

A Preliminary Study on the Function of Food Begging in Sichuan Snub-Nosed Monkeys (*Rhinopithecus roxellana*): Challenge to Begging for Nutritional Gain

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Key Words

Food begging · Social function · Food transfer · Sichuan snub-nosed monkeys · *Rhinopithecus roxellana*

Abstract

Several hypotheses have been developed to explain what benefits a donor may gain from sharing food with another individual, with nutritional gain assumed to be the sole benefit for the beggar. Recently, it has been proposed that begging behaviour serves a social function in non-human primates. In this study, the nutritional-gain assumption was again challenged based on observations on a captive group of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*), or golden snub-nosed monkeys. The major findings from this study are that (1) beggars sometimes left their own branches or passed by available branches to beg for similar food from other individuals, (2) beggars occasionally ignored branches that were acquired by begging and (3) food begging occurred more frequently in the all-male unit after the social rank had changed between 2 individuals in this unit. Overall, these preliminary findings suggest that some begging behaviours in captive golden snub-nosed monkeys were not driven by nutritional gain only; instead, we propose that these begging behaviours could be interpreted as attempts at deriving social benefits.

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Introduction

Food transfer, defined as allowing another individual to consume part of one's own monopolisable food [Stevens and Stephens, 2002; Stevens and Gilby, 2004], has been reported in many non-human primates, including chimpanzees (*Pan troglodytes*), capuchins (*Cebus apella*) and the Callitrichidae [de Waal, 1989; Fragaszy et al.,

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1997; Ruiz-Miranda et al., 1999; Brown et al., 2005]. Recently, a high frequency of food transfer was also reported in captive Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*), or golden snub-nosed monkeys [Zhang et al., 2008; Xue and Su, in press], expanding upon observations of this species' food transfer behaviour in the wild [Ren et al., 2000]. The conventional hypotheses explaining the functional basis of food transfer in non-human primates primarily focus on benefits accrued to the donor [Stevens and Gilby, 2004]. For example, the donor may either directly benefit through reciprocity [Trivers, 1971], trade [Noë and Hammerstein, 1994], avoiding harassment [Stevens and Stephens, 2002] or indirectly benefit through kin selection [Hamilton, 1964]. Because any benefits that the donor may acquire come at the cost of transferring food to the recipient, these hypotheses have implicitly assumed that nutritional gain must be the sole benefit accrued to the beggar [Slocombe and Newton-Fisher, 2005]. However, Slocombe and Newton-Fisher [2005] have recently hypothesised that begging behaviour may be driven by social benefits gained by the beggar. These authors suggested that when begging occurs despite there being an alternative way to obtain the same food at a lower cost of time and energy, this behaviour may be initiated to reinforce social relationships rather than only to obtain nutrition. Additionally, it has been observed in adult common marmosets that the beggar occasionally opened the possessor's mouth forcefully and took food out [Kasper et al., 2008]. However, the possessor had no refusal responses in this regard. This kind of tolerated mouth-to-mouth food transfer has been suggested to function socially as bond-testing [Kasper et al., 2008]. *R. roxellana*, as a species with high social tolerance [Ren et al., 1990; Li et al., 2006], exhibits a higher rate of food transfer in captivity than those reported for captive chimpanzees and capuchins, and the two peaceful methods (cofeeding and relaxed claim) are the most common ways for golden snub-nosed monkeys to beg food from others, as is the case for chimpanzees [Zhang et al., 2008]. The high food-related tolerance in captive golden snub-nosed monkeys led us to explore the possible function that begging may have in this species with the prediction that sometimes food begging may not serve a solely nutritional function in the captive context, and interpretation from the perspective of social function may be required to understand these begging behaviours, as has been suggested in chimpanzees [Slocombe and Newton-Fisher, 2005] and in common marmosets [Kasper et al., 2008].

Methods

Subjects and Housing

A group of captive golden snub-nosed monkeys housed at Shanghai Wild Animal Park was observed from April 18 to May 17, 2005 (this same group has previously been referred to as semi-captive [Zhang et al., 2008] as they have access to an outdoor enclosure). The 10-subject sample group, all located in the same enclosure, comprised a one-male unit (OMU) and an all-male unit (AMU). The OMU included 8 individuals: 1 adult male (No. 5), 2 adult females (No. 3 and 98-2), 2 juvenile males (No. 03-1 and 03-3), 2 juvenile females (No. 01-4 and 03-2) and a newborn infant that was not included in the study. The AMU consisted of 3 adult males (DWB, No. 97-1 and 98-1). This study was approved by the Peking University Institutional Animal Care Committee and the State Forestry Administration of China. In the wild, golden snub-nosed monkeys feed primarily on lichens and the leaves, fruit and seeds of a variety of plant species [Li, 2006; Guo et al., 2007]. The captive group in this study was fed regularly with freshly cut branches of privet at around 08.30, 13.00 and 16.45 h daily. Chopped steamed bread, eggs, fruit and eggplants were given to the monkeys at around 10.00 and 15.30 h. Water was available at all times.

Branch feeding, which is common in the wild, was chosen for the observation of food interactions from April 18 to May 17, 2005. Observations started from the time when the attendant came into the outdoor enclosure and dropped the privet branches into 4 separate piles (1 large pile for the OMU and 3 small piles for each adult male in the AMU). Observations ended either when no food interactions occurred (mean = 28.5 min, SD = 18 min) or a few minutes (mean = 5.8 min, SD = 2.7 min) after the monkeys had been fed in the afternoon prior to park closure. The feeding process was recorded by an observer (Z.Z.) with a digital video camera (Panasonic NV-DS30EN, Matsushita Electric Industrial Co. Ltd., Osaka, Japan). In total, 69 observation sessions were recorded over 27 days, including at least 2 sessions per day. Scan sampling was used to collect social-activity data outside the food sessions, and each individual had 3,494 min of behaviour recorded from April 18 to May 17, 2005 [for more details regarding the monkeys' living environment and the observation process, see Zhang et al., 2008].

Data on social activities were used to determine affiliative relationships and the social hierarchy of the group. In the AMU, it was inferred that one of the adult males (No. 97-1) replaced another (DWB) as the most dominant individual from May 5 onwards, based on a reversal in the direction of threats and submissive behaviours between these two monkeys. A third adult male (No. 98-1) was consistently the most subordinate individual in the AMU. In the OMU, the 3 adult monkeys had a consistent social rank throughout the study, with the male being ranked between 2 females in the following order: adult female (No. 3) > adult male (No. 5) > adult female (No. 98-2). Juveniles were subordinate to all adults in both the OMU and AMU.

All food interactions and behavioural categories were coded according to the classifications outlined by de Waal [1989, 1997]. In this study, begging behaviour was classified into the following 6 types: (1) cofeeding: the beggar joins the possessor to feed on the same branch; as a result, both individuals hold the branch; (2) relaxed claim: the beggar takes part or all of the branches from the possessor's hands or mouth in a relaxed manner without use of agonistic behaviour; (3) forced claim: the beggar grasps or pulls part or all of the branches from the possessor's hands or mouth forcefully, ignoring the possessor's agonistic signals and physical resistance, or supplants another individual from a possessed branch; (4) collect-near: the beggar collects small branches or leaves within arm's reach of the possessor; (5) steal: the beggar approaches the possessor (usually from behind, or from below when the possessor is on the perches), snatches food and runs off; (6) food interest: individual shows cheek-to-cheek begging, stares closely or sniffs at the possessor's food without attempting to take it [for more details on these begging behaviours as well as on possessors' responses, see Zhang et al., 2008]. A random sample of 457 (32.6%) food interactions was independently coded by another coder to assess interrater reliability. The kappa coefficients of observer agreement for behaviour type of the beggar, behaviour type of the possessor and whether the beggar initiated begging after either leaving their own branches or ignoring available food were 0.70, 0.71 and 0.79, respectively.

Results

Overall, 1,290 food interactions were analysed after excluding 111 interactions because the beggar/possessor relationship was unclear (typically due to the simultaneous approach of 2 individuals to a branch) or because there was an incomplete tape record. When analysing the food interactions, begging behaviour was unlikely to serve a nutritional function in the following 3 contexts, which will be presented in detail below.

Context I: The Beggar Left Its Own Branches or Passed by Available Branches to Beg from Others

In 122 (9.5%) of the 1,290 total food interactions, the beggars either left their own branches or ignored available branches to beg from an individual who possessed

food with comparable physical appearance and, thus, presumably with comparable nutritional quality. Almost all of these behaviours (113 of the 122 interactions; 92.6%) were observed in the OMU: 40 (35.4%) of the 113 interactions took place between adults, 42 (37.2%) between juveniles, and 31 (27.4%) between adults and juveniles. In addition, 5 such food interactions were observed in the AMU, and 4 were observed between the juvenile males in the OMU and the adults in the AMU.

It is notable that such begging in the OMU was observed when the beggar was subordinate as well as when it was dominant, although in the AMU only dominant individuals were observed to initiate such begging towards subordinates. In the OMU, within the 14 possible dyads, dominant individuals begged for branches from a subordinate individual after abandoning easily obtainable branches (total 49 cases, median frequency = 2.75) more frequently than the subordinate begged from the dominant in the same way (total 22 cases, median frequency = 0.5, Wilcoxon signed rank tests on paired data, $T = 17$, $n = 14$, $p < 0.05$). However, subordinate adults begged from dominant adults in 14 cases, while juveniles begged from adults in 8 cases. For dominant beggars, all 6 types of begging behaviour, except for stealing, were observed in this context. Cofeeding and relaxed claim were the 2 most common behaviours displayed by dominant beggars, amounting to 38.8% (19 of 49 cases) and 36.7% (18 of 49 cases), respectively. For subordinate beggars, cofeeding (16 of 22 cases; 72.7%) was the typical behaviour observed; relaxed claim and forced claim were not observed in this context. When such begging happened between juveniles, stealing was not observed, and cofeeding was also the most common method used by beggars (31 out of 42 cases; 73.8%). Juvenile males were also observed to beg from adults in the AMU in 3 cases by collect-near, cofeeding and forced claim (once each). As for the AMU, dominant beggars initiated such interactions towards subordinates by collect-near, relaxed claim or cofeeding in a total of 5 cases.

Context II: The Beggar Ignored the Acquired Branches after Begging

In 15 (1.2%) of the 1,290 total food interactions, the beggar took the possessor's branches away either by relaxed claim (10 out of the 15 cases; 66.7%) or by forced claim (5 cases), only to later abandon these food items. After some of these food interactions, the beggar and possessor engaged in further social interactions, including play between juveniles (3/15), affiliative behaviour, such as embracing each other or grooming, between a dominant adult beggar and subordinate adult possessor (4/15), and a confrontation between 2 adult males (1/15). In the remaining cases, the beggars abandoned the acquired branches and walked away alone. This happened between 2 juveniles (3/15), between a juvenile and an adult (3/15), and between 2 adults in the AMU (1/15).

Context III: The Frequency of Begging Behaviours Increased in the AMU after the Social Rank Changed within This Unit

Because the social-rank order of members of the AMU changed from May 5 onwards, food interactions before and after this change were counted separately. After the change in social hierarchy, the frequency of food interactions between members of the AMU remained constant between May 11 and May 17, and, therefore, observations ceased at this point. Twenty-four food sessions were recorded from May 5–8 and May 11–17, which were compared to 24 food sessions recorded closely before May 5 (April 26 to May 4).

Table 1. Frequency of food begging before and after (in parentheses) the change of social rank in the AMU

Beggar	Possessor			Beggar	Possessor					
	AM _A 1 (DWB)	AM _A 2 (No. 97-1)	AM _A 3 (No. 98-1)		AF1 (No. 3)	AM _O (No. 5)	AF2 (No. 98-2)	AM _A 1 (DWB)	AM _A 2 (No. 97-1)	AM _A 3 (No. 98-1)
AM _A 1 (DWB)	–	5 (8)	2 (12)	JM1 (No. 03-1)	17 (12)	9 (3)	10 (3)	10 (3)	2 (5)	0 (0)
AM _A 2 (No. 97-1)	0 (14)	–	5 (7)	JM2 (No. 03-3)	4 (1)	3 (1)	4 (1)	24 (12)	2 (18)	3 (4)
AM _A 3 (No. 98-1)	3 (9)	0 (0)	–							

Left column: food begging between adults in the AMU; right column: food begging initiated by juvenile males towards adults. Social rank in the AMU: original rank, AM_A1 (DWB) > AM_A2 (No. 97-1) > AM_A3 (No. 98-1)/changed rank, AM_A2 (No. 97-1) > AM_A1 (DWB) > AM_A3 (No. 98-1). AM_A = Adult male in AMU; AM_O = adult male in OMU; AF = adult female; JM = juvenile male.

When focusing on the 2 blocks of 24 selected food sessions, it was found that after the change in social rank, the total number of food interactions for the entire group dropped from 510 to 366 food interactions. However, food interactions in the AMU increased from 15 to 50 interactions. This increase was due to frequent food interactions between 2 pairs of adult males in this unit (DWB and No. 97-1, DWB and No. 98-1). After DWB's social rank had dropped, No. 97-1 began to show begging behaviour towards DWB, but DWB did not reduce his begging towards No. 97-1. Meanwhile, both DWB and No. 98-1 exhibited increased begging behaviour towards one another after the change in social hierarchy (table 1).

The effects of change in social rank on begging behaviour were also observed in the 2 juvenile males (No. 03-1 and 03-3), as they increased their begging behaviour towards the adult male (No. 97-1) after he had replaced another (DWB) as the dominant (table 1). This phenomenon was particularly obvious in No. 03-3; he begged from No. 97-1 significantly more often after No. 97-1 had become the new dominant (2/29 vs. 18/34, Fisher's exact test; $p < 0.001$, two-tailed). In contrast, the occurrence of food begging initiated by No. 03-3 decreased significantly towards the former dominant (DWB) after his social rank had dropped (24/29 vs. 12/34, Fisher's exact test; $p < 0.001$, two-tailed) or did not change significantly towards any other adults between the two phases [two-tailed Fisher's exact test; $p = 1.0$, for adult male in the AMU (No. 98-1, 3/29 vs. 4/34), adult male in the OMU (No. 5, 3/11 vs. 1/3) and adult females in the OMU (No. 3, 4/11 vs. 1/3; No. 98-2, 4/11 vs. 1/3)]. As to the other juvenile male (No. 03-1), the frequency of begging initiated by No. 03-1 towards No. 97-1 showed an increasing trend after No. 97-1 had become the new dominant (2/12 vs. 5/8, Fisher's exact test; $p = 0.06$, two-tailed). On the other hand, the begging frequency towards other adults either marginally decreased after the change of social rank [previous dominant in the AMU (DWB, 10/12 vs. 3/8): Fisher's exact test; $p = 0.06$, two-tailed], showed no significant difference between the two phases [adult male (No. 5, 9/36 vs. 3/18) and adult females (No. 3, 17/36 vs. 12/18; No. 98-2, 10/36 vs. 3/18) in the OMU; two-tailed Fisher's exact test; $p = 0.73, 0.25, 0.51$, respectively] or was never recorded either before or after the change of social rank (adult male in

the AMU, No. 98-1). Further exploration of this phenomenon indicated that the juvenile males (No. 03-1 and 03-3) initiated their interactions with the new dominant (No. 97-1) rather than in response to his begging from them. On the first day that the adult male No. 97-1 replaced another (DWB) as the dominant, both juvenile males begged for food from the new dominant No. 97-1 in a relaxed manner and kept doing so in the following days. However, 3 days later, the new dominant No. 97-1 began taking branches from the 2 juvenile males. Further analysis also revealed that the giving of grooming by the two juvenile males (No. 03-1 and 03-3) to the new dominant (No. 97-1) was influenced by the change in his social rank. Before the adult male No. 97-1 became the dominant one, neither of the juveniles groomed him. However, after this event, the 2 juvenile males groomed him 13 and 14 times, respectively. For 1 juvenile male (No. 03-1), 6 of the 13 (46%) grooming events happened on May 6, while the rest were observed on May 16. For the other one (No. 03-3), 11 of the 14 (79%) grooming events happened on May 6 and May 7, while the rest were observed on May 16.

Discussion

The major findings of this study indicate that there were contexts in which golden snub-nosed monkeys engaged in begging behaviours where it seemed that they did not beg primarily to obtain food. In addition, there was another context in which more begging behaviours were observed among certain individuals after the social rank order had changed in the AMU. Overall, these findings reveal that, in some contexts, the intention behind begging behaviour in captive *R. roxellana* was not for nutritional gain only. These contexts will be discussed in detail below.

In the first context, the dominant individuals abandoned their own branches or passed by available ones to take comparable food from a subordinate; however, the subordinates also initiated the same behaviours towards the dominants. Because it would not be adaptive for the subordinate to abandon easily obtainable food and instead take the risk of being attacked when taking food from the dominant individual, begging for nutritional gain inadequately explains the subordinate's behaviour, and we suggest that individuals – in particular, subordinate monkeys – may derive social benefits from begging. Even when such behaviour was initiated by the more dominant individuals, the underlying motivation for this behaviour may not have been to obtain food. For example, in the AMU, on the first day that the adult male No. 97-1 replaced another (DWB) as the dominant individual, DWB abandoned his branches and passed by available ones to peaceably cofeed with a third adult male (No. 98-1) for 33 s. Hence, the specific date, specific behaviour sequences of DWB and the specific identity of the possessor together imply that DWB's begging may not have been for nutritional gain only; instead, we suggest that DWB may have been attempting to procure some social benefits from begging.

Food interactions that took place in the second context, although rare, imply more directly that the purpose of begging is not always for nutrition. In some instances, the beggar ignored the food it had acquired and instead engaged in playful or affiliative behaviour with the possessor, indicating that begging is a way to initiate social interactions. Even in instances where the beggar walked away alone without engaging in any interaction with the possessor, this begging behaviour, we suggest,

may still only be understandable from the perspective of serving a social function. For example, in the AMU, on the second day that the adult male No. 97-1 replaced DWB as the dominant individual, he took away DWB's branches in a relaxed manner and walked away with them. After walking a few steps away, No. 97-1 left the acquired branches on the ground and continued to walk forward, indicating that his begging may have been a means to assess his new social rank.

In the final context, begging behaviour in the AMU also appears difficult to explain as being motivated by obtaining nutritional gain only, given that this behaviour greatly increased following changes in social rank within this unit. Because there was more begging behaviour between individuals whose rank order had reversed, we suggest that begging may have been a way to ascertain or assert the newly formed social rank. Moreover, given that increased begging was observed between the two currently subordinate individuals, we suggest that begging may be a way to establish affiliations between group members. In addition, juvenile males No. 03-1 and 03-3, especially the latter, begged more frequently from the new dominant of the AMU (No. 97-1), which is consistent with the observation that these juveniles subsequently began to groom No. 97-1. Because these juvenile males were 2 years old at the time of this study and would join the AMU about 1 year later (in fact, No. 03-3 was already being chased away by adults in the OMU because he had lost his mother when he was 1 year old), these behaviours may have been adaptive for them to establish a good relationship with the dominant individual in the AMU, especially for No. 03-3. This may be the reason why No. 03-3 initiated more begging and grooming behaviours towards the new dominant (No. 97-1) than did the other juvenile (No. 03-1) soon after No. 97-1's social rank changed. Therefore, juvenile males' begging behaviour towards the dominant individual in the AMU may be partially motivated by social benefits.

In conclusion, the results of the current study suggest that some begging behaviours in captive golden snub-nosed monkeys are not motivated by nutritional gain only; instead, these begging behaviours can be better interpreted as attempts to procure social benefits, as has also been proposed for some begging behaviours in chimpanzees [Slocombe and Newton-Fisher, 2005] and in common marmosets [Kasper et al., 2008]. In social primates living in large groups, food sharing may be a more complex behaviour than has been conventionally considered, in that it contributes significantly to the social lives of non-human primates. Exploring the motivations that drive begging behaviour will help to uncover the nature of food sharing in non-human primates [Slocombe and Newton-Fisher, 2005]. In the future, studies with a larger sample size and a longer observation period should be conducted on golden snub-nosed monkeys to provide direct evidence of the kinds of social benefits obtained by beggars via the initiation of food begging.

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