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NEWS AND PERSPECTIVES

Food-snatching behavior of free-ranging Japanese macaques observed on Shodoshima Island: a preliminary report

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Abstract We investigated the characteristics of a particular food-snatching behavior in which one individual forced another's mouth open and grabbed the food, as performed by free-ranging Japanese macaques (*Macaca fuscata*) in Choshikei Monkey Park on Shodoshima Island, western Japan. We conducted a survey in late June 2012 and observed one of two monkey troops, comprising 214 monkeys. We recorded the age classes and sexes of the individuals who performed the snatching behavior and were snatched from, and examined the effects of provisioned food distribution and quantity on the frequency of snatching trials and success. During the survey, we recorded 747 snatching trials, of which 609 were successful, all of which were performed by seven individuals: one adult male and six adult females. The snatching behavior occurred only during provisioning. The target animals were primarily juveniles (650 trials, 578 successful), while cases in which food was snatched from adult females (93 trials, 30 successful) and subadult females (4 trials, 1 success) were less frequent. Among the juveniles, small juveniles had food snatched more frequently than large juveniles. The higher frequency of snatching trials against juveniles was likely due to their subordinate nature. Neither the distribution nor quantity of the provisioned foods had significant effects on the number of snatching trials and successes, while the time elapsed after provisioning had significant negative effects, attributed to a decrease in the number of wheat grains left within the mouth pouch of the potential target animals.

Keywords Choshikei · Distribution · Japanese macaques · *Macaca fuscata* · Snatching behavior · Shodoshima

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Introduction

Food transfer is a common survival tactic adopted by many group-living animal species (Hadjichrysanthou and Broom 2012). It allows food resource distribution among group members, increasing their fitness. Food transfer among individual group members is sometimes voluntary; for example, from mothers to offspring (Feistner and McGrew 1989; Jaeggi et al. 2008). In other species, however, food transfer is involuntarily; several animals grab food from different species or conspecifics with harassment behavior (Brown 2004; Stevens 2004; Starin 2006; Gilby 2006, Kasper et al. 2008). Such food transfer is considered kleptoparasitism (Brockmann and Barnard 1979).

Nigi (2004) and Kurita (2007) described a new mode of food transfer in free-ranging Japanese macaques, *Macaca fuscata*, at Takasakiyama, southern Japan. Several monkeys, especially adult females, grabbed food from the cheek pouches of infants and juveniles, including their offspring. In this study, we call this "snatching behavior." Furthermore, Kurita (2007) suggested that the snatching behavior prevented increases in the body mass and growth rate of a target infant. Although intraspecific food transfer has been studied in several primate species (Brown 2004),

snatching behavior has been reported only for captive common marmosets (Kasper et al. 2008).

Kleptoparasitism in bird species is associated with several ecological conditions, including food availability, food item visibility, and the length of food shortage (Brockmann and Barnard 1979). Therefore, the occurrence of snatching behavior in Japanese macaques might be related to ecological factors; it is known that within-group contest-type competition occurs more frequently and severely in dietary patches that are smaller, less dense, and in a clumped distribution (Janson 1985; Koenig 2000; Vogel et al. 2007). Studies of free-ranging Japanese macaques, performed under both provisioned and wild conditions, support this prediction (Iwamoto 1987; Saito 1996; Tsuji and Takatsuki 2012). Therefore, we predicted that the snatching behavior occurred more frequently and successfully when food was provided in clumped and small quantities, and less frequently and successfully when food was provided in scattered and large quantities. Alternatively, age–sex class may affect the risk of having food snatched; for example, juveniles, which are physically weaker than adults, might be targeted more frequently (Kurita 2007).

In this study, as a first step in exploring the potential underlying social factors, we investigated the snatching behavior of members of a free-ranging Japanese macaque troop. We altered the distribution and quantity of provisioned food to evaluate environmental effects on the occurrence and success of the snatching behavior.

Methods

Study site and animals

We conducted field observations of Japanese macaques in Choshikei Monkey Park (34°31′N, 134°14′E) on Shodoshima Island (153.5 km^2), western Japan. The altitude of the park ranges from 340 to 420 m a.s.l. It is dominated by *Quercus salicina* community vegetation (Oota et al. 2011), with several evergreen plants, such as *Eurya japonica*. Two troops of Japanese macaque inhabit the park: troops A and B. One observer (IH) conducted three censuses of troop A after provisioning time, while troop B was censused four times before and after provisioning time. We classified the troop members based on age class and sex into infant, juvenile, subadult male, subadult female, adult male, and adult female, respectively. We treated the maximum number of individuals for each age class and sex as the individual number of given troop. Troop A consisted of 214 individuals: 7 adult (>8 years old) males, 84 adult females, 8 subadult (6–7 years old) males, 20 subadult females, 74 juveniles (1–5 years old), and 21 infants (<1 years old), while troop B consisted of 189 individuals: 6 adult males, 72 adult females, 4 subadult males, 24 subadult females, 59 juveniles, and 24 infants (Islamul Hadi, unpubl. data). These troops are habituated to the park staff and visitors, and we observed them within 5 m, undisturbed. Although their diet included natural food from the forest, the majority of their diet comprised provisioned food; wheat grains are supplied three times daily (in total ~20 kg/group) at feeding sites, and some sweet potatoes and vegetables are offered in the afternoon (Zhang 2011). During provisioning, monkeys of the two troops spend several hours at two 50 × 25 m feeding sites inside the park. Severe intertroop competition rarely occurs because the feeding site locations of the troops differ (C. Saeki, pers. comm.).

Feeding experiments and snatching data collection

We conducted a field survey and series of feeding experiments from 21 to 30 June 2012. Among the two troops, we selected troop A as our subject, since park staff had observed the snatching behavior in this troop more frequently, allowing easier data collection. We stayed with the central part of the troop and observed the monkeys for 1 h before and after the first (1100–1130 hours; "morning session" hereafter) and third (1630–1700 hours; "evening session" hereafter) provisioning times.

During the observations, one of the observers (IH) walked around the troop recording the snatching behavior that occurred before and after the feeding sessions using ad libitum sampling. For this study, we defined three terms related to snatching behavior: "snatching trial," when an individual approaches and tries to hold the target animal; "snatching success," when an individual successfully holds and snatches food from the target's cheek pouch orally or manually; and "snatching fail," when an individual approaches a target but fails to handle or collect food orally or manually. We recorded the sexes and age classes (infant, juvenile, subadult, or adult) of the participants in the snatching behavior whenever possible. We further classified juveniles, which comprised a large number of the snatching behavior targets, into small (25 individuals) and large (49 individuals) for further discussion. Most of the small juveniles were estimated to be one year old based on their distinct body size and shape. Individuals could not be identified in the limited study period and there were no precise historical recordings of the group members.

Feeding experiments were conducted to address the effects of the distribution and quantity of the provisioned food on the occurrence and success of the snatching behavior. We altered the food distribution ("scattered" vs. "clumped") and abundance ("large" vs. "small"), as outlined in Table 1. In the scattered condition, the wheat grains were served within the 50 × 25 m area (1250 m^2),

Table 1 Daily change in food distribution during the study period

Days	Food distribution	
	Morning (small amount)	Evening (large amount)
1	Preliminary observation	
2	S	S
3	S	S
4	C	C
5	S	S
6	C	C
7	S	S
8	C	C
9	C	S
10	–	C

C clumped distribution, *S* scattered distribution

corresponding to the normal provisioning condition for troop A. In the clumped condition, the wheat grains were served within a 20 × 10 m area (200 m^2). The quantities of wheat grain provisioned in the morning and evening sessions were 4 and 13 kg, respectively, except on the 21st, when 3 and 10 kg of wheat grain were served, respectively. Therefore, the amounts of food in the morning and evening sessions were designated "large" and "small," respectively (Table 1).

To evaluate the amount of available wheat grains gathered in the cheek pouch, one of the observers (YT) recorded the number of wheat grains gathered in 1 min by a randomly selected adult female or juvenile. After finishing the given recording session, the next focal animal was determined within 10 s. We tried to avoid collecting data from the same individuals repeatedly, but this may have occurred.

Statistical analyses

We conducted a chi-square test of independence to determine if the target animals were from a specific age class. We compared the observed compositions of the target age class and the troop age class. For juveniles, we tested whether the snatching behavior was directed more towards small or large individuals. Note that there were fewer data for the latter analysis than the former due to a lack of information from the first several days. Finally, we tested whether the rate of snatching success differed among animals.

To test our prediction of the frequency and success of the snatching behavior, we altered both the distribution and amount of provisioned food, as described above. Moreover, we included the time elapsed since provisioning as a possible environmental factor; to calculate its effect, we arbitrarily divided a feeding session into 5 min blocks. We used generalized linear mixed models (GLMMs) to address the effects of distribution, amount of provisioned food, time elapsed after provisioning, and an interaction between the distribution and amount of food on (1) snatching trials and (2) snatching successes. In these analyses, we assumed a Poisson distribution as the error structure and treated the snatching individuals as a random factor. Moreover, we treated the number of snatching trials as an offset term for the latter analysis to adjust its effect. Besides the snatching behavior, we determined whether the amount of wheat grains in a cheek pouch in the provisioning ground was affected by the distribution, amount of provisioned food, time elapsed after provisioning, and the interaction between the distribution and amount of food. For this analysis, we used a general linear model (GLM), assuming a negative binomial distribution as the error structure. To conduct the GLMM and GLM, we used the "glmmML" and "MASS" packages (Venables and Ripley 2002; Brostrom and Holmberg 2011). All statistical analyses were conducted with R, version 2.15 (R Developmental Core Team 2012), and the significance levels (α) of all analyses in this study were 0.05.

Results

During the feeding sessions, we recorded 747 snatching trials at a rate of 43.5 times $hour^{-1}$, of which 609 (35.8 times $hour^{-1}$) were successful. We observed no snatching behavior before the provisioning. We identified seven—one adult male and six adult females—among the 214 monkeys that performed the snatching behavior (Table 2). Two adult females in particular, Kanchee and Sarah, performed more than half of the snatching trials and had a higher rate of snatching success (Table 2).

The snatching animals tended to come to the feeding ground later than the other animals. Furthermore, they often looked for a target nearby. After finding a potential target, they usually grasped the head of the target from behind, pulled out and opening its mouth, and then took grains from the mouth pouch of the target manually (Fig. 1a) or orally (Fig. 1b). Often, they held the target animals tightly from behind on their belly using a foot and both elbows to prevent the target from struggling.

The target animals were mainly juveniles (86.9 % of snatching trials and 94.9 % of snatching successes), with a few cases of snatching targeted at adults (12.4 % of trials and 4.9 % of successes) and subadults (0.4 % of trials and 0.2 % of successes; Table 2). Infants, subadult males, and adult males were never snatched from during our observations. The age composition of the target animals differed significantly from the troop composition (chi-squared test for independence, $\chi^2 = 234.3$, $df = 2$, $p < 0.001$). Small

Table 2 Individuals who conducted the snatching behaviour and details of their target animals, as well as frequencies and success of the snatching

Name	Sex and age	Target animals (sex and age)								
		I	J[a]	J[b]		SAM	SAF	AM	AF	Total
				Small	Large					
Yana	AM	0	53 (36)	26 (14)	18 (15)	0	2 (1)	0	59 (8)	114 (45)
Kanchee	AF	0	294 (258)	183 (127)	48 (41)	0	0	0	6 (3)	300 (261)
Sarah	AF	0	260 (240)	170 (153)	42 (35)	0	1 (0)	0	3 (2)	264 (242)
Botak	AF	0	32 (32)	19 (19)	0 (0)	0	0	0	0	32 (32)
Traya	AF	0	0	0 (0)	0 (0)	0	0	0	5 (4)	5 (4)
Eni	AF	0	9 (9)	8 (7)	0 (0)	0	0	0	0	9 (9)
Intan	AF	0	3 (3)	1 (1)	2 (2)	0	0	0	20 (13)	23 (16)
Total		0	651 (578)	395 (350)	110 (93)	0	3 (1)	0	93 (30)	747 (609)

Numbers in parentheses show the snatching success

I infant, *J* juveniles, *Small* small juveniles, *Large* large juvenile, *SAM* subadult males, *SAF* subadult females, *AM* adult males, *AF* adult females

[a] Data on the frequencies of snatching in all juveniles collected June 22–30, 2012 (see "Methods")

[b] Data on the frequencies of snatching in small and large juveniles collected June 25–30, 2012 for further discussion

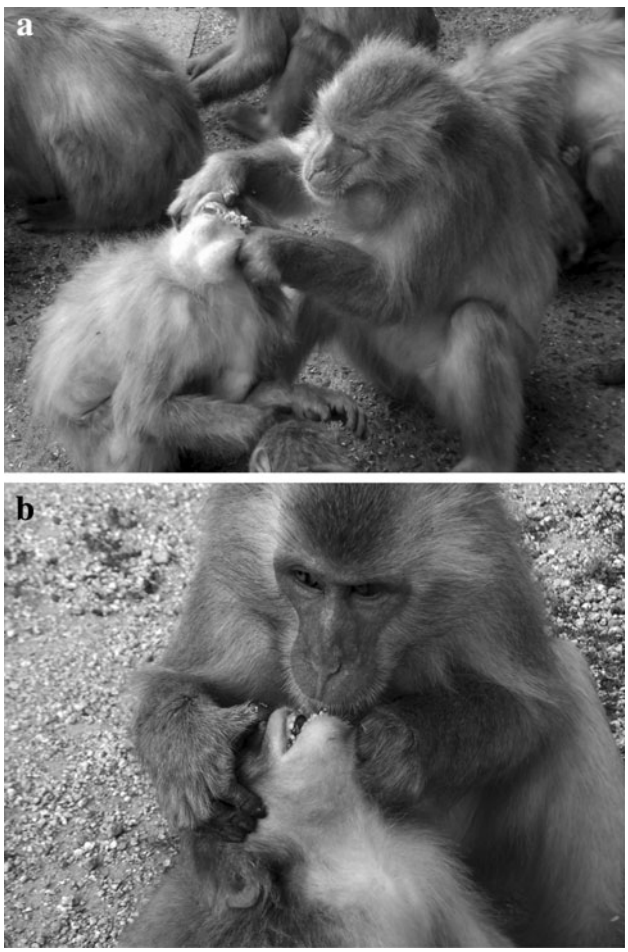

Fig. 1 **a** An adult female (Kanchee) snatching from a juvenile manually. **b** An adult female (Sarah) snatching from a juvenile orally

juveniles were snatched from more frequently than large juveniles ($\chi^2 = 61.8$, $df = 1$, $p < 0.001$). There was variation in the target animals: Yana (adult male), Traya (adult female), and Intan (subadult female) targeted adult females very often, Kanchee and Sarah mainly targeted juveniles, and Botak and Eni targeted only juveniles (Table 2). Regarding the four snatching individuals who targeted animals in multiple age classes, the composition of the target animals differed significantly from the troop composition (Yana: $df = 2$, $\chi^2 = 9.0$, $p = 0.011$; Kanchee: $df = 1$, $\chi^2 = 168.4$, $p < 0.001$; Sarah: $df = 2$, $\chi^2 = 186.5$, $p < 0.001$; Intan: $df = 1$, $\chi^2 = 105.0$, $p < 0.001$).

Both the frequency of snatching and its success decreased with time after provisioning (GLMM, $df = 247$, occurrence: $z = 2.5$, $p < 0.001$; success: $z = -4.4$, $p < 0.001$), while the effects of the provisioned food distribution and quantity and their interaction did not have any significant effects ($p > 0.05$ for each analysis). In addition, the amount of wheat grains in the cheek pouch decreased with time after provisioning (GLM, $df = 464$, $z = -14.6$, $p < 0.001$). The amount of wheat grains in the cheek pouch was greater when the provisioned foods were scattered ($df = 464$, $z = 6.1$, $p < 0.001$), while no other variables had significant effects on the amount of wheat grains in the cheek pouch ($p > 0.05$ for each).

Discussion

In Choshikei Monkey Park, seven individuals (one adult male and six adult females) among the 214 troop members

of the subject troop (3.2 %) performed the snatching behavior. This small number of snatching individuals was similar to that reported in Takasakiyama, southern Japan, where ~10 of 1300 individuals from three troops (0.8 %) performed the snatching behavior (Kurita 2007). We predict that such exploitative behavior will not become a major strategy among the troop members since, if it were to occur, the target animals would eventually adopt counteracting behavioral tactics to evade the snatching.

By nature, Choshikei monkeys gather in small spaces (Yamada 1966; Zhang and Watanabe 2007). Large clusters consisting of 10–100 monkeys were observed normally. At the feeding site, the distance between individuals was very short and they often passed on the heads of other monkeys. Such habitual crowding of Choshikei monkeys might influence the frequency of the snatching behavior. Takasakiyama monkeys snatched wheat grains very often from their own infants (Kurita 2007). We observed only one case of snatching from own-offspring (conducted by Sarah). Since individual identification was not conducted in this study, the kin/non-kin relationships of the target animals could not be evaluated. However, due to its clustering nature, non-kin individuals were readily available, and this could have encouraged the higher occurrence of snatching behavior in Choshikei.

The target animals in this study were mainly juveniles (81.8 % of trials). The snatching animals targeted juveniles—especially small juveniles—frequently because the small juveniles seemed to be easier to catch and handle due to their smaller size. Among the subadults and adults, females were selected as targets more than males, perhaps due to their weaker physical strength. Snatching from infants was not observed, perhaps because the study season (late June) corresponded to 2–3 months after the birth season, when the infants depended mainly on milk (Iwamoto 1982), so there would be no reward for the snatching animals.

Brockmann and Barnard (1979) suggested some ecological factors that facilitate the evolution of kleptoparasitism in birds: (1) large concentrations of target animals, (2) food in large quantities, (3) food of high quality, (4) food supplied in a predictable manner, (5) food visibility, and (6) food shortage. All of these factors, except for (6), were applicable to the snatching behavior of the Japanese macaques in Choshikei Monkey Park, because (1) the density of the monkeys was high, (2) large amounts of food were supplied, (3) provisioned foods like wheat grain are high in energy and nutrition (Iwamoto 1987), (4) the provision time was fixed, and (5) food was supplied at an open feeding site. Food shortage did not seem to have a role because the food environment of the provisioned macaques was stable and the energy intakes of the Japanese macaques under provisioning were greater than those of wild Japanese macaques (Iwamoto 1987; Tsuji 2010). The snatching is an effective feeding strategy for dominant individuals to obtain a great amount of energy, and the crowded condition of Chosikei might would allow them to perform this behavior.

Based on foraging ecology theories and previous studies (Janson 1985; Koenig 2000; Vogel et al. 2007), we predicted that the snatching behavior occurred more frequently and perhaps more successfully in food supply conditions involving a clumped distribution and small quantities. In practice, however, neither the distribution nor the amount of food provisioned affected the frequency of the snatching behavior and its success, and only time elapsed since provisioning had significant negative effects; that is, snatching occurred frequently and successfully immediately after the provisioning. One likely reason for this is the amount of provisioned food inside the mouth pouch; regardless of the food distribution and quantity, target animals gathered the provisioned food in their cheek pouches. Mouth pouch contents would be swallowed and made unavailable to the snatching animals after the target animals had stopped picking up the food and had left the feeding site. Therefore, to obtain provisioned foods effectively, the snatching animals attacked the targets immediately after provisioning, when the amount of wheat grains in cheek pouch was higher.

In this study, we were unable to identify each target; therefore, we were unable to establish their relationships to the snatching individuals. In the future, individuals should be identified and kinship relationships and social rank relationships among the troop members should be clarified in order to address the social background of the snatching behavior. Specifically, determining whether the snatching behavior is transmitted from a mother to her offspring and whether it is only performed by high-ranking individuals would help us to understand why few monkeys perform this behavior. Another challenge is to determine the implications of it for the foraging success of the target animals. A long-term study would reveal the effects of the snatching behavior on the mortality and reproductive success of the participants.

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