall of their enclosures.

The semi-closed feeding containers were made from plastic 355-mL bottles with a 5 cm × 7.5 cm hole cut into the cylindrical portion. They were filled with the same fruit and vegetable mix, but with only half the amount normally given in the monkeys' regular feeding dishes. Added to these containers were shredded pieces of paper. These containers were also attached to the inside wall of the enclosures. Restricting the accessibility of the food by using these containers and the shredded paper, and also reducing the amount of food, allowed testing the effects of a putatively more expensive food on food transfer behavior. In addition to the provisioned food, the monkeys were able to forage for leaves that grew inside or adjacent to their enclosure, as well as for small arthropods and lizards that entered their enclosure.

Data Collection

Feeding trials began immediately following the presentation of food and ended when all of the fruit and vegetable mix was eaten or the monkeys ceased feeding for 5 min. All food interactions, as well as the type of food involved (fruit, monkey chow, leaf, or arthropod), were recorded.

A food interaction is defined as two monkeys being within arm's reach and one monkey's face being oriented toward a food item held in the mouth or hand of the other monkey. Each participant was categorized as either a possessor or a potential recipient. The possessor is defined as the individual holding food in its mouth or hand, and the potential recipient is defined as the individual not holding food in its mouth or hand at the beginning of an interaction. For each food interaction, the time, the age/sex class of participants, and the identity of the

individual that approached (i.e., reduced the interindividual distance to within arm's reach) were noted. Interactions in which the possessor approached the potential recipient are referred to as possessor-initiated interactions, whereas interactions in which the potential recipient approached the possessor are referred to as recipient-initiated interactions.

The presence or absence of resistance and whether or not the food item was transferred were recorded for each food interaction. Resistance is 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 is defined as the movement of food from the hand or mouth of the possessor to the hand or mouth of the recipient. Any overt eye contact between the possessor and potential recipient, as well as any vocalizations emitted by either individual, were also noted. Begging is defined here as the potential recipient reaching its hand or open mouth toward the food item held by the possessor, regardless of whether the interaction was initiated by an approach of the potential recipient or the possessor. Because begging can be both fleeting and subtle, its interobserver reliability is low, so it was noted but not systematically scored in this study. To ensure the interobserver reliability of all the other data gathered, initially the most experienced observer (A.F.) worked with a less experienced observer (C.K.W.) twice a week for 2 hr of observations. They discussed each food interaction and resolved differences until those differences vanished after 1 month of training, at which time the trainee also began to gather data independently. To gauge the suitability of such training, we later examined data that were scored simultaneously and independently by two observers (the now-experienced C.K.W. and a student intern trainee) on two different kinds of groups (a pair and a family with two offspring) on 1 day at the beginning of training and again 2 weeks later, for a total of six observation periods (two the first day and four on the later one, totaling 127 min). There was 100% agreement for both days regarding which individual approached (13/13 interactions), and only one disagreement over identities, occuring on the very first interaction observed on the first day (12/13 over both days agree). Identity disagreements vanished after another 2 weeks of training. Agreement about the time of and occurrence of food interactions was not as high on either day (5/6 and 8/11; the trainer recorded two interactions that were not scored by the trainee on the first day, and one on the second one; the trainee scored one on the second day that was not scored by the trainer). Because the criterion for the existence of an interaction is an interindividual distance estimate, the lower degree of agreement is not surprising since the animals must occasionally be very close to the criterion distance.

Sampling

Owl monkey pairs and families were observed for a combined total of 64.5 hr divided among 133 feeding trials. Feeding trial lengths ranged from 7 to 87 min, with mean trial lengths per each pair or family ranging from 20.5 to 60.0 min, and an overall mean of 30.9 min. Pairs and families were not sampled with equal intensity, with the number of feeding trials for each group (pair or family) ranging from six to 21, and the total observation time per group ranging from 213 to 552 min. Thus, each variable represents a proportion of interactions for each group so that the groups are equally weighted for statistical comparisons. One pair was observed feeding only with an open dish, yielding six pairs and four families used in comparisons of feeding trials with an open dish or a semi-closed container.

Statistical Analyses

All statistical tests were performed using Systat version 11 (Systat Software, Inc., Richmond, CA). The effects of food presentation (open dish or semi-closed feeding container) on the proportion of interactions resulting in transfer, the proportion of interactions with resistance, and the proportion of interactions that were possessor-initiated were examined using Wilcoxon matched-pairs signed-ranks tests. There is no difference in the proportion of the interactions that resulted in transfer between feeding trials with an open dish (median = .56) or semi-closed container (median = .53, $T_s = 19$, n = 10, $P = .386$). There is also no difference in the proportion of the interactions with resistance between feeding trials with an open dish (median = .11) and semi-closed container (median = .14, $T_s = 14$, n = 8, $P = .888$). The proportion of interactions that were possessor-initiated also does not differ between feeding trials with an open dish (median = 0, range = 0–.38) and a semi-closed container (median = 0, range = 0–.47, $T_s = 9$, n = 6, $P = .753$). Because data collected from food presented in the open dishes and the semi-closed containers were comparable, these data were combined for all further analyses.

Comparisons using Mann-Whitney tests were made between pairs and families regarding feeding trial length, food transfer rates, number of food interactions per observation period, proportion of interactions resulting in a transfer, proportion of interactions with resistance, and proportion of interactions that were possessor-initiated. Patterns of age/sex classes in terms of possessors and potential recipients were examined with the use of log-likelihood ratio statistics (G-test [Sokal & Rohlf, 1995]). The pooled observed frequencies were compared with the expected frequencies that were generated from the total number of individuals in each age/sex class (four males: four females: five juveniles: four infants). Using a binomial test, the number of instances in which males and females were possessors during food interactions between adults in the families was compared with the null hypothesis that each sex has an equal probability of being a possessor. A Kruskal-Wallis test was used to determine whether or not the age/sex class of the possessor affected the proportion of interactions that were resisted.

For the seven pairs, Mann-Whitney tests were used to compare the proportion of the interactions in each pair with males as possessors to the proportion of the interactions in each pair with females as possessors. For the pairs and families combined, Mann-Whitney tests were used to compare the proportion of interactions with adult males and females as possessors that resulted in transfer, occurred with resistance, or were possessor-initiated.

RESULTS

Food interactions resulted in transfer in all 11 groups of captive owl monkeys (median = 54% of food interactions). Food was transferred from adults to dependent offspring (median = 63% of food interactions) as well as between mates (median = 59% of food interactions). All types of food were transferred, including leaves and arthropods that the monkeys obtained through foraging. Transferred food items were not those that were previously discarded by the possessors, and they were all invariably ingested by the recipients, thereby indicating that they were of normal and acceptable quality. No vocalizations were emitted immediately before, during, or immediately after food interactions, nor was any overt eye contact observed during food interactions. Few transfers occurred with resistance from the possessor (median = 14% of food interactions;

cf., "theft" in Feistner and McGrew [1989]). Food transfers were often a result of recipient-initiated interactions, but occasionally also resulted from possessor-initiated interactions (median = 4% of food interactions). When begging occurred, it was brief (i.e., either food transfer or resistance occurred immediately).

Families vs. Pairs

Feeding trial length did not differ between families (median = 27 min) and pairs (median = 28 min, $U = 18$, $n_1 = 4$, $n_2 = 7$, $P = .450$). Food transfer rates in families (median = 5.0 transfers/hr) and pairs (median = 1.7 transfers/hr) also did not differ ($U = 5$, $n_1 = 4$, $n_2 = 7$, $P = .089$). The number of food interactions per feeding trial was greater in families (median = 3.5) than in pairs (median = 2.0, $U = 3$, $n_1 = 4$, $n_2 = 7$, $P = .038$), reflecting the fact that families had more individuals participating in food interactions.

A comparison of food interactions between mates reveals no difference in the proportion of interactions with males as possessors in pairs (median = .46) and families (median = .68, $U = 7.0$, $n_1 = 7$, $n_2 = 4$, $P = .186$). There is no statistical difference in the proportion of interactions resulting in transfer in pairs (median = .54) and families (median = .62, $U = 12.0$, $n_1 = 7$, $n_2 = 4$, $P = .705$). There were very few possessor-initiated interactions in pairs (median = 0, range = 0–.30), which is not statistically different from the proportion of possessor-initiated interactions in families (median = .09, $U = 6.5$, $n_1 = 7$, $n_2 = 4$, $P = .143$). The proportion of interactions with resistance, however, is greater in families (median = .18) than in pairs (median = .08, $U = 3.5$, $n_1 = 4$, $n_2 = 7$, $P = .046$).

Food Sharing Within Families

Within families, the adult males, adult females, juveniles, and, on rare occasion, infants were possessors during transfers (Fig. 1). The frequency of age/sex classes being possessors during food interactions is independent of family ($G = 15.7$, $n = 239$, $df = 9$, $P = .073$; Fig. 1). A G-test of the pooled data suggests that infants are possessors during food interactions less often than would be expected with a uniform likelihood of each individual being a possessor during food interactions ($G = 52.7$, $n = 239$, $df = 3$, $P < .001$). Even when the age/sex class that deviates the most from the expected (infants) is removed from the analysis, adult males are possessors more often than would be the case if each individual in a family were equally likely to be a possessor ($G = 8$, $n = 236$, $df = 2$, $P < .05$). The frequency of age/sex classes being potential recipients during food interactions varies by family ($G = 29.6$, $n = 239$, $df = 9$, $P = .001$; Fig. 1), so whether the infant or juvenile was most often the recipient during food interactions depended on the particular family involved.

The age/sex of possessors did not affect the proportion of interactions that met resistance ($H = 4.27$, $P = .118$; juvenile median = .32, adult male median = .15, adult female median = .15).

Food Sharing Between Mates Within Pairs and Families

Males and females were equally likely to transfer food to their partners. There is no difference in the proportion of interactions that resulted in transfer when males were possessors (median = .50) and when females were possessors (median = .56, $U = 45.5$, $n_1 = 11$, $n_2 = 11$, $P = .193$). There is also no difference in the proportion of interactions with resistance when males were possessors
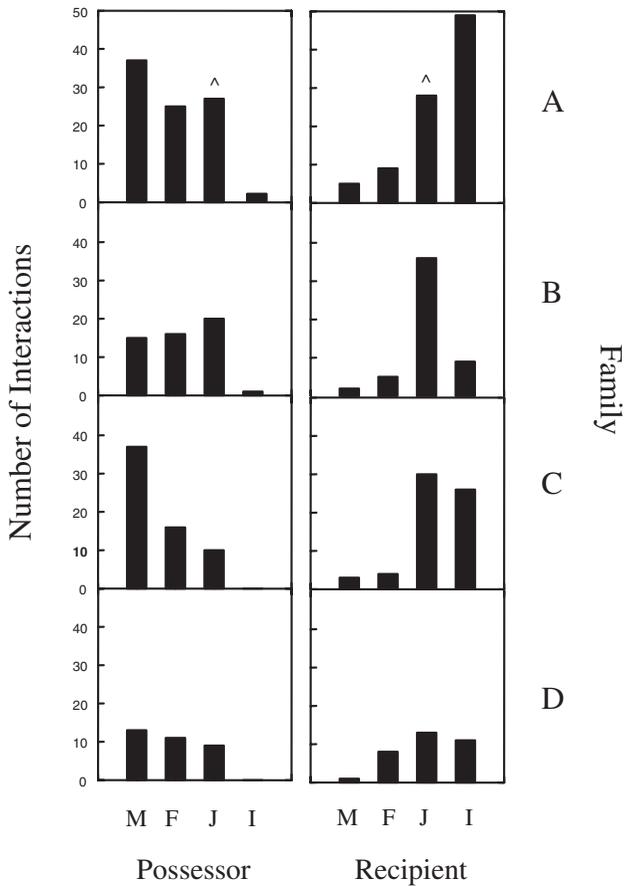
Fig. 1. Frequencies of males (M), females (F), juveniles (J), and infants (I) as possessors and recipients during food interactions in four families (A: n = 91; B: n = 52; C: n = 63; and D: n = 33). ^ There are two juveniles in family A.

(median = .13) and when females were possessors (median = 0, range = 0–.25, $U = 73.0$, $n_1 = 11$, $n_2 = 11$, $P = .388$). There is no difference in the proportion of interactions that were possessor-initiated when males were possessors (median = 0, range = 0–.50) or when females were possessors (median = 0, range = 0–.37, $U = 45.5$, $n_1 = 11$, $n_2 = 11$, $P = .166$).

In pairs without offspring, there was no difference in the proportion of interactions with females as possessors (median = .54) and males as possessors (median = .46, $U = 15$, $n_1 = 7$, $n_2 = 7$, $P = .225$; Fig. 2). Possessor-initiated interactions were observed between mates in three of the seven pairs. In each of the three pairs, females were always the possessor during possessor-initiated interactions.

In families, the frequency of food interactions between mates when males were possessors as compared to when females were possessors is independent of family ($G = 6.2$, $df = 3$, $P = .104$). Pooled data on the 18 food interactions between adult mates not in families revealed that the 13 instances in which the male was the possessor did not differ from the null expectation of nine of these 18 interactions ($P = .096$; Fig. 2). Possessor-initiated interactions between mates
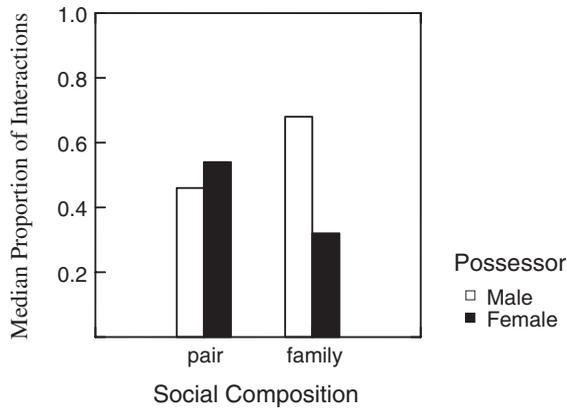
Fig. 2. Sex of the possessor of food during food interactions between adults in social units of pairs (n = 7) and families (n = 4). There were a total of 107 food interactions between adults in pairs, and 18 food interactions between adults in families.

were observed only in one family, in which the male initiated food transfers to his mate three times.

DISCUSSION

Food Sharing Between Mates

Captive adult owl monkeys regularly transfer food to their mates, and these transfers often occur with little resistance. The proportion of food interactions between adult males and females resulting in transfer (59%) is higher than that reported for chimpanzees (44% [Mitani & Watts, 2001]) and twice that of capuchins (27% *C. capucinus* [Rose, 1997]). In contrast to chimpanzees, food sharing between captive adult owl monkeys does not appear to occur only when there is intense begging for a highly prized food item, such as large fruits or meat (*P. paniscus* [White, 1994; Hohmann & Fruth, 1996] and *P. troglodytes* [Teleki, 1973; Mitani & Watts, 2001]), but is regularly observed to occur under normal feeding conditions with little or no begging.

Female owl monkeys with offspring are pregnant or lactating for approximately 9 months a year [Dixson, 1994; Dixson & Fleming, 1981; Fernandez-Duque et al., 2002]. Food sharing between adults may function to increase nutrition to pregnant and lactating females. Males were observed to transfer food to females not only in families, but also in pairs. Some of the females in the pairs may have been pregnant during the course of this study (their status was incompletely known due to the high spontaneous abortion rate). The females in families were all nursing their infants. Therefore, it is not known whether males transfer food more often to females during pregnancy and lactation than when females are neither pregnant nor lactating. In addition to potentially providing added nutrition to females during pregnancy and lactation, food sharing between adults may aid in social bonding. In pairs and families, both males and females transferred food to their mates. Therefore, neither hypothesis regarding the function of food sharing between captive adult owl monkeys can be ruled out at this time.

The relationship between food sharing and sociosexual behaviors has not been examined in a monogamous mammal. When no offspring are present, female

owl monkeys transfer food to males. A similar pattern was found in captive golden lion tamarins [Brown & Mack, 1978]. Several affiliative behaviors that are commonly observed in monogamous species, such as grooming and duetting, are rare in owl monkeys [Juarez et al., 2003; Schwindt et al., 2004], and frequent food transfers may be playing a role in pair-bonding instead. Male and female bonobos transfer food to one another when females are without infants, suggesting that food transfers may be associated with sexual receptivity [White, 1994]. Indeed, male bonobos have been reported to share food with females immediately after copulating with them [Kuroda, 1984]. Males of a monogamous species may be more likely to share food with females than males of a polygamous species, perhaps as a consequence of a greater certainty of paternity. This type of exchange should be examined in a monogamous species.

Transfers to Offspring

Adult males were most often the possessors, and infants and juveniles were most often the potential recipients during food interactions that occurred in families (Fig. 1). A similar pattern has been described in dusky titi monkeys (*Callicebus torquatus torquatus*) [Starin, 1978] and golden lion tamarins [Brown & Mack, 1978]. Lactating females have increased nutritional requirements [Thompson, 1992] and thus their cost of sharing food is likely to be high. One might expect females to be more likely than adult males or older siblings to resist begging infants, but the results from this study suggest that females are equally likely as males and possibly less likely than juveniles to resist during food interactions. Transferring food to an infant may increase its independence from its mother, leading to earlier weaning [Rapaport, 1997; Starin, 1978], a shorter interbirth interval, and greater reproductive success over the course of the parental pair's lifetime.

Possessor-Initiated Interactions

Possessor-initiated interactions, although rare, occurred with both offspring and adults as recipients. No apparent food calls accompanied this behavior, in contrast to reports for many callitrichid species [Feistner & McGrew, 1989]. Feistner [1985] described this behavior as ''offering'' in cotton-top tamarins (the donor (possessor) sits and holds a food item in one hand while emitting a rhythmic, high-pitched food call and making eye contact with a potential recipient). No food calls or overt eye contact were observed during possessor-initiated interactions in our study (possessor-initiated transfers simply consist of the possessor carrying food to another individual while holding the food in its hand).

Food Sharing in Captive vs. Wild Populations

The patterns of food sharing in captive owl monkeys may differ than from those in natural populations. Ruiz-Miranda et al. [1999] compared food sharing in wild and reintroduced golden lion tamarins, and found that although reintroduced monkeys transferred food twice as often as their wild counterparts, the pattern of transfer was similar. Wild golden lion tamarins were observed to transfer food to pregnant females, supporting the idea that food transfers may serve an important nutritional function. Food sharing with infants has been observed in free-ranging owl monkeys [Rotundo et al., in press]. Natural populations of owl monkeys experience seasonal fluctuations of insects, fruit,

flowers, and leaf flush [Fernandez-Duque et al., 2002]. It is possible that these food items, which vary in abundance, are transferred not only to infants but also between adults during times of the year when they are rare or when female nutritional demand is high.

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REFERENCES

Brown K, Mack D. 1978. Food sharing among captive *Leontopithecus rosalia*. Folia Primatol 29:268–290.

DeNault L, McFarlane D. 1995. Reciprocal altruism between male vampire bats, *Desmodus rotundus*. Anim Behav 49:855–856.

Dixson A. 1994. Reproductive biology of the owl monkey. In: Baer JF, Weller RE, Kakoma I, editors. Aotus: the owl monkey. San Diego: Academic Press. p 113–132.

Dixson A, Fleming D. 1981. Parental behaviour and infant development in owl monkeys (*Aotus trivirgatus griseimembra*). J Zool 194:25–39.

Feistner A. 1985. Food-sharing in the cotton-top tamarin (*Saguinus oedipus oedipus*). Master's thesis, University of Stirling, Stirling, UK. 41p.

Feistner A, McGrew W. 1989. Food-sharing in primates: a critical review. In: Seth PK, Seth S, editors. Perspectives in primate biology. Vol. III. New Delhi: Today and Tomorrow's Printers and Publishers. p 21–36.

Fernandez-Duque E, Rotundo M, Ramirez-Llorens P. 2002. Environmental determinants of birth seasonality in night monkeys (*Aotus azarai*) of the Argentinean chaco. Int J Primatol 23:639–656.

Fragaszy D, Feuerstein J, Mitra D. 1997. Transfers of food from adults to infants in tufted capuchins (*Cebus apella*). J Comp Psychol 111:194–200.

Gonzalez-Solis J, Sokolov E, Becker P. 2001. Courtship feedings, copulations and paternity in common terns, *Sterna hirundo*. Anim Behav 61:1125–1132.

Gwynne D. 1984. Courtship feeding increases female reproductive success in bushcrickets. Nature 307:361–363.

Gwynne D. 1986. Courtship feeding in katydids (Orthoptera: Tettigondiidae): invest-

ment in offspring or in obtaining fertilizations? Am Nat 128:342–352.

Hohmann G, Fruth B. 1996. Food sharing and status in unprovisioned bonobos. In: Wiessner P, Schiefenhoevel W, editors. Food and the status quest. Providence: Berghahn Books. p 47–67.

Juarez C, Rotundo M, Fernandez-Duque E. 2003. Behavioral sex differences in the socially monogamous night monkeys of the Argentinean chaco. Revista Etol Supl 5:174.

Kleimann D. 1977. Monogamy in mammals. Q Rev Biol 52:39–69.

Kunkele J. 2000. Energetics of gestation relative to lactation in a precocial rodent, the guinea pig (*Cavia porcellus*). J Zool 250:533–539.

Kuroda S. 1984. Interaction over food among pygmy chimpanzees. In: Susman R, editor. The pygmy chimpanzee: evolutionary biology and behavior. New York: Plenum Press, p 301–323.

McGrew W, Feistner A. 1992. Two nonhuman primate models for the evolution of human food sharing: chimpanzees and callitrichids. In: Barkow J, Cosmides L, Tooby J, editors. The adapted mind: evolutionary psychology and the generation of culture. New York: Oxford University Press. p 229–243.

McNab B. 1973. Energetics and the distribution of vampires. J Mammol 54:131–144.

Mitani C, Watts D. 2001. Why do chimpanzees hunt and share meat? Anim Behav 61:915–924.

Moynihan M. 1964. Some behavior patterns of playtyrrhine monkeys. I. The night monkey (*Aotus trivirgatus*). Smithsonian Misc Collections 146:1–84.

Nisbet I. 1973. Courtship-feeding, egg-size, and breeding success in common terns. Nature 241:141–142.

Nisbet I. 1977. Courtship-feeding and clutch size in common terns *Sterna hirundo*. Evol Ecol 2:101–109.

Ogden T. 1994. Ophthalmologic research in the owl monkeys. In: Baer JF, Weller RE, Kakoma I, editors. Aotus: the owl monkey. San Diego: Academic Press. p 263–286.

Price E, Feistner A. 1993. Food sharing in lion tamarins: tests of three hypotheses. Am J Primatol 31:211–221.

Rapaport L. 1997. Food sharing in golden lion tamarins (*Leontopithecus rosalia*): provisioning of young, maintenance of social bonds, and resource constraints. Ph.D. dissertation, University of New Mexico, Albuquerque, NM. 209p. Available from UMI; AAT 9736124.

Rooney J, Lewis S. 2002. Fitness advantage from nuptial gifts in female fireflies. Ecol Entomol 27:373–377.

Rose L. 1997. Vertebrate predation and food sharing in *Cebus* and *Pan*. Int J Primatol 18: 727–765.

Rotundo M, Fernandez-Duque E, Gimenez M. 2002. Biparental care in the night monkey (*Aotus azarai*) of Formosa, Argentina. Neotrop Primates 10:70–72.

Rotundo M, Fernandez-Duque E, Dixson A. 2005. Infant development and parental care in free-ranging groups of owl monkeys (*Aotus azarai azarai*) in Argentina. Int J Primatol DOI: 10.1007/s10764-005-5329-2.

Ruiz-Miranda C, Kleimann D, Dietz J, Moraes E, Grativol A, Baker A, Beck B. 1999. Food transfers in wild and reintroduced golden lion tamarins, *Leontopithecus rosalia*. Am J Primatol 48:305–320.

Schwindt D, Carrillo G, Bravo J, DiFiore A, Fernandez-Duque E. 2004. Comparative socioecology of monogamous primates in the Amazon and Gran Chaco. Folia Primatol 75(S1):412.

Silk J. 1979. Feeding, foraging, and food sharing behavior of immature chimpanzees. Folia Primatol 31:123–142.

Sokal R, Rohlf F. 1995. Biometry. 3rd ed. New York: W.H. Freeman and Company. 887p.

Starin E. 1978. Food transfer by wild titi monkeys (*Callicebus torquatus torquatus*). Folia Primatol 30:145–151.

Stevens J. 2002. The behavioral ecology of food sharing. Ph.D. dissertation, University of Minnesota, Minneapolis, MN. 151p. Available from UMI; AAT 3072688.

Tasker C, Mills J. 1981. A functional analysis of courtship feeding in the red-billed gull, *Larus novaehollandiae scopulinus*. Behaviour 77:220–241.

Teleki G. 1973. The predatory behavior of wild chimpanzees. Lewisburg: Bucknell University Press. 232p.

Thompson S. 1992. Gestation and lactation in small mammals: basal metabolic rate and the limits of energy use. In: Tomasi TE, Horton TH, editors. Mammalian energetics. Ithaca: Cornell University Press. 276p.

de Waal F. 1997. Food transfers through mesh in brown capuchins. J Comp Psychol 111: 370–378.

de Waal F. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. Anim Behav 60:253–261.

Westergaard G, Suomi S. 1997. Transfer of tools and food between groups of tufted capuchins (*Cebus apella*). Am J Primatol 43: 33–41.

White F. 1994. Food sharing in wild pygmy chimpanzees, *Pan paniscus*. In: Roeder J, Theirry B, Anderson J, Herrenschmidt N, editors. Current primatology. Vol. II. Strasbourg: Université Louis Pasteur. p 1–10.

Wilkinson G. 1984. Reciprocal food sharing in the vampire bat. Nature 308:181–184.

Wilson C. 1976. Food sharing behavior in primates: another species added. Proc Ark Acad Sci 30:95–96.

Wright P. 1984. Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In: Small MF, editor. Female primates: studies by women primatologists. New York: Alan R. Liss, Inc. p 59–75.

Wright P. 1985. The costs and benefits of nocturnality for *Aotus trivirgatus* (the night monkey). Ph.D. dissertation, City University of New York, New York, NY. 339p. Available from UMI; AAT 8601707.