Title: **First report of food sharing among Nicobar long-tailed macaques**

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Abstract- The sharing of food is an essential component of human societies and has likely played a key role for the evolution of several human traits such as reduced sexual dimorphism, a more flexible maturational pace in relation to environmental variation and an increase in human tolerance and co-operation. For this reason, the investigation of the evolutionary origins of food sharing in humans has been a central topic in biological anthropology. Since behaviour does not fossilize, investigations on food sharing in non-human primates are key in providing a window into the evolution of food sharing and co-operation in humans. Among non-human primates, apes and New World monkeys have mostly shown evidence of non-kin food sharing, but in Old World monkeys, it is a very rare phenomenon. Here we provide the first descriptive report of food sharing in wild macaques. We studied two free-ranging groups of Nicobar long-tailed macaques from two different islands (i.e., Great Nicobar and Katchal), that have very different ecological settings and vegetation, for over 168 days. Using focal animal sampling, we observed a total of 18 food sharing events, that revolved around monopolizable food items (coconut and termite log) and mostly involved males. Females, even when present near the food owner, took very little interest in observing the event. The macaques shared food only among the individuals who sat close to the food owner, who, in turn, displayed very little aggression against bystanders. Given that, among Nicobar macaques, males have been previously described as forming strong social relationships, and since harassment was rarely observed in the present study, we argue that our observations could support the reciprocal exchange rather than the harassment hypothesis. While more observations are needed to better clarify the ultimate function of food sharing in this species, our study on Nicobar long-tailed macaques, highlighting some features that might make this species an ideal model to study the evolution of human behavior.

Keywords- co-operation, rewards, begging, social learning, non-kin, harassment

1. **Introduction**

The sharing of food is an essential component of human societies (Kaplan et al., 1985; Kaplan and Gurven, 2005). While food sharing is found across many group-living species, from insects to birds and mammals (reviewed in Stevens and Gilby, 2004), it plays a much more important nutritional role in humans than in other animals. Chimpanzees (*Pan troglodytes*), for example, commonly hunt other animals and share their meat (Mitani and Watts, 2001; Gilby, 2006), but, in this species, food obtained through food sharing constitutes only a small proportion of all calories consumed, as chimpanzees largely obtain their food themselves after weaning (Kaplan et al., 2000; Hohmann, 2009; Luca et al., 2010). In contrast, in human societies, individuals largely depend on food obtained by others long after weaning, generating a society in which some people produce much more than they consume while other people consume much more than they produce (Kaplan, 1997; Crittenden and Schnorr, 2017). This type of economy likely emerged in human societies as a result of a heavy reliance on food sources that are difficult to acquire, such as meat or extracted food items (e.g., tubers), and so it helped to balance the uncertainty of foraging for high-risk/high-reward foods (Kaplan and Hill, 1985; Stanford et al., 2011).

The emergence of an economy that largely relies on food sharing has likely played a key role in human evolution, by favoring, for example, a reduction in sexual dimorphism, a more flexible maturational pace in relation to environmental variation and an increase in human tolerance and co-operation (Kramer, 2018). For this reason, the evolutionary origins of food sharing have been a central topic in biological anthropology. While archaeological and paleontological studies have been influential in providing some indirect evidence on when an economy based on food sharing might have evolved in humans, by investigating, for instance, when human diet might have started relying more on meat and extracted food items (Backwell and d'Errico, 2001; Leakey and Clark, 2009; Pickering and Domínguez-Rodrigo, 2012), behaviour does not fossilize. Therefore, investigations on food sharing in non-human primates are vital in providing a window into the evolution of food sharing and co-operation in humans (Isaac, 1978; Jaeggi and Gurven, 2013).

Food sharing in non-human primates can take different forms: it can be active, when an individual either gives food to a partner or produces a call to attract partners to a food source (Feistner and McGrew, 1989; Stevens and Gilby, 2004), as well as passive when an individual obtains food from a group member without the food owner's active help (e.g., tolerated theft; Blurton Jones, 1987). Since food sharing is beneficial to the recipient but costly to the donor, the selective pressures that have promoted the evolution of this type of co-operative interaction in primates, including humans, have been a matter of debate for decades (reviewed in Stevens and Gilby, 2004; Jaeggi and van Schaik, 2011). While the evolution of food sharing among kin (including between mothers and infants) can be accounted for by mechanisms of kin selection (Hamilton, 1964), the evolution of food sharing among non-kin is more puzzling as it is unclear how actions that benefit the recipient at no apparent advantage to the actor can be maintained by natural selection if co-operators do not share alleles (Dugatkin, 2002; Hammerstein, 2003; Clutton-Brock, 2009).

Non-kin food sharing among primates, to date, has largely been described in apes (e.g., chimpanzees, *Pan troglodytes*; bonobos, *Pan paniscus*: Jaeggi et al., 2010; Goldstone et al., 2016), and in New World Monkeys (e.g., golden lion tamarins, *Leontopithecus rosalia*: Wilson, 1976; spider monkeys, *Ateles geoffroyi*: Pastor-Nieto, 2001; tufted capuchins, *Sapajus apella*: de Waal et al., 1993; de Waal, 2000; white-faced capuchins, *Cebus capucinus*: Perry and Rose, 1994). Food sharing among Old World monkeys, in contrast, has rarely been reported (e.g., Guinea baboons, *Papio papio*: Goffe and Fischer, 2016; olive baboons, *Papio anubis*: Strum, 1975). The investigation of food sharing in both apes and monkeys can shed light on whether at least some of the factors regulating food sharing in human societies were present not only in the common ancestor of humans and other apes living around 6-8 million years ago, but also in the common ancestor between apes and Old World monkeys dating back to around 32 million years ago (Pozzi et al., 2014). Additionally, the study of non-human animals can help us better understand whether and to what extent human behavior is unique.

Here we provide the first report of food sharing among Nicobar long-tailed macaques (*Macaca fascicularis umbrosus*). We have evaluated our observations in the light of two main hypotheses that have been put forward to date to explain the evolution of food sharing among primates, namely the reciprocal exchange hypothesis and the harassment hypothesis. Under the reciprocal exchange hypothesis, donors offer food in order to receive either food (capuchin monkey: de Waal, 2000) or some other service or commodity in return, such as coalitionary support (chimpanzee: Mitani and Watts, 2001; Mitani, 2006), mating opportunities (chimpanzee: Hockings et al., 2007; Gomes and Boesch, 2011) or grooming (chimpanzee: Mitani, 2006b). The harassment hypothesis, on the other hand, suggests that donors are forced to share food in order to decrease the costs of defending the food item against group members. These two hypotheses are not necessarily mutually exclusive as both harassment and reciprocity can regulate the tendency to share food in non-human primate populations (Stevens and Gilby, 2004). To date, there has been evidence to support both the reciprocal exchange hypothesis (capuchin monkey: de Waal, 1997; chimpanzee: Mitani and Watts, 2001; Hockings et al., 2007; Gomes and Boesch, 2011) and the harassment hypothesis (chimpanzee: Stevens and Stephens, 2002; chimpanzee: Gilby, 2006; reviewed in Stevens and Gilby, 2004).

Long-tailed macaques provide an excellent study model to test both hypotheses and compare the factors driving food sharing in this species with those that regulate the sharing of food in apes, especially chimpanzees. In fact, while there are many socio-ecological differences between long-tailed macaques and chimpanzees (unlike macaques, for example, female chimpanzees commonly disperse to neighbouring groups while males remain in the group and form strong social bonds; Nishida, 2011), there are also many similarities between the two species. Both chimpanzees and long-tailed macaques, for example, form strong social relationships in which individuals exchange several services such as grooming and agonistic support (Mitani, 2006; Kaburu and Newton-Fisher, 2015; Gumert and Ho, 2008; Mishra et al., 2020). Furthermore, both species use tools (Whiten et al., 1999; Malaivijitnond et al., 2007) and forage on food items that are difficult to acquire and/or extract such as meat in chimpanzees (Mitani and Watts, 2001) and coconut in macaques (Pal et al., 2017b; Mazumder and Kaburu, 2020). This creates the situation in which only a handful of individuals have access to specific resources, which might be one of the conditions that can favour the emergence of food sharing.

2. Methodology

2.1. Study site and subjects

The study was conducted between December 2018 and March 2019 and between September 2019 and January 2020. We observed two wild groups of Nicobar long-tailed macaques named BQ and FV living on two different Nicobar Islands, Great Nicobar and Katchal Island, respectively (Fig. 1). BQ group had 28–44 individuals, including 4–8 males, 5–8 females, 5–11 subadults, 5–13 juveniles, and 0–4 infants, while the FV group had 32-54 individuals, including 4–10 males, 1–16 females, 6–12 subadults, 9–14 juveniles, and 3–7 infants. Pedigree information of the groups is unknown. BQ group was found between 7°1′6.35″N and 7°0′35.47″N latitude and between 93°56′2.36″E and 93°56′13.88″E longitude, whereas FV was restricted between 7°59'42.83"N and 7°59'0.24"N latitude and between 93°21'51.11"E and 93°21'9.74"E longitude. Both islands have very different habitats. More specifically, the Great Nicobar island has comparatively fewer coconut trees, is hilly, and beaches are long yet narrow. Katchal island, on the other hand, has vast extents of land covered with coconut trees, along with flat terrain and small beaches with water currents.

2.2. Ecological survey

In order to estimate the differences in the abundance of plant species between the two islands, we conducted line surveys in the groups' areas. We conducted surveys on ten trails per island, with each trail ranging between 444-558 m and covering a total of 5.1 km and 4.9 km for Great Nicobar and Katchal islands, respectively. We surveyed 17 species of plants that are commonly eaten by the long-tailed macaque populations living on the islands. We chose these plants after carefully observing the foraging behavior of the macaques. We took photographs of the plants and noted the plant features for identification. Later we consulted with local people to identify the plants. We subsequently consulted works by Alappatt (2017) and Mathew (2018). During the survey, at every 1.5 m, we stopped, then took a count of the plants located within 2 meters from each side of the transect line (i.e., 4m in width) (Umapathy et al., 2003). We surveyed each trail twice, and then the average was calculated from all ten trails on each island. The terrain was very un-even and vegetation cover was very thick, therefore conducting more than two surveys on the same trail was difficult.

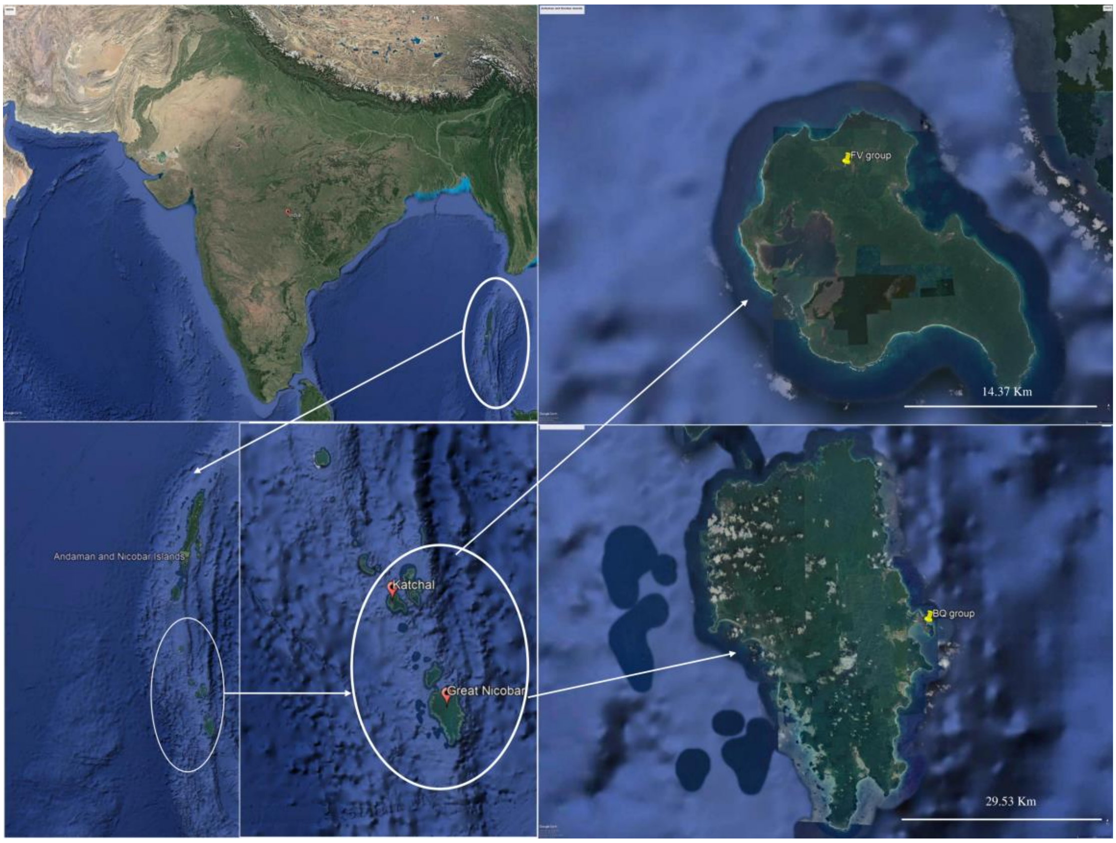

Fig. 1. Field site © Google Earth

2.3. **Behavior data collection**

We collected the behavioural data between 04:00–13:00 h and 14:30–17:00 h through 15-min focal animal sampling (Altmann, 1974; Setchell and Curtis, 2011) using HanDBase software (Version 4.1.5d). Animals were habituated to human presence and we could observe them from a minimum distance of 10 m. The order of focal animals to sample was predetermined and randomized every day before data collection started. When only one subject was visible, we sampled this subject, then searched for other focal subjects. When the focal animal was engaged in foraging behavior, we recorded the following information: 1) the type of food item eaten; 2) the technique used for foraging; 3) the number and identity of other individuals observing or sitting close to the food owner/processor; 4) whether the food possessor shared food with other individuals of the group; and 5) the activity of the other individual (s), namely begging, food snatching, grooming, sitting in contact with the food owner, both during and after the food owner processed or shared the food. Following Boesch and Boesch's (1989) definition, we defined food sharing as *active* if an individual B took the food that was held by an individual A who made an effort to facilitate B's action, or *passive*, if an individual B took the food that A had dropped on the ground or that A held without making any movement to facilitate B's action. If the food sharing event continued for more than 15 min, we kept recording the behavior until it terminated. We defined harassment as be those cases in which bystanders followed the food owner and begged for food by reaching out and extending their arm with an open palm (adjusted from Gilby, 2006). In order to determine the dominance rank in both macaque groups, we recorded both aggressive (chase, bite, hit), and submissive interactions (number of flees, move away). We then compiled the data and then transformed the score percentages. We calculated the rank by calculating the percent of aggression given and submission received by an individual (Zumpe and Michael, 1986). Since we could not identify all the individuals in the group, we could not classify the dominance rank relative to another individual (i.e., we divided the individual's score in a stratified hierarchy, by cataloguing each of their percentile scores into sets and then assigned a rank to it). For example, the individuals who scored 5.0% or less were given low rank. Those in between 5.1 and 10.0% were given intermediate rank, and those who scored equal to or greater than 10.01% were considered as high-rank individuals. The grades were cumulatively calculated for all individuals in a group to determine the cut-off, which was relative to one another. The cut-offs were determined using a cumulative grading system, and the calculation gave us the rank of all the individuals (both males and females) for both groups, from which only 25 members' ranks have been mentioned in this paper.

2.4. **Ethical note**

IISER Mohali Research Committee approved the study, and the permit (No. CWLW/WL/134/332) was issued by the Andaman and Nicobar Forest Department, India. The study complied with all the guidelines set forth by the Government of India, Andaman and Nicobar Island Territory Forest Department. The study was purely observational and followed the best practices of field primatology set forth by the International Primatological Society. There was no conflict of interest during any phase of this study or article preparation.

3. **Results**

We observed food-sharing events occurring among 15 individuals (eight from BQ group and seven from the FV group) while foraging on either coconuts or termites. We observed both active and passive food sharing of coconut meat among the members of the BQ group, whereas we observed passive food sharing of termite logs among FV group members of Katchal island. Our ecological survey revealed that coconut (*Cocos* sp.) was more abundant in Katchal, whereas termite logs were more available to the BQ groups from Great Nicobar Island (Fig. 2).

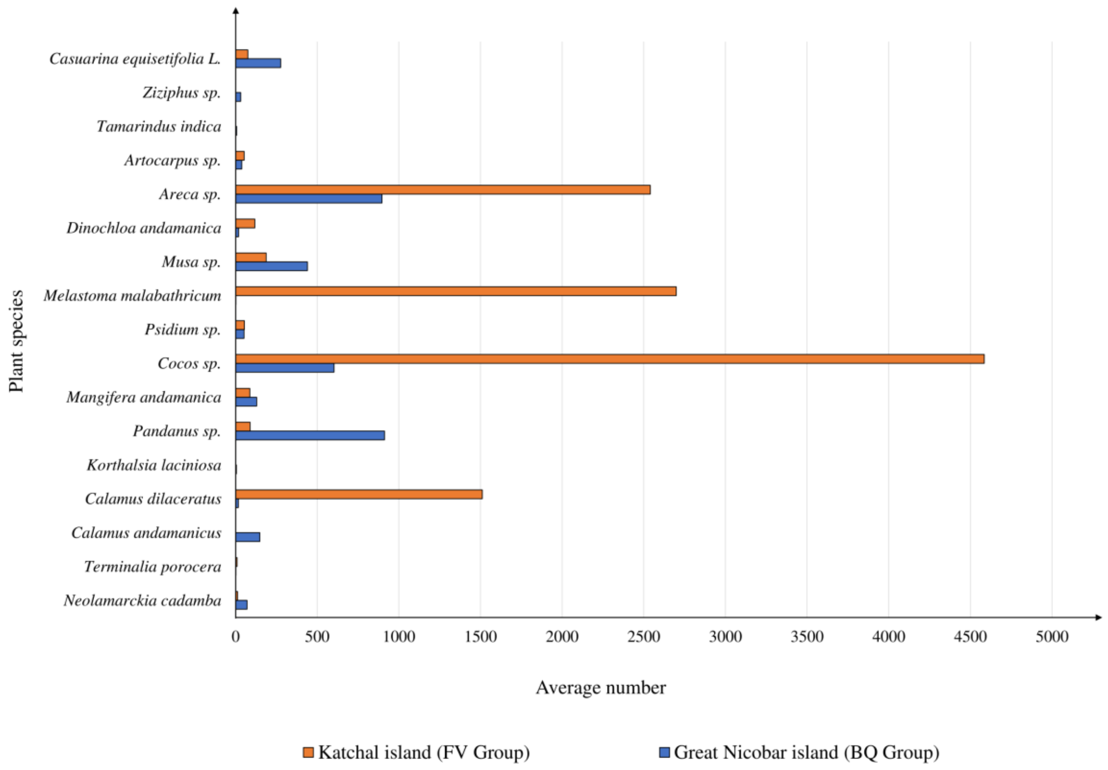

Fig. 2. Average number of plants surveyed at Great Nicobar (BQ group) and Katchal (FV group) islands, India. Only plants that were commonly foraged by the macaques are included.

During the study period, we observed a total of 1450 foraging incidents. Of these, in 26 cases macaques foraged on either coconut (*Cocos* sp.) (BQ group) or termite logs (FV group), involving 15 individuals out of which only 11 individuals (six from BQ group and five from FV group) across the two groups shared the food. Of these cases, only 18 cases involved food sharing events (69.23%). Food sharing was higher (80%) among BQ members than among FV members (60%) (Fig. 3). In both groups, the majority of the food donors were males and we observed them sharing food most often with other males. Finally, we observed food donors sharing food more often (69.23%) with the individuals who actively observed them foraging without harassing them (Table in supplementary file and Figure 3).

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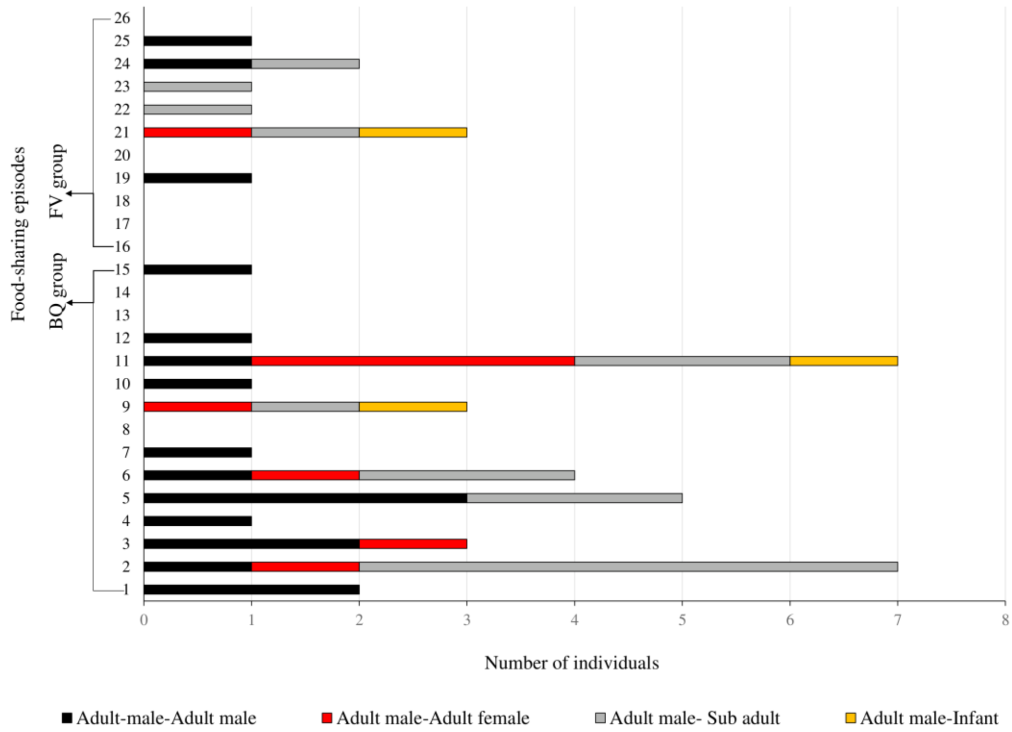

Fig. 3. Number of food-sharing cases by Nicobar long-tailed macaques at Great Nicobar and Katchal islands, India. Cases have been divided by age-sex class categories.

Not every member of the group was able to forage on coconuts or termite logs, and only a handful of group members could feed on them either by using a unique technique to extract food or by guarding the food against other members (Mazumder and Kaburu, 2020). The food owner shared their food (either actively or passively) with other members who sat close to them while they were foraging on the food. We observed food sharing occurring more frequently among low ranking individuals (Figure 4), although other members from higher ranks also shared some part of their food (Supplementary file and Figure 4 and 5).

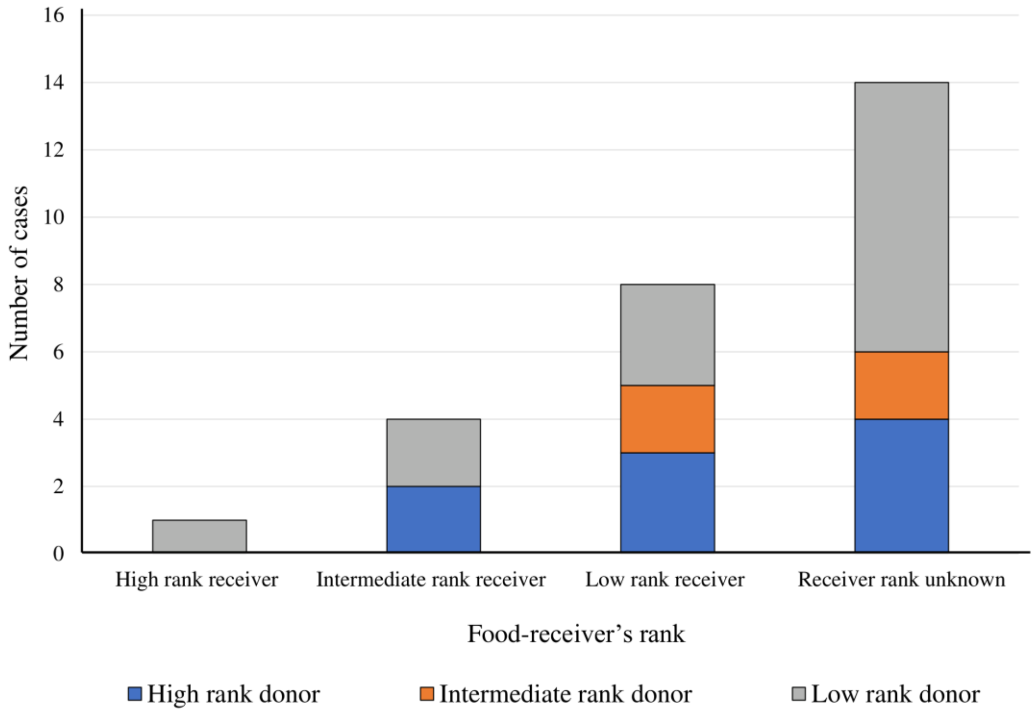

Fig. 4. Food-sharing events between group members of different ranks.

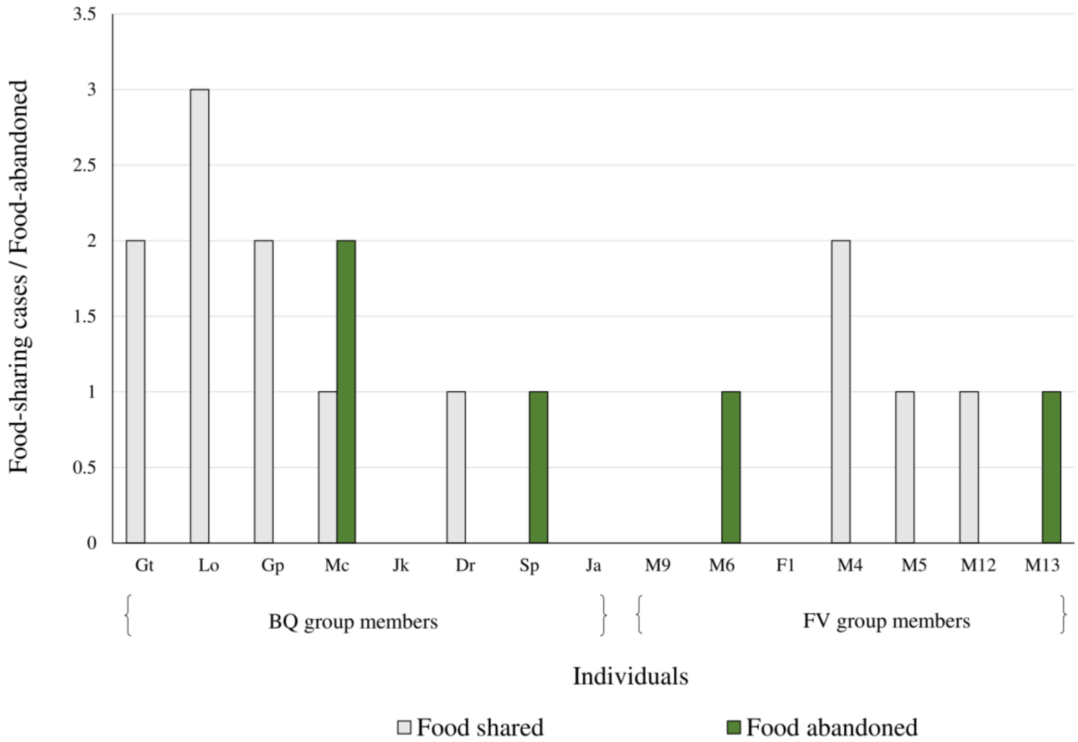

Fig. 5. Number of times the individuals shared or abandoned the food at Great Nicobar and Katchal islands, India.

3.1. **Coconut sharing**

The members of the BQ group often foraged on mature coconuts by using a pounding or a rolling substrate (Fig. 6). In all cases of coconut pounding, the individual pounded the coconut and broke it into pieces of unequal size (Mazumder and Kaburu, 2020). In 87% of the cases of coconut pounding (13 out of 15), after the food was processed this way, we observed the food possessor keep the coconut unguarded without threatening anyone who tried to pick the food from the substrate, and had also given some part of the food to members sitting close. The other macaques sitting nearby collected bits of a portion of the shredded coconut from the substrate (i.e., passive sharing). They ate it while the food processor was still eating the coconut. At the same time, we observed the food owner actively sharing the food among the individuals sitting close by. Group members who were sitting far away (i.e., farther than 5 m from the food processor/ owner) did not attempt to steal food. However, in only two of the 15 cases of coconut pounding observed, the food owner was harassed by the females, who continuously followed the food owner and begged for food. In another case, the food owner climbed the topmost point of the tree to protect his food from another member who followed him. In none of these cases, the food owner gave away pieces of coconut to the harassers. We observed the food owner eventually abandon the food leaving it with the other member who then foraged on the discarded food (Supplementary file).

Fig. 6. Nicobar long-tailed macaque pounding coconut using a pounding substrate while other macaques observe the food owner processing the coconut in Great Nicobar island.

3.2. Termite sharing

The members of the FV group often foraged on termites from a termite log (Fig. 7) and shared it among a restricted number of group members. In all termite foraging bouts, the food owner searched for the termites and processed the log by biting off the portions without any termite with its teeth or by probing with its fingers to reach the food source. During this process, the individual prevented other group members from approaching (closer than 1 m) the termite logs through aggressive display or threats. During the food process, the food owner had to orient its body and mouth in different positions to maximize the success rate. Furthermore, no individual begged or tried to harass the food owner in any manner, but bystanders sat at the proximity of less than 3 m but greater than 1 m from the owner. These individuals were first threatened and then chased away by the food owner when they tried to approach (< 1 m) the food source or the food owner. After the successful extraction of the food, the food owner fed on the food, and after a few minutes, only a handful of other individuals were allowed to forage on the termite exposed wood portions which it had processed.

Fig. 7. Termite log foraged by Nicobar long-tailed macaques in Katchal

Out of the 26 observed cases of foraging on either coconuts or termite logs, six were characterized by harassment from bystanders. In only two cases did we observe the individual who had received a piece of food grooming the food owner. More specifically, the grooming session was recorded 1 hour 22 minutes and 1 hour 38 minutes after the food sharing events. These grooming sessions lasted for 17 min 33 seconds and 9 min 16 seconds, respectively. In another case food sharing occurred immediately after a fight between the members. We did not observe any female who received the food mating with the food owner.

4. **Discussion**

Here, we have reported 18 cases of food sharing among wild Nicobar long-tailed macaques. To date, cases of food sharing among non-kin in non-human primates have been described in apes and New World monkeys while only a limited number of cases of food sharing have been reported for Old World monkeys (Goffe and Fischer, 2016; Strum, 1975), and our study provides the first report of food sharing among free-ranging macaques. To date, two main hypotheses have been proposed to explain the emergence of food sharing among non-kin in animals: the reciprocal exchange and the harassment hypotheses (Feistner and McGrew, 1989; Stevens and Gilby, 2004; Jaeggi and van Schaik, 2011). According to the reciprocal exchange hypothesis, food sharing has evolved as a form of trading of services in which food is used as a commodity to be exchanged for other services, such as coalition support, mating opportunities or grooming, while the harassment hypothesis posits that food possessors share food with harassers in order to minimize the costs of defending a food source. There seems to be evidence in support of both hypotheses: by examining 68 primate species, Jaeggi and van Schaik (2011), for example, showed that food sharing is more likely to occur in primate species that form multi-male societies (as opposed to one-male groups) and in species where males form coalitions, supporting the meat-for-sex and meat-for-support hypotheses. Similarly, among chimpanzees from the Ngogo community in Uganda, males were found to trade meat for agonistic support (Mitani and Watts, 2001), while chimpanzees of the Taï forest exchanged meat for both agonistic support and sex (Gomes and Boesch, 2009; 2011). Likewise, among chimpanzees of the Bossou community, males share cultivated fruits with reproductive females, which might be a strategy males use to increase their mating opportunities (Hockings et al., 2007). On the other hand, males of the chimpanzee communities of Mahale (Kaburu and Newton-Fisher, 2015), Kanyawara (in Kibale National Park, Uganda) and Gombe (Gilby, 2006; Gilby et al., 2010) did not exchange meat for other services. In fact, among Gombe chimpanzees, males were found to be more likely to share meat when under pressure, supporting the harassment hypothesis (Gilby, 2006). Similarly, experimental evidence on chimpanzees and squirrel monkeys (*Saimiri boliviensis*) showed that experimentally inducing higher levels of harassment increase the likelihood of sharing by the food possessor (Stevens, 2004; Silk et al., 2013). Collectively, these studies show that a variety of factors can affect the likelihood of food sharing, including the degree of relatedness, relationship quality and rank difference between donor and recipient as well as the frequency of begging (Silk et al., 2013).

Here we argue that the low proportion of harassment observed in food context among Nicobar long-tailed macaques is more likely to support the reciprocal exchange rather than harassment hypothesis. During our study, we observed harassment in the form of begging behaviour in only two cases of coconut pounding (out of 15), and in these few cases, the harassers did not receive any food. The majority of food transfers, in contrast, were directed to bystanders who were not harassing the food owners. Furthermore, we recorded the majority of food sharing events occurring between males. We have previously shown a strong male-bias in object manipulation and tool use among Nicobar long-tailed macaques (Mazumder and Kaburu, 2020) and we argued that, for at least some of these behaviours, such as coconut pounding, this male-bias might be explained by the extra strength required in manipulating coconuts. Given that male macaques are normally bigger than females, they can more easily lift and pound the coconuts compared to females. Notwithstanding, this cannot explain why males tend to share food more often with other males rather than with females. Although we do not have data on the groups' pedigree, among macaques males usually disperse at puberty, and, consequently, adult males tend to be unrelated to each other (Ruiter and Geffen, 1998; Kulik et al., 2015). This suggests that the food sharing event we observed likely occurred among non-kin, thereby excluding the kin-selection hypothesis. At the same time, male Nicobar macaques form strong social relationships (Mishra et al., 2020), and so it is possible that the quality of the social relationship among group members might determine whether food is shared or not, which would support the reciprocal exchange hypothesis. The prevalence of food donations among low-ranking macaques offers further support to the reciprocal exchange hypothesis since subordinates are more likely to trade services for rank-restricted commodities, such as agonistic support or tolerance (Mitani and Watts, 2001; Mitani, 2006a; Carne et al., 2011; Kaburu and Newton-Fisher, 2015). More work is needed, however, to examine the pattern of exchange of social services among Nicobar macaques in order to assess whether donors use food as a commodity to receive other services in return.

To our knowledge, our study is the first to report the sharing of food among free-ranging macaques sharing among macaques has been previously investigated among captive populations in experimental conditions (e.g., Schaub, 1996; Massen et al., 2010). This raises the question of why food sharing can be experimentally induced in captive macaques, while it is rare in wild populations. Here we argue that the presence of food sharing in our study population might be due the combination of two particular features that characterize the Nicobar macaque population: 1) the presence of monopolizable food sources that can be accessed by only a limited number of individuals, namely those macaques who are particularly skilful in breaking a coconut open; and 2) the ability to use tools and manipulate objects (Mazumder and Kaburu, 2020). Coconuts, like many other cultivated fruits, tend to have a higher nutritional value compared to many wild plants, and, for this reason, they tend to be preferred food items for wild animals (Siex and Struhsaker, 1999; Pal et al., 2017a; Das et al., 2020). However, accessing the coconut meat can be challenging and, among Nicobar macaques, only a few individuals are often able to open coconuts using complex manipulative techniques (Pal et al., 2017b; Mazumder and Kaburu, 2020). This gives food owners enormous leverage as they can have control over access to the coconut, and, therefore, they can use this food item as a commodity to be exchanged for other services. At the same time, we have recently shown that Nicobar macaques use tools and manipulate objects in several contexts, ranging from food to hygiene and play contexts (Mazumder and Kaburu, 2020). Even though we could not provide conclusive evidence that the ability to use tools is socially learned in this macaque population, we did occasionally observe bystanders trying to replicate the behavior of tool users. Given that social learning requires proximity between the tool user and any bystander who is attempting to learn how to use the tool, it is likely that social learning promotes social tolerance among group members (Coussi-Korbel and Fragaszy, 1995; van Schaik et al., 1999).

While long-tailed macaques are commonly classified as a despotic species with strict dominance, low tolerance, and nepotistic relations (Thierry, 2000; Thierry et al., 2004), this classification has been based exclusively on female social relationships, since females form the core of macaque societies (Thierry et al., 2004). In contrast, a similar classification for male macaques is currently missing. In fact, accumulating evidence suggests that the egalitarian-despotic gradient model proposed for female social relationships might not reflect male-male relationships among macaques. Among black crested macaques (*Macaca nigra*) and stump-tailed macaques (*Macaca arctoides*), for instance, while females have been classified as tolerant (Thierry et al., 1994), males have been found to form strict dominance hierarchies with low-rates of affiliative and high rates of aggressive interactions that are typical of despotic species (Reed et al., 1997; Richter et al., 2009). Interestingly, there seems to be strong variation even in female social relationships across different populations. For example, while female Barbary macaques are commonly classified as tolerant (Thierry and Aureli, 2006), some studies have found a strict dominance hierarchy among females of some wild Barbary macaque populations (Kaburu et al., 2012). Future studies will therefore need to examine the social relationships among Nicobar long-tailed macaques in order to investigate the degree of tolerance this population displays and understand whether a high level of tolerance might explain the emergence of food sharing in this macaque population.

Our observations, along with our recent report on tool use in Nicobar macaques (Mazumder and Kaburu, 2020) suggest several similarities between food sharing in Nicobar macaques and chimpanzees since both species use tools (although to a different extent) and share food that is monopolizable and difficult to access. Chimpanzees, for example, exhibit strong inter-individual differences in the ability to successfully hunt and kill other animals (Mitani and Watts, 1999; Watts and Mitani, 2002; Nishida, 2011). The other type of food sharing not related to meat that has been described in chimpanzees involved cultivated fruits (Hockings et al., 2007), which are costly to acquire since they tend to be protected by farmers, and are more likely to be acquired by males than females (Hockings, 2011). Interestingly, Hockings and colleagues (2007) showed that males tend to share cultivated fruits with sexually receptive females suggesting that males might use food as a way to increase their mating opportunities. In contrast, male Nicobar macaques were not observed sharing food with sexually reproductive females, ruling out the food-for-sex hypothesis for this population. Finally, another interesting parallelism between the Nicobar macaque population and chimpanzees is the presence of inter-population differences in food sharing. In particular, while the BQ population was observed sharing coconut meat both actively and passively, the FV population was never observed processing or sharing coconut, but they were observed passively sharing termites. Similar behavioral differences in hunting and sharing food have been described in chimpanzees (Takahata et al., 1984). We argue that the FV macaque population might have evolved alternative foraging strategies, given the complexity of the processing of coconut fruits and the presence of alternative probably equally nutritious food items, such as termites.

In the context of human evolution, while the majority of the studies have focused on non-kin food sharing in apes, especially chimpanzees, our observations of non-kin food sharing among Nicobar macaques suggest that food sharing in humans might have an evolutionary origin that is much earlier than hitherto thought. Importantly, there are clear differences in food sharing between human and non-human. Isaac (1978), for example, highlighted how in hunter-gatherer societies, people collect the edible items from different places and bring them back home, where the food would be shared. This is in contrast to the pattern observed in great apes and other primates who have been seen to consume the food at the spot where it has been acquired. Other differences in food sharing behaviours are the division of labour in human societies, which is based upon the age and sex of the individuals (Kaplan and Gurven, 2005; Marlowe, 2007; Stutz, 2018). Despite these differences, there are also many similarities between food sharing in human and non-human primates, such as the tendency to share hard-to-acquire food items or the tendency to share food with closely bonded group members.

In conclusion, our study provides the first observation of food sharing in macaques, showing several similarities with food sharing in chimpanzees. Our preliminary observations seem to rule out the harassment hypothesis as the reason behind food sharing in Nicobar macaques. In contrast, we suggest that food sharing in macaques might be explained under the reciprocal exchange hypothesis since the majority of food sharing events occurred between males, and recent work on male Nicobar macaques has shown that they form strong social relationships (Mishra et al., 2020). More work, however, is needed to more formally test this hypothesis. Finally, this study on food sharing in Nicobar macaques, along with our recent report on tool use and object manipulation in this same population (Mazumder and Kaburu, 2020) paint an interesting picture of this macaque population, highlighting some features such as tool use and food sharing, that might make this species an ideal model to study the evolution of human behavior.

5. **Data availability**

The data collected during the current study are available from the corresponding author on reasonable request.

Acknowledgements: We thank the Forest Department of Andaman and Nicobar Island, Andaman for permitting us to conduct the work. The Leaky Foundation (Doctoral Research Grant), International Primatological Society (Research Grant), Indian Institute of Science Education and Research, Mohali awarded to Jayashree Mazumder (PhD student, IISER Mohali) financially supported the present study. We also thank Pondicherry University (Port Blair Campus), the local people of Port Blair, Campbell Bay, Nancowry and Katchal. We also want to thank Mr Amit Kerketta and forest department officials as Great Nicobar and Katchal islands for their support and help during the study. We would also like to thank the native people as well the government officials in Katchal, Nancowry and Great Nicobar without their support; this work would not have been possible. We would also like to thank Parth R. Chauhan for his guidance and support during the study and article preparation. We also thank Nirmal Nath Upadhyay, S.S.V. Kiran and Diksha Mandlik for their help during the second phase of the fieldwork. Finally, we are grateful to the two anonymous reviewers for providing constructive feedback on a previous draft of the manuscript.

References

Alappatt, J.P., 2017. Common Forest Plants of Andaman and Nicobar Islands. Department of Environment and Forest, Andaman and Nicobar Administration, Port Blair.

Altmann, J., 1974. Observational Study of Behavior: Sampling Methods. Behaviour 9, 227–267.

Backwell, L.R., Errico, F. d', 2001. Evidence of termite foraging by Swartkrans early hominids. Proceedings of the National Academy of Sciences 98, 1358–1363. doi:10.1073/pnas.98.4.1358

Blurton Jones, N.G., 1987. Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. Social Science Information 26, 31–54. doi:10.1177/053901887026001002

Boesch, C., Boesch, H., 1989. Hunting behavior of wild chimpanzees in the Taï National Park. American Journal of Physical Anthropology 78, 547–573. doi:10.1002/ajpa.1330780410

Boyd, R., Silk, J.B., 2017. How Humans Evolved. W W NORTON, Place of publication not identified.

Carne, C., Wiper, S., Semple, S., 2011. Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. American Journal of Primatology 73, 1127–1133. doi:10.1002/ajp.20979

Clutton-Brock, T., 2009. Cooperation between non-kin in animal societies. Nature 462, 51–57. doi:10.1038/nature08366

Coussi-Korbel, S., Fragaszy, D.M., 1995. On the relation between social dynamics and social learning. Animal Behaviour 50, 1441–1453. doi:10.1016/0003-3472(95)80001-8

Crittenden, A.N., Schnorr, S.L., 2017. Current views on hunter- gatherer nutrition and the evolution of the human diet. American Journal of Physical Anthropology 162, 84–109. doi:10.1002/ajpa.23148

Das, S., Harpalani, M., Chaudhuri, B., Negi, R., Ali, S.T., Singh, M., 2020. Use of an Embedded Fruit by the Nicobar Long-tailed Macaque (*Macaca fascicularis umbrosus*): I. Familiarity to Coconuts (*Cocos nucifera* L.) and Temporal Patterns of Coconut Foraging. Primate Conservation 34, 1–22.

Dugatkin, L.A., 2002. Cooperation in animals: An evolutionary overview. Biology & Philosophy 17, 459–476. doi:10.1023/A:1020573415343

Feistner, A., McGrew, W.C., 1989. Food-sharing in primates: a critical review. In: Seth, P.K., Seth, S. (Eds.), Prespectivesw in Primate Biology. Today & Tomorro's Printers and Publishers, New Dehli, pp. 21–36.

Gilby, I.C., 2006. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. Animal Behaviour 71, 953–963. doi:10.1016/j.anbehav.2005.09.009

Gilby, I.C., Emery Thompson, M., Ruane, J.D., Wrangham, R., 2010. No evidence of short-term exchange of meat for sex among chimpanzees. Journal of Human Evolution 59, 44–53. doi:10.1016/j.jhevol.2010.02.006

Gilby, I.C., Machanda, Z.P., O'Malley, R.C., Murray, C.M., Lonsdorf, E.V., Walker, K., Mjungu, D.C., Otali, E., Muller, M.N., Emery Thompson, M., Pusey, A.E., Wrangham, R.W., 2017. Predation by female chimpanzees: Toward an understanding of sex differences in meat acquisition in the last common ancestor of Pan and Homo. Journal of Human Evolution 110, 82–94. doi:10.1016/j.jhevol.2017.06.015

Goffe, A.S., Fischer, J., 2016. Meat sharing between male and female Guinea baboons (*Papio papio*). Primate Biology 3, 1–8. doi:10.5194/pb-3-1-2016

Goldstone, L.G., Sommer, V., Nurmi, N., Stephens, C., Fruth, B., 2016. Food begging and sharing in wild bonobos (*Pan paniscus*): assessing relationship quality? Primates 57, 367–376. doi:10.1007/s10329-016-0522-6

Gomes, C.M., Boesch, C., 2009. Wild Chimpanzees Exchange Meat for Sex on a Long-Term Basis. PLoS ONE 4, e5116. doi:10.1371/journal.pone.0005116

Gomes, C.M., Boesch, C., 2011. Reciprocity and trades in wild West African chimpanzees. Behavioral Ecology and Sociobiology 65, 2183–2196. doi:10.1007/s00265-011-1227-x

Hamilton, W.D., 1964. The genetical evolution of social behaviour. I. Journal of Theoretical Biology 7, 1–16. doi:10.1016/0022-5193(64)90038-4

Hammerstein, P., 2003. Why is reciprocity so rare in social animals? A protestant appeal. In: Hammerstein, P. (Ed.), Dahlem Workshop Report. Genetic and Cultural Evolution of Cooperation. MIT Press, pp. 83–93.

Hockings, K.J., 2011. The crop-raiders of the sacred hill. In: The Chimpanzees of Bossou and Nimba. Springer, Tokyo, pp. 211–220.

Hockings, K.J., Humle, T., Anderson, J.R., Biro, D., Sousa, C., Ohashi, G., Matsuzawa, T., 2007. Chimpanzees Share Forbidden Fruit. PLoS ONE 2, e886. doi:10.1371/journal.pone.0000886

Hohmann, G., 2009. The Diets of Non-human Primates: Frugivory, Food Processing, and Food Sharing. In: Hublin, J.-J., Richards, M.P. (Eds.), The Evolution of Hominin Diets, Vertebrate Paleobiology and Paleoanthropology. Springer Netherlands, Dordrecht, pp. 1–14. doi:10.1007/978-1-4020-9699-0_1

Jaeggi, A.V., Gurven, M., 2013. Natural co-operators: Food sharing in humans and other primates: Natural Cooperators: Food Sharing in Humans and Other Primates. Evolutionary Anthropology: Issues, News, and Reviews 22, 186–195. doi:10.1002/evan.21364

Jaeggi, A.V., Van Schaik, C.P., 2011. The evolution of food sharing in primates. Behavioral Ecology and Sociobiology 65, 2125–2140. doi:10.1007/s00265-011-1221-3

Jaeggi, A.V., Stevens, J.M.G., Schaik, C.P. van, 2010. Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. American Journal of Physical Anthropology 143, 41–51. doi:10.1002/ajpa.21288

Kaburu, S.S.K., Newton-Fisher, N.E., 2015. Egalitarian despots: hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, Pan troglodytes. Animal Behaviour 99, 61–71. doi:10.1016/j.anbehav.2014.10.018

Kaplan, H., 1997. The evolution of the human life course. In: Between Zeus and the Salmon: The Biodemography of Longevity,. National Academy Press, Washingto DC, pp. 175–211.

Kaplan, H., Gurven, M., 2005. The Natural History of Human Food Sharing and Cooperation: A Review and a New Multi-Individual Approach to the Negotiation of Norms. In: Gintis, H., Bowles, S., Boyd, R., Fehr, E. (Eds.), Moral Sentiments and Material Interests - The Foundations of Cooperation in Economic Life, Economic Learning and Social Evolution. MIT Press, London, pp. 75–113.

Kaplan, H., Hill, K., Cadeliña, R.V., Hayden, B., Hyndman, D.C., Preston, R.J., Smith, E.A., Stuart, D.E., Yesner, D.R., 1985. Food Sharing Among Ache Foragers: Tests of Explanatory Hypotheses [and Comments and Reply]. Current Anthropology 26, 223–246. doi:10.1086/203251

Kaplan, H., Lancaster, J., Hurtado, A.M., 2000. A theory of human life history evolution. In: Diet, Intelligence, & Longevity, 9. Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, pp. 156–185.

Kramer, K.L., 2018. The co-operative economy of food: Implications for human life history and physiology. Physiology & Behavior 193, 196–204. doi:10.1016/j.physbeh.2018.03.029

Kulik, L., Amici, F., Langos, D., Widdig, A., 2015. Sex Differences in the Development of Social Relationships in Rhesus Macaques (*Macaca mulatta*). International Journal of Primatology 36, 353–376. doi:10.1007/s10764-015-9826-4

Leakey, M.D., Clark, J.D., 2009. Olduvai Gorge. Vol. 3, Vol. 3,. Cambridge University Press, Cambridge.

Luca, F., Perry, G.H., Di Rienzo, A., 2010. Evolutionary adaptations to dietary changes. Annual Review of Nutrition 30, 291–314. doi:10.1146/annurev-nutr-080508-141048

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., Hamada, Y., 2007. Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). American Journal of Primatology 69, 227–233. doi:10.1002/ajp.20342

Marlowe, F.W., 2007. Hunting and Gathering: The Human Sexual Division of Foraging Labor. Cross-Cultural Research 41, 170–195. doi:10.1177/1069397106297529

Massen, J.J.M., Berg, L.M. van den, Spruijt, B.M., Sterck, E.H.M., 2010. Generous Leaders and Selfish Underdogs: Pro-Sociality in Despotic Macaques. PLoS ONE 5, e9734. doi:10.1371/journal.pone.0009734

Mathew, S., 2018. On floristic diversity of Andaman-Nicobar Islands with special reference to insular germplasm conservation outside the islands. Abrahamia: An International Journal of Plant Sciences 3, 104–130.

Mazumder, J., Kaburu, S.S.K., 2020. Object Manipulation and Tool Use in Nicobar Long-Tailed Macaques (*Macaca fascicularis umbrosus*). International Journal of Primatology 41, 141–159. doi:10.1007/s10764-020-00141-y

Mishra, P.S., Pal, A., Velankar, A.D., Kumara, H.N., Singh, M., 2020. Do males bond? A study of male-male relationships in Nicobar long-tailed macaques *Macaca fascicularis umbrosus*. Journal of Biosciences 45, 22. doi:10.1007/s12038-020-9995-y

Mitani, J.C., 2006a. Demographic influences on the behavior of chimpanzees. Primates 47, 6–13. doi:10.1007/s10329-005-0139-7

Mitani, J.C., 2006b. Reciprocal exchange in chimpanzees and other primates. In: Kappeler, P.M., Schaik, C.P. van (Eds.), Cooperation in Primates and Humans. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 107–119. doi:10.1007/3-540-28277-7_6

Mitani, J.C., Watts, D.P., 1999. Demographic influences on the hunting behavior of chimpanzees. American Journal of Physical Anthropology 109, 439–454. doi:10.1002/(SICI)1096-8644(199908)109:4<439::AID-AJPA2>3.0.CO;2-3

Mitani, J.C., Watts, D.P., 2001. Why do chimpanzees hunt and share meat? Animal Behaviour 61, 915–924. doi:10.1006/anbe.2000.1681

Nishida, T., 2011. Chimpanzees of the lakeshore: natural history and culture at Mahale. Cambridge University Press, Cambridge ; New York.

Pal, A., Kumara, H.N., Mishra, P.S., Velankar, A.D., Singh, M., 2017a. Extractive foraging and tool-aided behaviors in the wild Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*). Primates. doi:10.1007/s10329-017-0635-6

Pal, A., Kumara, H.N., Mishra, P.S., Velankar, A.D., Singh, M., 2017b. Extractive foraging and tool-aided behaviors in the wild Nicobar long-tailed macaque (Macaca fascicularis umbrosus). Primates. doi:10.1007/s10329-017-0635-6

Pastor-Nieto, R., 2001. Grooming, kinship, and co-feeding in captive spider monkeys (*Ateles geoffroyi*). Zoo Biology 20, 293–303. doi:10.1002/zoo.1029

Perry, S., Rose, L., 1994. Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capucinus*. Primates 35, 409–415. doi:10.1007/BF02381950

Pickering, T.R., Domínguez-Rodrigo, M., 2012. Can we use chimpanzee behavior to model early hominin hunting? In: Dominguez-Rodrigo, M. (Ed.), Stone Tools and Fossil Bones. Cambridge University Press, Cambridge, pp. 174–198. doi:10.1017/CBO9781139149327.008

Pozzi, L., Hodgson, J.A., Burrell, A.S., Sterner, K.N., Raaum, R.L., Disotell, T.R., 2014. Primate phylogenetic relationships and divergence dates inferred from complete mitochondrial genomes. Molecular Phylogenetics and Evolution 75, 165–183. doi:10.1016/j.ympev.2014.02.023

Reed, C., O'Brien, T.G., Kinnaird, M.F., 1997. Male Social Behavior and Dominance Hierarchy in the Sulawesi Crested Black Macaque (*Macaca nigra*). International Journal of Primatology 18, 247–260. doi:10.1023/A:1026376720249

Richter, C., Mevis, L., Malaivijitnond, S., Schülke, O., Ostner, J., 2009. Social Relationships in Free-Ranging Male *Macaca arctoides*. International Journal of Primatology 30, 625–642. doi:10.1007/s10764-009-9364-z

Ruiter, J.R.D., Geffen, E., 1998. Relatedness of matrilines, dispersing males and social groups in long–tailed macaques (*Macaca fascicularis*). Proceedings of the Royal Society of London. Series B: Biological Sciences 265, 79–87. doi:10.1098/rspb.1998.0267

Schaik, C.P. van, Deaner, R.O., Merrill, M.Y., 1999. The conditions for tool use in primates: implications for the evolution of material culture. Journal of Human Evolution 36, 719–741.

Schaub, H., 1996. Testing kin altruism in long-tailed macaques (Macaca fascicularis) in a food-sharing experiment. International Journal of Primatology 17, 445–467. doi:10.1007/BF02736631

Setchell, J.M., Curtis, D.J., 2011. Field and laboratory methods in primatology: a practical guide. Cambridge University Press, Cambridge; New York.

Siex, K.S., Struhsaker, T.T., 1999. Colobus monkeys and coconuts: a study of perceived human-wildlife conflicts. Journal of Applied Ecology 36, 1009–1020. doi:10.1046/j.1365-2664.1999.00455.x

Silk, J.B., Brosnan, S.F., Henrich, J., Lambeth, S.P., Shapiro, S., 2013. Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. Animal Behaviour 85, 941–947. doi:10.1016/j.anbehav.2013.02.014

Stanford, C.B., South Calif, U., Wrangham, R.W., Harvard, U., 2011. Detailed Critical Review of: The Hunting Apes Meat Eating and the Origins of Human Behavior, and, Catching Fire How Cooking Made us Human. Multifactor Health and Education Initiative.

Stevens, J.R., 2004. The selfish nature of generosity: harassment and food sharing in primates. Proceedings of the Royal Society of London. Series B: Biological Sciences 271, 451–456. doi:10.1098/rspb.2003.2625

Stevens, J.R., Gilby, I.C., 2004. A conceptual framework for non-kin food sharing: timing and currency of benefits. Animal Behaviour 67, 603–614. doi:10.1016/j.anbehav.2003.04.012

Stevens, J.R., Stephens, D.W., 2002. Food sharing: a model of manipulation by harassment. Behavioral Ecology 13, 393–400. doi:10.1093/beheco/13.3.393

Strum, S.C., 1975. Primate Predation: Interim Report on the Development of a Tradition in a Troop of Olive Baboons. Science 187, 755–757. doi:10.1126/science.187.4178.755

Stutz, A., 2018. Division of Labor in the Evolution of Human Foraging Societies. Presented at the Science conference, UISPP, p. 184950.

Takahata, Y., Hasegawa, T., Nishida, T., 1984. Chimpanzee predation in the Mahale mountains from August 1979 to May 1982. International Journal of Primatology 5, 213–233. doi:10.1007/BF02735758

Thierry, B., 2000. Covariation of conflict management patterns across macaque species. In: Aureli, F., Waal, F.B.M. de (Eds.), Natural Conflict Resolution. University of California Press, California, pp. 106–128.

Thierry, B., Anderson, J.R., Demaria, C., Petit, O., 1994. Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. Current Primatology 2, 103–117.

Thierry, B., Mewa Singh, Kaumanns, W. (Eds.), 2004. Macaque societies: a model for the study of social organization, Cambridge studies in biological and evolutionary anthropology. Cambridge University Press, Cambridge ; New York, NY.

Umapathy, G., Singh, M., Mohnot, S.M., 2003. Status and Distribution of *Macaca fascicularis umbrosa* in the Nicobar Islands, India. International Journal of Primatology 24, 281–293. doi:10.1023/A:1023045132009

Waal, F.B.M. de, 1997. Food transfers through mesh in brown capuchins. Journal of Comparative Psychology 111, 370–378. doi:10.1037/0735-7036.111.4.370

Waal, F.B.M. de, 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. Animal Behaviour 60, 253–261. doi:10.1006/anbe.2000.1471

Waal, F.B.M. de, Luttrell, L.M., Canfield, M.E., 1993. Preliminary data on voluntary food sharing in brown capuchin monkeys. American Journal of Primatology 29, 73–78. doi:10.1002/ajp.1350290108

Watts, D.P., Mitani, J.C., 2002. Hunting Behavior of Chimpanzees at Ngogo, Kibale National Park, Uganda. International Journal of Primatology 23, 1–28. doi:10.1023/A:1013270606320

Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. Nature 399, 682–685. doi:10.1038/21415

Wilson, C.G., 1976. Food Sharing Behavior in Primates: Another Species Added,. Journal of the Arkansas Acedemy of Science 30, 95–96.

Zumpe, D., Michael, R.P., 1986. Dominance index: A simple measure of relative dominance status in primates. American Journal of Primatology 10, 291–300. doi:10.1002/ajp.1350100402

Figure 1

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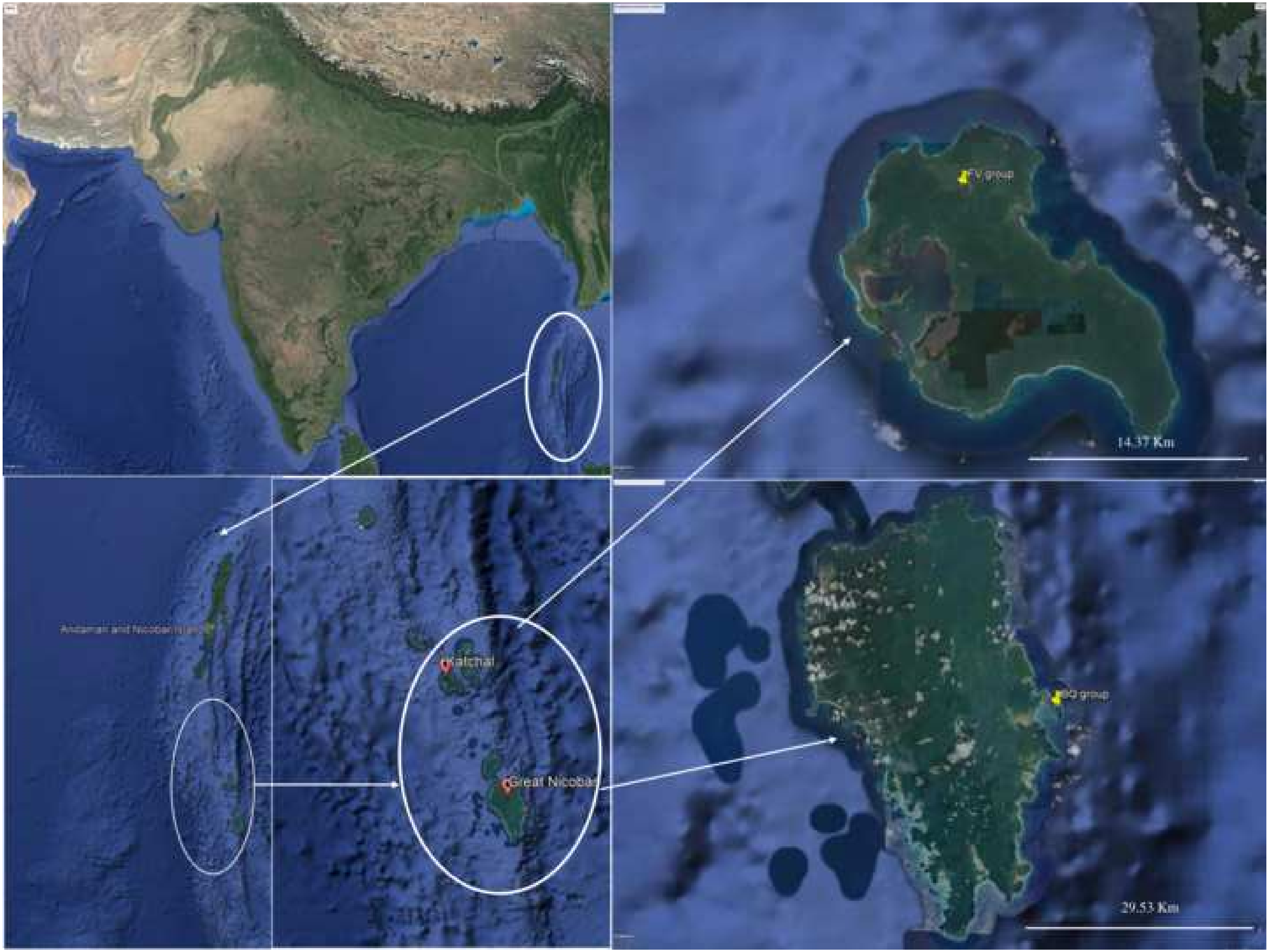
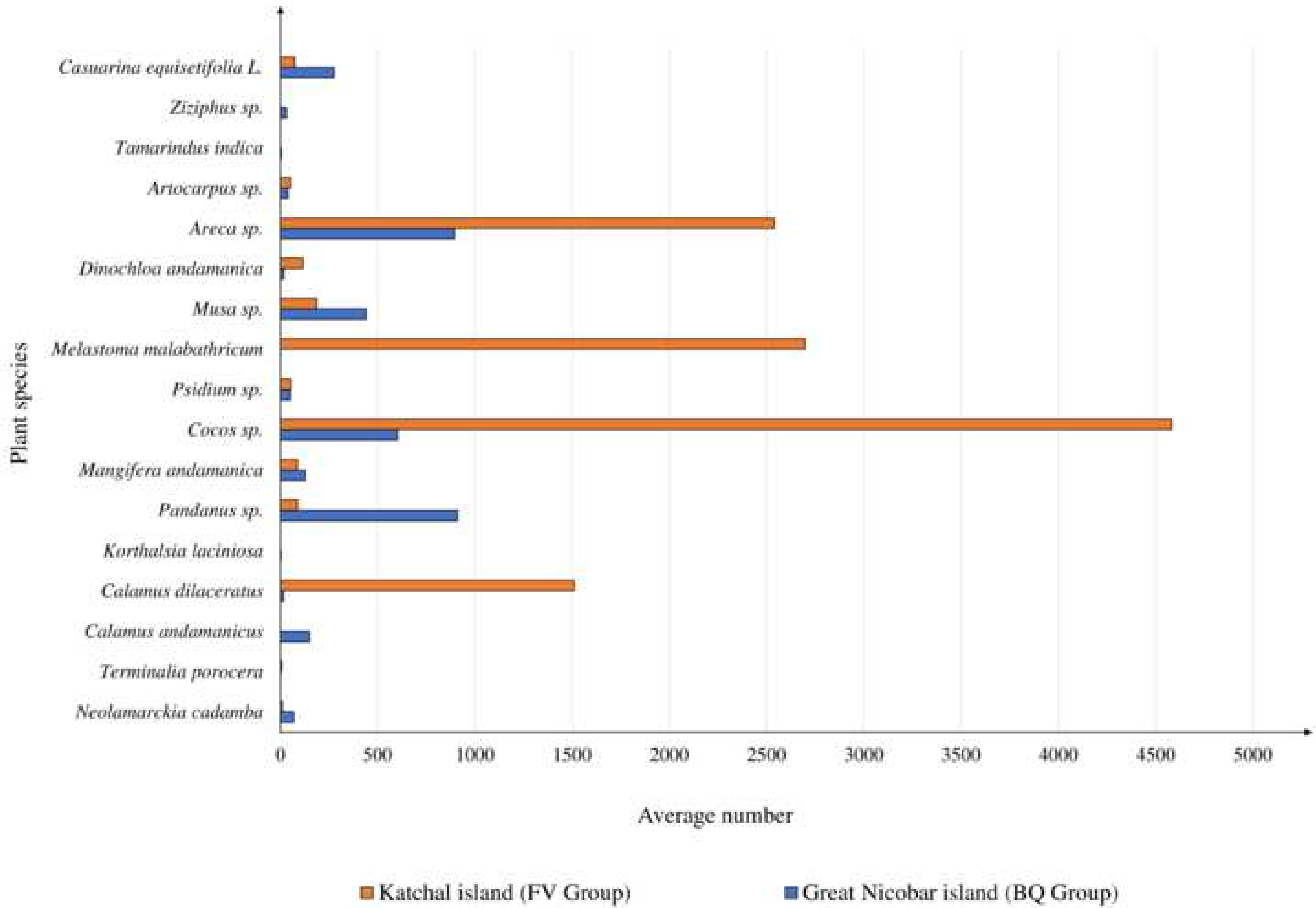


Figure 2



Casuarina equisetifolia L.
Ziziphus sp.
Tamarindus indica
Artocarpus sp.
Areca sp.
Dinochloa andamanica
Musa sp.
Melastoma malabathricum
Psidium sp.
Cocos sp.
Mangifera andamanica
Pandanus sp.
Korthalsia laciniosa
Calamus dilaceratus
Calamus andamanicus
Terminalia porocera
Neolamarckia cadamba
Plant species
0
500
1000
1500
2000
2500
3000
3500
4000
4500
5000
Average number
Katchal island (FV Group)
Great Nicobar island (BQ Group)

Figure 3

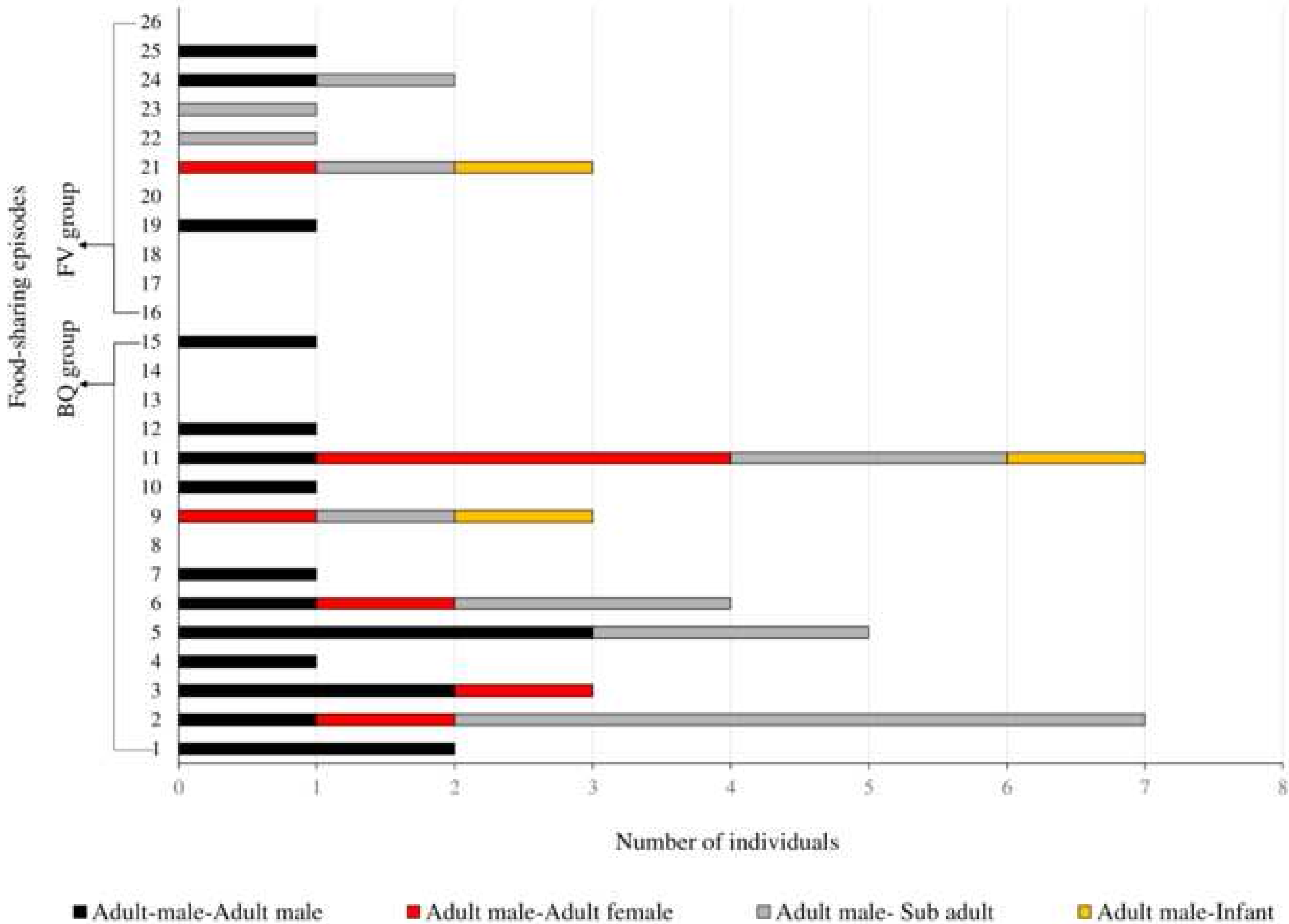

Food-sharing episodes
FV group
BQ group
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
1
2
3
4
5
6
7
8
Number of individuals
Adult-male-Adult male
Adult male-Adult female
Adult male- Sub adult
Adult male-Infant

Figure 4

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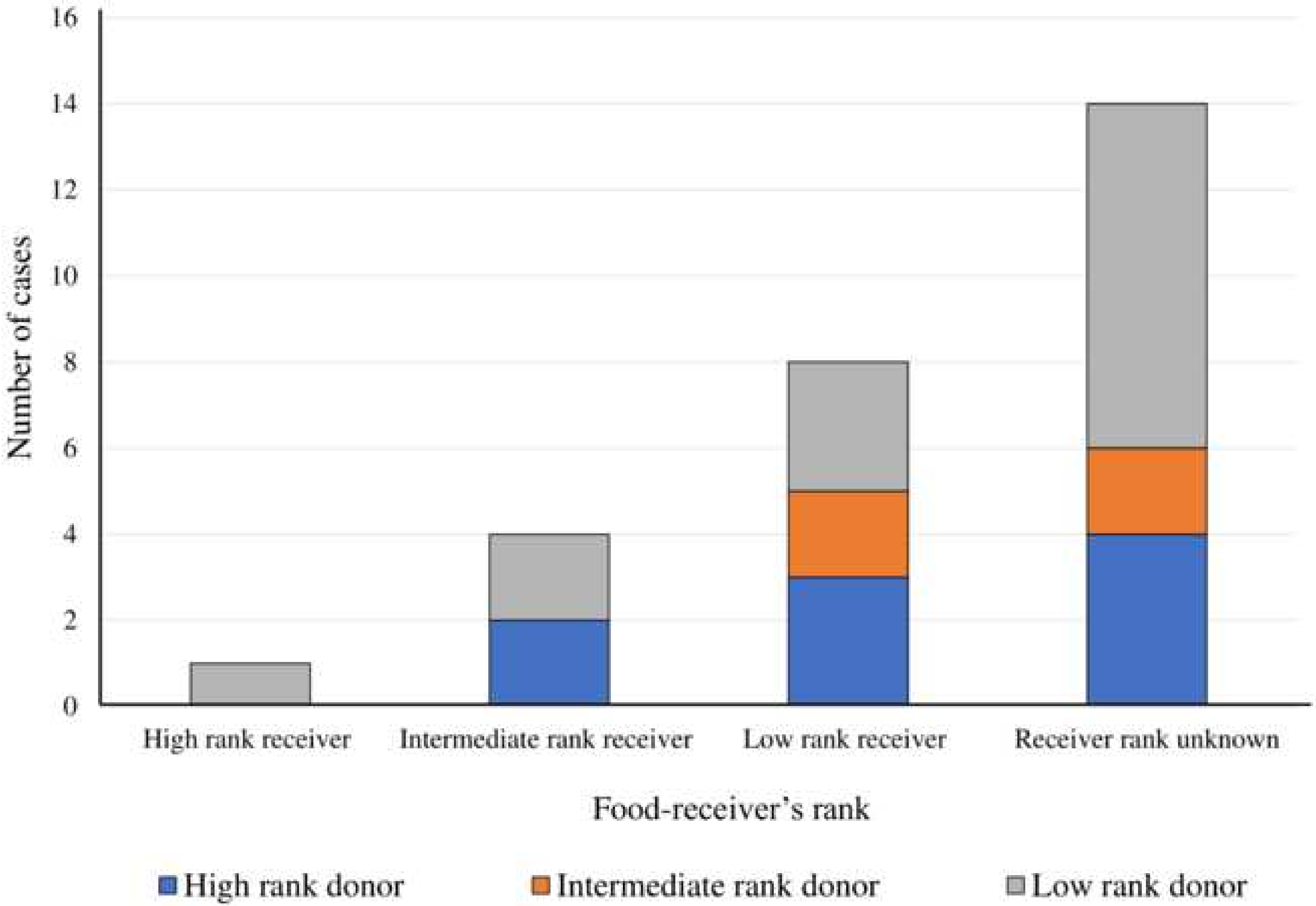
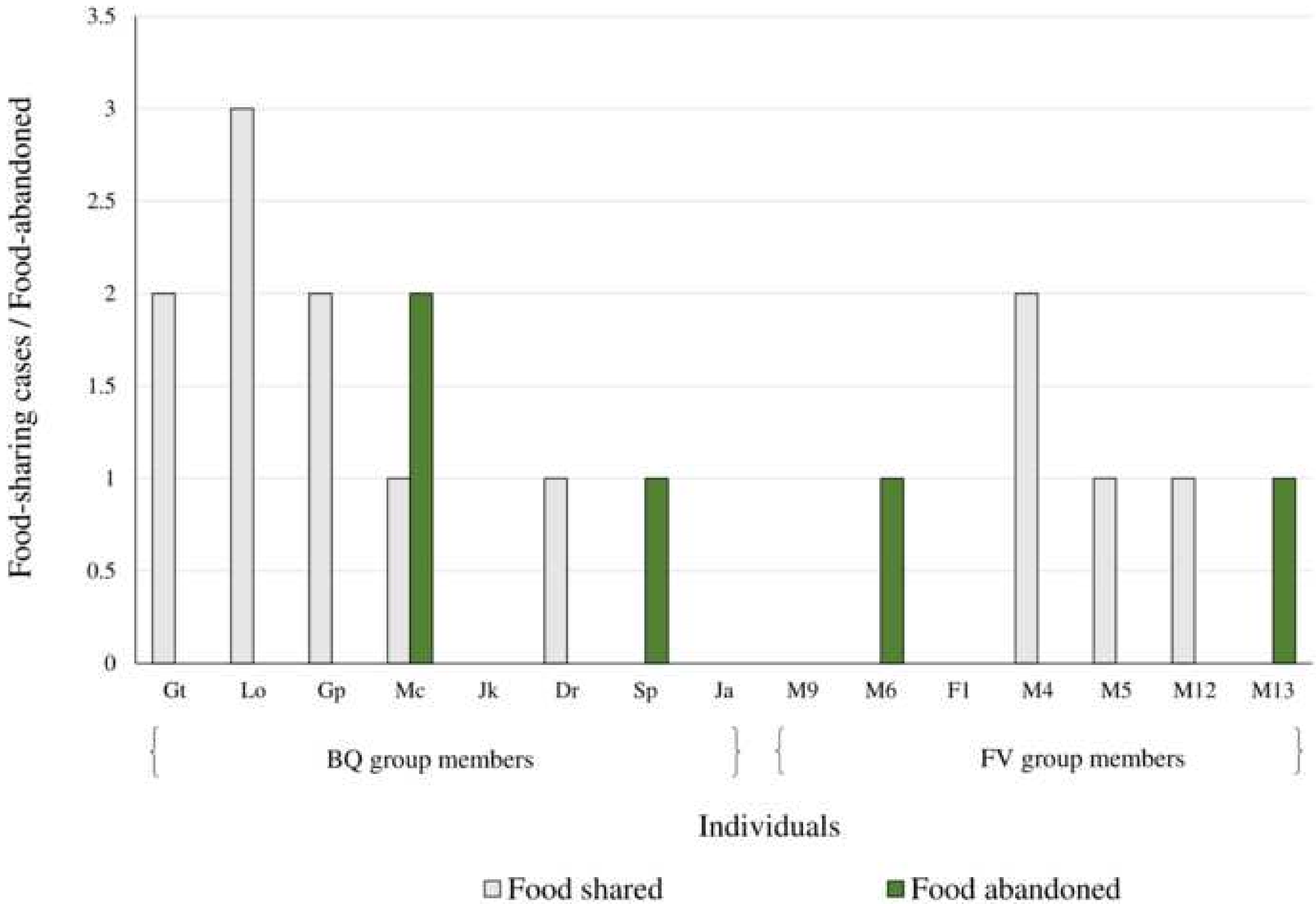


Figure 5



Food-sharing cases / Food-abandoned
3.5
3
2.5
2
1.5
1
0.5
0
Gt
Lo
Gp
Mc
Jk
Dr
Sp
Ja
M9
M6
F1
M4
M5
M12
M13
BQ group members
FV group members
Individuals
Food shared
Food abandoned

Figure 6

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Supplementary Table

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Table
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