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Dads do not pay for sex but do buy the milk: food sharing and reproduction in owl monkeys (*Aotus* spp.)

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Sharing food is costly, and animals rarely share food with unrelated individuals. Males may share food with females when females are fertile or when female nutrition will affect offspring. Such benefits are known for insects and birds, but not for mammals. This study examined the effect of female reproductive state (ovarian cycling, pregnancy, lactation) on food sharing between mates in monogamous owl monkeys, *Aotus* spp. Male–female pairs of captive owl monkeys at the DuMond Conservancy (Miami, FL, U.S.A.) were regularly observed feeding from October 2003 to November 2004. To determine the onset and duration of pregnancy, urine was collected from females and analysed for the progesterone metabolite pregnanediol-3α glucuronide using enzyme immunoassay. Food transfers from females to males did not vary across reproductive state, and males did not transfer food most often to females when females could potentially become pregnant. Conversely, females most often begged for food when they were lactating, and males most often transferred food to females when their mates were lactating. Compared to males of polygamous species, male owl monkeys are relatively certain of paternity. In addition to providing infant care directly, male owl monkeys would benefit from ensuring that their mates receive adequate nutrition because it indirectly provides nutrition for offspring by enhancing the quantity and/or quality of the mates' milk.

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Food sharing is an affiliative social behaviour in which food donors experience a reduction in potential energetic intake while food recipients acquire additional food resources. There are obvious fitness advantages of sharing food with offspring, and this type of food sharing is common (Feistner & McGrew 1989). Nonkin food sharing, however, is rare but may also offer reproductive benefits to food donors and recipients. Sharing food with potential mates may result in increased mating opportunities (Gwynne 1984a; Kuroda 1984) and/or increased offspring production (Royama 1966; Gwynne 1984b, 1986).

In mammals, the reproductive benefits of sharing food with adults have been investigated only in bonobos, *Pan paniscus*, and chimpanzees, *Pan troglodytes*. Male bonobos share food with females, possibly in exchange for mating opportunities (Kuroda 1984; Hohmann & Fruth 1996). Male chimpanzees, however, do not preferentially share food with oestrous females (Mitani & Watts 2001), and males that share food with females do not sire more offspring than males that do not share food with females (Hemelrijk et al. 1999).

Sharing food with females that are pregnant or lactating may have important nutritional benefits and may ultimately affect female reproductive success. Female mammals face substantially higher energetic costs during

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pregnancy than during normal metabolic maintenance (Thompson 1992), and there can be reproductive consequences of failing to meet these energetic demands (Tardif et al. 2004). Lactation is even more costly than gestation (Randolph et al. 1977; Michener 1989; Thompson 1992; Künkele 2000). To help offset these extra costs, pregnant or lactating females may behaviourally compensate by spending more time foraging (guinea pigs, *Cavia porcellus*: Künkele 2000) or by limiting their physical activity (Thompson 1992). On the other hand, if these females receive food from other individuals, they may increase their energy intake while avoiding the additional time and energy expenditures of increased foraging (Royama 1966). Females that increase their energetic intake may produce more nutritious milk, thereby accelerating offspring growth and reducing the time their infants are dependent (Laurien-Kehnen & Trillmich 2004). Females that receive more food from males may subsequently have shorter interbirth intervals than females that receive less or no food from males (Brown & Mack 1978). Females with the shortest interbirth intervals could ultimately produce the largest number of offspring.

Males may benefit by relinquishing food to their mates when there is certainty of paternity. Although extrapair copulations and fertilizations can occur in socially monogamous species, monogamous males can be fairly certain of paternity to the extent that they can monopolize their mates and monitor their activities (Birkhead & Møller 1992). If females gain reproductive benefits from receiving food, males that share food and sire offspring with those females also benefit. In some pair-bonded species, males share food with pregnant and lactating females (golden lion tamarins, *Leontopithecus rosalia*: Brown & Mack 1978; Ruiz-Miranda et al. 1999; wolves, *Canis lupus*: Mech et al. 1999; man, *Homo sapiens*: Marlowe 2003). Yet, to date, the quality or type of food shared across female reproductive states has not been considered nor have researchers observed the same subjects over time.

We examined food sharing in monogamous owl monkeys (*Aotus* spp.) to determine whether males share food with females when females are most likely to conceive (a payment for sex) and/or when females are most energetically needy (helping to pay the costs of milk production). We also examined the potential effect of these food transfers on reproductive success by relating the frequency of the food transfers to females with the interbirth intervals. Owl monkeys are socially monogamous, with males investing in parental care (Wright 1984; Rotundo et al. 2005). Males not only groom and carry infants but also regularly share food with them (Wright 1984; Feged et al. 2002; Wolovich et al. 2006).

Both captive and wild owl monkeys (*Aotus* spp.) transfer food between mates (Feged et al. 2002; Wolovich et al. 2006). We expected females to beg for food most often when they were lactating and we expected males to transfer food most often to females when females were lactating. We predicted that the highest rate of food transfers would occur from females to males when females were experiencing ovarian cycles and hence potentially fertile. If food transfers to females affected reproductive success, we expected a negative relationship between the rates of food transfers from males to lactating females and interbirth intervals.

METHODS

Subjects and General Procedures

We observed 14 adult male−female pairs of captive owl monkeys, *Aotus nancymaae* and *A. azarai*, at the DuMond Conservancy for Primates and Tropical Forests, Inc. (Miami, FL, U.S.A.) from October 2003 to November 2004. We included *A. nancymaae*, *A. azarai* and two hybrid individuals because previous work investigating the patterns of food sharing in captive owl monkeys did not indicate any differences between them (Wolovich et al. 2006) and because they all belong to the red-necked group of owl monkeys (Brumback 1973; Hershkovitz 1983). Species of *Aotus* can be genetically distinguished (Torres et al. 1998; Delfer & Bueno 2003), but there are at least two areas of hybridization in natural populations of owl monkeys (Pieczarka et al. 1993; Ford 1994; Torres et al. 1998); therefore, data gathered from hybrid individuals can be biologically meaningful.

Eight of the 14 pairs had offspring present at some point in the study, whereas six of the pairs had no offspring present at any time during this study. Two of the females were older than the others and had given birth successfully to at least three offspring, whereas the other females were all less than 10 years old and had given birth once or never prior to this study. Pairs of owl monkeys consisting of one adult male and one adult female were maintained in 2.4-m-diameter × 2.4-m-height cylindrical wire mesh enclosures. Families of owl monkeys (pairs of adults with offspring) were housed in 3 × 3-m cylindrical wire mesh enclosures. Each enclosure contains a nestbox and a variety of perches and platforms. The enclosures are visually separated from one another by dense foliage, but vocalizations are heard from conspecifics in nearby enclosures.

Observations began during dusk or within 2 h after sunset, the period when the monkeys were normally fed and most active (Wright 1985). We used flashlights with lenses covered by red cellophane to aid in observing behaviours and in identifying individuals. The monkeys were previously habituated to the presence of observers (Wolovich et al. 2006).

Apple Feedings

For each trial, we placed 24 small cubes of apple (3.4 cm^3) into an empty plastic 355-ml juice container with a 5-cm × 7.5-cm hole cut into the cylindrical portion. We used apple because the monkeys reliably eat it, it can be cut into exact pieces, it does not break apart when handled by the monkeys and it is available year round. The juice container was used to slow the rate of food extraction, thereby facilitating observations. At the start of the feeding trial, the feeding container was placed on the inside wall of the monkeys' enclosure 1.5 m from the ground. We began recording data immediately following food presentation until all the apple pieces were eaten

or when the monkeys ceased feeding for 5 consecutive minutes. For each food interaction, we scored 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 or transfer (Table 1).

Determination of Female Reproductive State

To accurately assess female reproductive state, we conducted hormonal assays from noninvasively collected urine samples. This technique enabled the detection of any pregnancies that ended in abortion that would have otherwise been undetected (Málaga et al. 1997).

Urine collection and storage

We trained the monkeys to urinate via positive reinforcement with marshmallows soon after awakening in the late afternoons. We collected urine from the adult female of each pair being observed that evening. Urine was caught in a clean plastic bowl by holding it directly under the urinating monkey. We transferred the urine into microcentrifuge tubes using sterile pipettes and stored the samples at $-20°C$ until analysis (Kesner et al. 1995).

Hormone assays

The Endocrine Bioservices Laboratory at the University of Nebraska at Omaha assayed the urine samples for levels of pregnanediol-3α glucuronide (PdG), a progesterone metabolite, using an enzyme immunoassay that has been well characterized elsewhere (Munro et al. 1991; French et al. 1996). Briefly, microtitre plates were coated with 50 μl of PdG antibody (P1126), and 50 μl of sample (diluted 1:200 in double-distilled water) or PdG standard preparations (ranging from 10 000 to 78 pg/well in

halving dilutions) were added. PdG-horseradish peroxidase (50 μl) was then added to each well. After 2 h of incubation, unbound hormone was removed from the wells by washing (4×), and 100 μl of substrate (ABTS$-H_2O_2$) was added to determine the amount of conjugate bound to the antibody. Plates were gently shaken until the absorbance in wells with 0 pg of the standard reached 1.0. Absorbance for all wells was then measured on a Dynatech MR5000 plate reader and sample concentrations were calculated using a four-parameter sigmoid line fit function.

Assay quality control was monitored by assaying a urine pool on each plate at two concentrations (approximately 70 and 30%, respectively, for the low concentration and high concentration pool). Intraassay coefficients of variation were 8.25 and 8.19%, and interassay coefficients of variation were 11.06 and 23.63%, for the high and low pools, respectively. The assay of serial dilutions of single samples collected from six females in varying reproductive conditions produced displacement curves that were parallel to the displacement curve produced by the PdG standard. To control for variable fluid intake and output, urine samples were assayed for creatinine (Cr) concentration using a modified Jaffé reaction (description in French et al. 1996). PdG concentrations are thus expressed as μg PdG/mg Cr.

Based upon the PdG profiles, we categorized each female as cycling or pregnant. Females were classified as lactating from the time an infant was born until the infant was 6 months old, the typical length of nursing in *Aotus* (Dixson & Fleming 1981, personal observation). We made an attempt to use each of the 14 groups of monkeys in at least eight apple trials for each of the three female reproductive states (ovarian cycling, pregnant and lactating).

Sampling

We observed the owl monkey pairs for a combined total of 89 h divided among 512 apple trials (median = 37 trials per pair, range 24−43). One pair was observed during only 24 apple trials because the older male in the family died in May 2004. Mean apple trial length ranged 4.7−14.7 min with an overall mean of 10.6 min.

We collected urine successfully from 10 of the 14 females. Urine was collected from each of these females approximately once every 4 days with a total of 445 urine samples collected and analysed for PdG (median = 44 samples/female, range 25−60). Only seven of these females gave birth and were included in analyses comparing food interactions among the three female reproductive states. Because it was impossible to know whether females were pregnant at the time of the observations, there was unequal sampling among the groups for the number of apple trials for each female reproductive state (ovarian cycling median = 12 trials, range 7−20; pregnant median = 8 trials, range 4−14; lactating median = 14 trials, range 9−20).

Ovarian Cycle Length and Gestation Period

We calculated ovarian cycle lengths for all females that had at least three distinct consecutive rises and falls in

Table 1. Description of food-sharing terms for owl monkeys

Term	Definition
Food interaction	Two monkeys within arm's reach and one monkey holds food in its mouth or hand and another monkey's face is oriented towards the food
Possessor (P)	Holds food in mouth or hand at the beginning of interaction
Potential recipient (PR)	Does not hold food in mouth or hand at the beginning of interaction
Approach	One monkey reduces the distance between it and another monkey to within arm's reach
Beg	PR extends hands towards a food item held by P or moves mouth towards item and opens mouth
Investigate	PR moves mouth towards mouth of P but does not open mouth
Resist	P turns away from PR, moves hand with food away from PR, or moves body away from PR
Transfer	Food is moved from the hand or mouth of the possessor to the hand or mouth of the recipient

PdG. Cycle length was defined as the number of days between the successive nadir samples that occur immediately prior to the peaks. We calculated the mean peak value for PdG for each female and used it to determine an overall mean peak value in PdG. PdG rises just after conception and remains elevated during pregnancy, allowing for the detection of the onset and duration of pregnancy (Hunter et al. 1979). We used the PdG levels of all females that successfully gave birth to calculate gestation lengths (the number of days between parturition and the previous rise in PdG that was not followed by a dip in PdG to near zero). We determined the mean values of PdG during pregnancy for each female and used them to calculate an overall mean PdG during pregnancy.

Interbirth Intervals

We measured interbirth interval as the time between a female's first and second births. Because interbirth interval can decrease as a function of female parity and age (S. Evans, unpublished data), only females under 10 years of age were included in this calculation. All females that fit these criteria were *A. nancymaae*.

Statistical Analyses

We used SYSTAT version 11.0 (SYSTAT, San Jose, CA, U.S.A.) for all statistical tests. We used nonparametric statistics because our data did not meet the assumptions necessary to use parametric tests. Wilcoxon signed-ranks tests were used to examine food interactions with the males as a possessor and with the females as a possessor for the following food interaction variables: the numbers of food interactions, investigates, begs and transfers, the rate of food transfers (number of transfers/h), the proportion of begs with resistance and the proportion of begs resulting in transfer. Bonferroni corrections were applied to alpha levels to control for the number of statistical tests used (adjusted $\alpha = 0.007$ for an overall $\alpha = 0.05$).

For comparisons among female reproductive states, each variable is represented as the number of occurrences per feeding trial for each pair for each female reproductive state so that pairs are weighted equally. Only females that exhibited all three female reproductive states were used for comparisons. We used Friedman's two-way analysis of variance by ranks to compare food transfers per feeding trial among female reproductive states to determine whether there is an overall effect of female reproductive state on the number of food transfers per feeding trial. Additional Friedman's two-way analyses of variance by ranks were used to compare the other food interaction variables to describe better the variation, if any, in the quality of food interactions. If a significant overall effect was found, we used Wilcoxon signed-ranks tests to compare between food interactions between each possible combination of the three female reproductive states (ovarian cycling, pregnant, lactating). We used a Spearman rank correlation to examine the relationship between the number of food transfers per hour from males to lactating females and the interbirth interval.

RESULTS

Ovarian Steroid Hormone Profiles

Cycle length

Six of the 10 females (three *A. nancymaae*, one *A. azarai*, two hybrids) had at least three consecutive detectable ovarian cycles and were included in the determination of ovarian cycle length. Figure 1 illustrates typical successive nonconceptive ovarian cycles of an *A. nancymaae* female. The mean ± SD cycle length for *A. nancymaae* was 18.5 ± 1.3 days with a mean peak PdG value of 33.6 ± 21 µg/mg Cr. The female *A. azarai* had a longer mean cycle length of 25.0 days with a mean peak PdG value of 89 µg/mg Cr, but this estimate was based on only three consecutive cycles. The two hybrid females had a mean cycle length of 18.3 days with a mean peak PdG value of 70.9 µg/mg Cr.

Gestation period

Four *A. nancymaae* females and one *A. azarai* female gave birth during this study. The four *A. nancymaae* females had a mean gestation length of 117 ± 8 days, and the one *A. azarai* female had a gestation length of 121 days. The mean PdG during pregnancy for the four *A. nancymaae* females was 65.7 ± 42 µg/mg Cr, and the mean PdG for the one *A. azarai* female was 59.4 µg/mg Cr. Median levels of PdG during pregnancy were significantly greater than those during normal ovarian cycling (Wilcoxon signed-ranks test: $T = 0$, $N = 7$, $P = 0.018$; Fig. 2).

Overall Patterns of Food Sharing between Mates

There was no difference in the mean number of apple pieces that the male and female of pairs retrieved from the
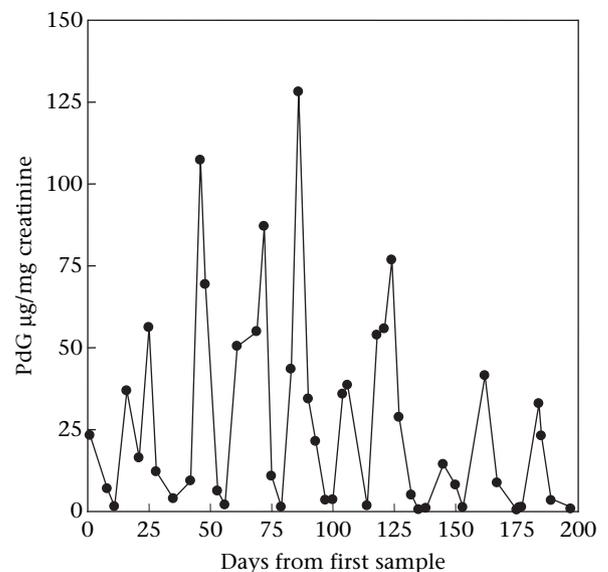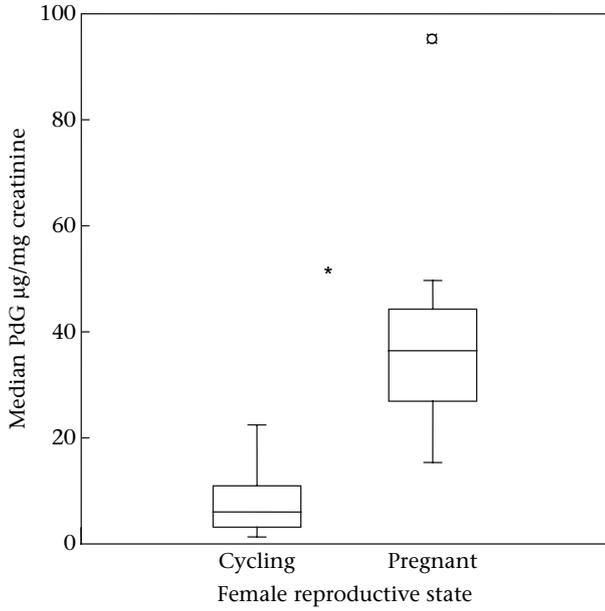

Figure 1. Fluctuation of urinary pregnanediol-3α glucuronide (PdG) from a reproductively mature female *A. nancymaae*. This female had experienced successive nonconceptive ovarian cycles.

Figure 2. Concentrations of pregnanediol-3α glucuronide (PdG) in the urine of female owl monkeys ($N = 7$) during normal ovarian cycling and during pregnancy. Horizontal lines within box plots represent median values, boxes represent the interquartile range, and whiskers represent the range of values within 1.5 times the interquartile range. ¤ = outlier (value that fell beyond three times the interquartile range). *$P < 0.05$.

container (medians = 8.0 and 9.6 pieces, respectively; Wilcoxon signed-ranks test: $T = 35$, $N = 14$, $P = 0.27$). Food sharing between mates was observed in 13 of the 14 pairs with a mean rate of 0.98 transfers per hour. The total number of food interactions varied among pairs ($N = 14$ pairs, median = 39 interactions/pair, range 4−160). Food transfers within pairs were symmetrical, occurring both from males and females to their mates. Across all observations, there were no significant differences in the number of food interactions (Wilcoxon signed-ranks test: $T = 29$,

$N = 13$, $P = 0.278$), investigations ($T = 41$, $N = 14$, $P = 0.507$), begs ($T = 10$, $N = 10$, $P = 0.92$) or transfers ($T = 31$, $N = 13$, $P = 0.529$) when either the male or the female of pairs were potential recipients. There were also no differences in the rate of transfers ($T = 42$, $N = 13$, $P = 0.807$), proportion of begs with resistance ($T = 27$, $N = 12$, $P = 0.594$) or the proportion of begs that resulted in transfer ($T = 9$, $N = 9$, $P = 0.110$) when the male or female of pairs were potential recipients.

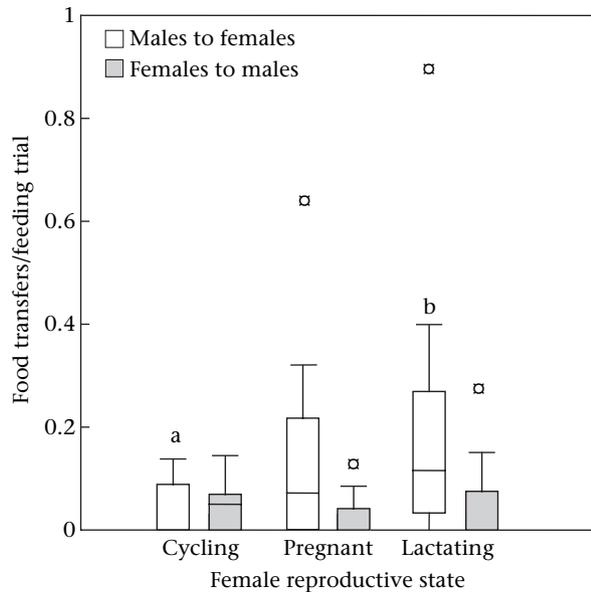## Food Transfers and Female Reproductive State

We report the median values of all food interaction variables for each female reproductive state in Table 2. The number of food transfers from males to females per feeding trial varied significantly across the three female reproductive states (Friedman test: $\chi_2^2 = 7.68$, $N = 7$, $P = 0.02$; Fig. 3). Post hoc analyses revealed that the number of food transfers from the male to the female in pairs did not differ when females were cycling (median = 0.00/trial) and when females were pregnant (median = 0.07) (Wilcoxon signed-ranks test: $T = 2$, $N = 5$, $P = 0.14$), but the number of food transfers from the male to female in pairs was greater when females were lactating (median = 0.12/trial) than when females were cycling (median = 0.00/trial) (Wilcoxon signed-ranks test: $T = 0$, $N = 5$, $P = 0.04$). The number of food transfers from females to males per feeding trial, however, did not vary among the three female reproductive states (Friedman test: $\chi_2^2 = 0.11$, $N = 7$, $P = 0.95$).

When males were possessors and females potential recipients, there were no differences in the number of investigations and the proportion of begs that resulted in transfer across the three female reproductive states (Table 2). The total number of food interactions and the number of female begs, however, varied among female reproductive states. The number of food interactions per trial with males as possessors was significantly greater

Table 2. Variation in food interactions with female reproductive state when females or males were possessors and males or females were potential recipients, respectively

	Female reproductive state				
	Cycling	Pregnant	Lactating	χ_2^2	P value
Female possessor, male potential recipient					
No. male investigates/feeding trial	0.19 (0−1.1)	0.17 (0−1.5)	0.14 (0−0.8)	0.33	0.846
No. male begs/feeding trial	0.14 (0−0.3)	0.17 (0−0.4)	0.15 (0−0.8)	0.22	0.895
Proportion of male begs resulting in transfer	0.50 (0−1.0)	0.00 (0−1.0)	0.00 (0−1.0)	3.00	0.223
No. food interactions/feeding trial	0.49 (0.1−1.3)	0.33 (0−1.9)	0.36 (0−1.5)	1.41	0.495
Male possessor, female potential recipient					
No. female investigates/feeding trial	0.06 (0−0.3)	0.14 (0−0.6)	0.10 (0−0.6)	1.65	0.438
No. female begs/feeding trial	0.00 (0−0.3)	0.10 (0−1.1)	0.21 (0−1.7)	6.40	0.041
Proportion of female begs resulting in transfer	0.00 (0−0.5)	0.50 (0−1.0)	0.50 (0−1.0)	4.80	0.091
No. food interactions/feeding trial	0.19 (0−0.4)	0.55 (0−1.6)	0.45 (0−1.8)	6.33	0.042

Values represent medians for seven pairs of owl monkeys. Values in parentheses represent ranges. The values for each variable were compared among the three female reproductive states using Friedman two-way analyses of variance, yielding the chi-square values and P values reported for each of the four variables. α = 0.05.

Figure 3. Food transfers within male−female pairs during different female reproductive states. Horizontal lines within box plots represent median values (*N* = 7 pairs), boxes represent the interquartile range, and whiskers represent the range of values within 1.5 times the interquartile range. ⌷ = outliers (values that fell beyond three times the interquartile range). Different letters denote significant differences between median values across reproductive states. Comparisons were made using Friedman tests and Wilcoxon signed-ranks tests (α = 0.05).

when females were pregnant and when they were lactating than when they were cycling (Wilcoxon signed-ranks test: $T = 0$, $N = 6$, $P = 0.028$; $T = 1$, $N = 6$, $P = 0.046$, respectively). The number of female begs per trial was greatest when females were lactating and least when they were cycling (Wilcoxon signed-ranks test: $T = 0$, $N = 5$, $P = 0.04$). During food interactions with females as possessors and males as potential recipients, there were no differences in the number of investigations, begs or total food interactions across the three female reproductive states (Table 2). The proportion of male begs that resulted in transfer also did not vary with female reproductive state.

Food Sharing and Interbirth Intervals

There was an association between the frequency of food transferred to lactating females and the interbirth interval, with females that received the most food from males having the shortest interbirth interval. This negative relationship between the rate of food transfers to lactating females and the interbirth interval is significant (Spearman rank correlation: $r_S = -0.81$, $N = 6$, $P < 0.05$).

DISCUSSION

We examined patterns of food sharing systematically in the same pairs of individuals across female reproductive states while controlling for food quality. Although food transfers in owl monkeys occur both from males to

females and from females to males, there is an important biological difference. Female owl monkeys transferred food to their mates irrespective of reproductive status. Males transferred food to females when they were lactating rather than when they were cycling and could potentially conceive. Therefore, we conclude that males do not pay for sex but do buy the milk. This conclusion is supported by the finding that there is no association between observation periods with mating and those with food sharing in captive owl monkeys (Wolovich & Evans 2007). We found a negative relationship between interbirth interval and the rate of food transfers from males to lactating females. This finding suggests that sharing food with lactating females may be related to overall lifetime reproductive success.

Food Sharing with Females and Potential Reproductive Advantages

Owl monkeys live in socially monogamous groups with each male having access to only one female. It may benefit a male to remain with a single female by ensuring his paternity and successful rearing of his offspring. These males would also benefit by investing both in their offspring and in their mates. Even though this study focused on captive monkeys that could easily acquire food, the females increased their rate of begging when they were lactating. Males responded by transferring food to lactating females; thus males provision their mates with food when their mates require the most energy for successful reproduction (Randolph et al. 1977; Michener 1989; Thompson 1992; Künkele 2000). Other pair-bonded mammals have been reported to share food with pregnant and lactating females. Male wolves regurgitate food not only to pups but also to lactating females (Mech et al. 1999). In the wild, male golden lion tamarins have been observed to transfer food to pregnant females (Ruiz-Miranda et al. 1999), and in captivity, males transfer food to their mates most often after their mates give birth (Brown & Mack 1978). This pattern has also been observed in human societies. Hadza men with nursing wives bring more food home than do Hadza men with nonnursing wives (Marlowe 2003). Our results support these findings and suggest a nutritional function of sharing food with female mammals.

These patterns of food sharing are similar to those described for insects and birds because males transfer food to females most often when females require additional energy for reproduction. Food transfers from adult males to adult females may improve maternal condition and provide extra nutrients for egg production (Royama 1966). In many orders of insects, males offer nuptial gifts to females during or directly after copulations (Vahed 1998). Females that consume nuptial gifts produce larger eggs and larger clutch sizes than females that do not receive nuptial gifts (Gwynne 1984b). Courtship feeding in birds has a similar effect. In common terns, *Sterna hirundo*, and red-billed gulls, *Larus novaehollandiae*, food provided by males increases the number of eggs that females can produce (Nisbet 1973, 1977; Tasker & Mills 1981; Gonzalez-Solis et al. 2001) as well as the time between successive

clutches (Wendeln 1997). Females that receive more courtship feedings also lay their eggs earlier in the season than females that receive fewer courtship feedings (Tasker & Mills 1981; Wendeln 1997; Gonzalez-Solis et al. 2001), possibly allowing for additional clutches later in the season.

Until now, there has been little evidence in mammals supporting any fitness advantage associated with food transfers to adult females (Hemelrijk et al. 1999). We found a significant negative relationship between the rate of food transfers from males to lactating females and the length of interbirth intervals in owl monkeys. By having short interbirth intervals, a pair can theoretically produce a greater number of offspring over the course of their lifetimes than a pair with long interbirth intervals. Our results suggest that the nutritional function of sharing food with females may be more widespread among animal taxa than previously thought.

Food Sharing with Males and Potential Social Advantages

Male owl monkeys did not alter their rate of begging with respect to their mate's reproductive condition, and females did not decrease their rate of transferring food to males when they were pregnant or lactating. Furthermore, across all pairs, the overall rate of food transfers from females to males was equal to that from males to females. There are several possible interpretations as to why there was no effect of female reproductive state on the pattern of these food transfers. During lactation, the females in this study may have not been food limited, or they may have been selective in the food items that they relinquished. Because females begged for food from males most often during lactation and because the type of food was held constant, neither of these explanations seems likely. It is possible, however, that the patterns of food transfer in the wild may be different and females may not share food resources during pregnancy and lactation. Preliminary data from observations in the wild, however, do not suggest this to be the case. Two pregnant females have been observed to transfer food to their mates (Wolovich et al., in press), a rare behaviour across the animal kingdom.

An alternative explanation as to why food sharing from females to males does not vary with female reproductive state is that food sharing may play a role in social bonding (Wolovich et al. 2006). A social bonding hypothesis of food sharing 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 humans (Lovejoy 1981). Furthermore, complex reciprocal social exchanges of food have been observed for grooming in chimpanzees (de Waal 1997; Mitani 2006) and for sex in bonobos (Kuroda 1984; Parish 1994; Hohmann & Fruth 1996). Female owl monkeys may transfer food to males in exchange for future paternal care, with the food transfers acting as an incentive for the males to remain with them to help raise offspring.

Ovarian Cycle Length and Gestation Period

Our estimates of ovarian cycle lengths for *A. nancymaae* as 18.5 days and for *A. nancymaae* × *azarai* as 18.3 days are slightly longer than previous reports of cycle length for *A. lemurinus* (16 days) (Bonney et al. 1980). The one *A. azarai* female used in this study had an even longer cycle length, but she was an older female and we used only three consecutive cycles for determining her mean cycle length. There are potential species differences in cycle length but there are also methodological differences that could account for the variation between the cycle lengths observed in this study and those in previous studies. Bonney et al. (1980) measured levels of oestrone and progesterone both in plasma and in urine samples that were collected daily. It is unlikely that this previous estimate is incorrect especially because the samples in our study were collected approximately every 4 days, allowing for a higher level of error in calculating cycle length.

The gestation length estimates of 117 days for *A. nancymaae* and 121 days for *A. azarai* are shorter than previous reports for *Aotus* (126 days, Hall & Hodgen 1979; 133 days, Hunter et al. 1979). Even accounting for an approximate level of error of ±4 days in this study, the *A. nancymaae* and *A. azarai* gestation periods were still shorter than those previously reported for owl monkeys. If our findings are correct, *Aotus* has the shortest gestation period of any New World primate (Hartwig 1996). As a result, *Aotus* neonates may be more altricial than other New World primates. It is interesting that newborn owl monkeys are held in a unique position on the warm groin area of adults (Dixson & Fleming 1981). This carrying position coupled with the newborns' completely bare ventrums (personal observation) may suggest that they are not able to thermoregulate. If owl monkey infants are altricial, then sharing food with lactating females may be even more important for females to produce a high-quality milk that would be vital for infants to develop rapidly, especially during the first few weeks of life. Some other infant characteristics, however, do not support the idea that owl monkey infants are particularly altricial (Hartwig 1996). Continued investigation into the variation of ovarian cycle lengths, gestation periods and milk composition among *Aotus* species should be conducted to determine potentially significant biological differences and add to our understanding of the importance of food sharing in this genus.

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