ANIMAL BEHAVIOUR, 2008, **75**, 1155–1163
doi:10.1016/j.anbehav.2007.09.023

Available online at www.sciencedirect.com
ScienceDirect

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

CHRISTY K. WOLOVICH*, SIAN EVANS† & JEFFREY A. FRENCH‡
*Department of Biology, University of Miami
†DuMond Conservancy for Primates and Tropical Forests, Inc., Miami
‡Department of Psychology, University of Nebraska at Omaha

(Received 28 April 2007; initial acceptance 6 July 2007; final acceptance 5 September 2007; published online 30 January 2008; MS. number: A10759)

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.

Keywords: *Aotus*; food transfer; lactation; monogamy; owl monkey; paternal care; pregnanediol-3α glucuronide

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

Correspondence and present address: C. K. Wolovich, Department of Biology, Bucknell University, Lewisburg, PA 17837, U.S.A. (email: c.wolovich@bucknell.edu). S. Evans is at DuMond Conservancy, 14805 SW 216 St., Miami, FL 33170, U.S.A. J. A. French is at 419 Allwine Hall, Department of Psychology, University of Nebraska at Omaha, 6001 Dodge Street, Omaha, NE 68182-0274, U.S.A.

0003–3472/08/$34.00/0

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