Intergroup food transfers in wild golden lion tamarins (*Leontopithecus rosalia*)

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Abstract

Transfers of food between adults are uncommon in primates. Although golden lion tamarins (*Leontopithecus rosalia*), are unique among primates in the extent of food transfers, reports of food transfers between adults have so far been restricted to captive or reintroduced individuals. Here, I report the first six recorded events of adult-adult food transfers between individuals belonging to different groups. Given that individuals emigrate from their natal group to find reproductive opportunities, I suggest that those intergroup food transfers could be a way for individuals to estimate the quality or availability of potential mates or social partners. Here I propose an additional function of food transfers in wild golden lion tamarins: to create and strengthen social bonds outside of the family group.

Keywords: food transfers; social bond; intergroup interaction; golden lion tamarins; tolerance

Introduction

Within-group food transfers are common in primates, particularly in apes and callitrichids (G. R. Brown et al., 2004), and can serve several functions. Most transfers are passive, where the donor allows the receiver to take food from their possession (G. R. Brown et al., 2004), and most occur between mothers and infants (G. R. Brown et al., 2004; Feistner & McGrew, 1989); adult-adult food transfer is rare and is only present in species that also transfer food to their young (Jaeggi & Van Schaik, 2011). A common function of transfers is hence providing food or information to young, but between adults, food transfers can be used to avoid harassment or as a reciprocal exchange (G. R. Brown et al., 2004; Feistner & McGrew, 1989; Jaeggi & Van Schaik, 2011). In support of this second function, most adult-adult food transfers in primates are predicted by dominance, with higher ranking individuals raking food from lower ranking individuals, with relinquishing food being the least costly strategy for the lower ranking individual (G. R. Brown et al., 2004). Thirdly, some work in chimpanzees suggest that food transfers between group members are used for social support, or as exchange food for sexual interactions (Mitani & Watts, 2001; Nishida et al., 1992). Finally, in captivity there is also evidence of reciprocal altruisms involving food transfers in capuchins and tamarins (G. R. Brown et al., 2004). Although Cheney and Seyfarth (1990) suggest that reciprocity in primates is more likely to involve social interactions rather than physical objects, such as food.

By contrast, between-group food transfers are almost unknown in primates. Recently, Fruth & Hohmann (2018) reported an event where an individual bonobo (*Pan paniscus*) possessing an antelope shared with members of its own group as well as members of the neighbouring community. But comparable observations do not exist for many other commonly studied primates. We might expect to see between-group transfers when there is high tolerance between groups such as when the cost of aggression is high, or when resources are not defensible (Robinson & Barker, 2017).

Callitrichids are a unique family not only for their extensive transfer of food to juveniles, potentially for both nutritional and informational benefits (G. R. Brown et al., 2005; Feistner & Chamove, 1986; Moura et al., 2010; Moura & Langguth, 1999; Rapaport, 1999; Troisi, 2017; Troisi et al., *In prep*; Voelkl et al., 2006), but also the prevalence of active transfers initiated by adults (G. R. Brown et al., 2004; Feistner & McGrew, 1989), especially towards

juveniles and pregnant females (Guerreiro Martins et al., 2019; Ruiz-Miranda et al., 1999). Recent work has shown that in callitrichids food transfers can also be used to reinforce cooperative bonds within a group (Guerreiro Martins et al., 2019).

Golden lion tamarins (*Leontopithecus rosalia*) are an endangered Neotropical callitrichid native to the Atlantic forest on the south-eastern coast of Brazil. They are territorial cooperative breeders living in small family groups, with an average group size of five to seven individuals (Dietz et al., 1994; Dietz & Baker, 1993; Tardiff et al., 2002; Troisi, 2017; Troisi et al., *In prep*, 2018). Golden lion tamarins have a rapid reproductive turnover, often giving birth to twins, and an intense parental investment (Dietz et al., 1994). Golden lion tamarins defend a territory of approximately 45.2 ± 15.5 ha against other golden lion tamarin groups (Dietz et al., 1997), and have regular, highly vocal encounters with neighbouring groups (Peres, 1989). Most golden lion tamarins disperse from their natal groups, mainly immigrating to neighbouring groups, with 60% of individuals dispersing from their natal group by three years of age and 90% after four years (Baker et al., 2002).

Unlike most primates, golden lion tamarins actively provision young and other group members with solid foods (Rapaport & Brown, 2008), and adults vocalise to infants to offer food (K. Brown & Mack, 1978; Rapaport, 2011; Rapaport & Ruiz-Miranda, 2002). Experimental studies show that golden lion tamarins preferentially transfer to juveniles food items that are rare, that they have tried before, or that are difficult to process or novel (Price & Feistner, 1993; Rapaport, 1999, 2006; Troisi, 2017; Troisi et al., *In prep*) but adults also transfer food to pregnant females (Ruiz-Miranda et al., 1999). However, despite food transfers being common, all reported transfers occurred between members of the same group, and transfers between adults have only been reported in captive or reintroduced individuals. Here I report six events in the wild where monopolisable food was shared between members of different groups in a cooperatively breeding species: the golden lion tamarin.

Methods

Six groups of 3-10 free living golden lion tamarins (N=42-46 individuals) were observed in two locations of the Atlantic forest, Brazil (Table S1 in the ESM for list of individuals). All electronic supplementary materials are available on OSF at https://osf.io/8w5gj/. All

individuals in each group were related to the breeding pair of their groups, except in three of the groups where in each case one individual was not. Three groups were located at the Poço das Antas Biological Reserve (22 °30'-22 °33' S; 42 °15'–42 °19' W), and three groups in a pocket of Atlantic forest at the Fazenda Afetiva-Jorge, Imbaú region (22°37' S, 42°28' W). Both sites are within the municipality of Silva Jardim, Rio de Janeiro, Brazil, are less than 30 km apart, and possess similar plant species (Carvalho et al., 2006). The groups were habituated to human presence and monitored by members of the Associação Mico-Leão-Dourado. To keep track of the population, every group was regularly surveyed to record births and deaths, and captured twice a year, during which individuals were weighed, measured and individually marked with Nyanzol dye on the tail and body. Individuals were also tattooed at first capture as part of the management of the species by the Associação Mico-Leão-Dourado (Ruiz-Miranda et al., 1999).

The observations reported here were made during two experiments looking at teaching behaviour in golden lion tamarins, during which food was provided to wild groups (see Troisi, 2017; Troisi et al., *In prep*, 2018). In the first experiment, golden lion tamarins were provided with small samples of different types of food: banana, apples, grapes, meal worms and crickets in January-February 2014, and additionally pears and papayas in August-September 2014 (Troisi, 2017; Troisi et al., *In prep*). The fruits were cut into small pieces/slices, and the insects were dehydrated. All food items were provided in pots (Figure 1.A). The aim of the experiment was to examine the function of adult to juvenile within-group food transfers. However, during some of the experimental trials some territorial encounters took place, allowing me to make the observations that I report below. In this experiment, very few individuals ate the dehydrated insects, and all of the transfers observed were of fruits. In the second experiment, the same golden lion tamarins groups were provided with a novel substrate containing slices of bananas in February-March 2014 and September-October 2014 (Troisi et al., 2018) (Figure 1.B), with the aim of determining whether juvenile golden lion tamarins learn substrate properties from food-offering calls (Troisi et al., 2018).

Ethical approval

All experiments were performed in accordance with the American Society of Primatologists' (ASP) Principles for the Ethical Treatment of Primates and the Association for the Study of

Animal Behaviour (ASAB) guidelines. The Animal Welfare and Ethics Committee of the University of St Andrews approved the studies. Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) approved the ethics for project number 17409–10, "Manejo de metapopulação do mico-leão-dourado: pesquisa e ações," and the ethics adhered to the legal requirements of Brazil.

Report

I observed six food-transfers between individuals of different groups (Table 1, ESM Video). All of the transfers reported below involved six unique donors, and six unique receivers. The first three observations were made during the first experiment investigating food transfers using different types of food (Troisi, 2017; Troisi et al., *In prep*), and the remaining three during the second experiment looking at the function of food-offering calls (Troisi et al., 2018).

Observation 1

The first observation occurred on the 1st February 2014 at the Fazenda Affetiva-Jorge. Five individuals, four from group AF2 and one from group 'Super', were foraging on provisioned fruits at a platform before briefly dispersing. Individuals from the group AF2 present were AF2T3, a sub-adult male, AF2T13 a juvenile male, AF2T2 a juvenile female, and AF2T34 a sub-adult female. The individual from group Super was SuperT3, a sub-adult female (1 year and 3 months). After the dispersal to branches around the platform, SuperT3 approached individual AF2T3, who was foraging on a piece of grape. SuperT3 extended her arm and hand four times towards AF2T3 and vocalised, before AF2T3 appeared to let her take the food from its hand.

Observation 2

The second observation occurred 21:48 minutes after the first one. Two individuals from AF2 (AF2T2, a juvenile female, and AF2T14, an adult male) and one individual from Super (SuperT3, from observation 1) were foraging on a platform when they were approached by individual SuperT13, a sub-adult female (1 year and 3 months old) from group Super. AF2T12, an adult female carrying two infants, and AF2T23, an adult female, were also present in the vicinity. SuperT13 first inspected some of the food on the platform before

approaching AF2T14. SuperT13 first attempted to take a grape from AF2T14's mouth. AF2T14 showed some resistance, but then AF2T14 appeared to let SuperT13 take the food from its hand. SuperT13 was then approached by a juvenile from the AF2 group, potentially to take the food, which led SuperT13 to leave the platform. During this entire period, SuperT3 was foraging on another food patch less than 15cm away from where the food transfer took place.

Observation 3

The third observation took place on the 6th September 2014 at the Poço-das-Antas research station. AFT3, a sub-adult female from group AF, was foraging in the presence of two other individuals (AFT234, an adult female from group AF, and an unidentified individual, potentially from group AF too), when BO2T13, an adult male from group BO2, approached the pot of food where AFT3 (11 months old) was foraging. BO2T13 started extracting a piece of grape from the pot, but AFT3 took it from BO2T13's hands, and ate it, with little resistance from BO2T13. During the transfer, BO2T2, a sub-adult male from group BO2, was in the vicinity.

Observation 4

This observation, and the following two, were made during the food-offering call experiment (Troisi et al., 2018) where a novel substrate, containing bananas, was provided to the groups. On the 19th February 2014 at the Fazenda Affetiva-Jorge, three individuals were foraging at the novel substrate: one from group Super (SuperT0C, an adult male) and two from group AF2 (AF2T4, a sub-adult male, and AF2T34 a sub-adult female). AF2T34 obtained food from the substrate and was eating some banana, when SuperT0C (3 years and 4 months) arrived to investigate the substrate, then tried to get some banana from AF2T34's hands. AF2T34 showed some resistance, but SuperT0C obtained food nonetheless. SuperT3, a sub-adult female, and SuperT1, a juvenile female, both from group Super, approached the group during the transfer.

Observation 5

The firth observation occurred on the 14th September 2014 at the Poço-das-Antas research station. Four individuals from the group AF were present: AFT3, a sub-adult female, AFT0C,

an adult male, AFT234, an adult female, and AFT1234, an adult female; as well as one individual from group BO2: BO2T3, a sub-adult female. AFT234 was extracting food from the novel substrate when BO2T3 (12 months old) intercepted the food as it was coming out of the substrate, and obtained part of the slice of banana that AFT234 had been trying to get out. BO2T3 actually attempted to get food from AFT0C, an adult male from group AF, and from AFT3, a sub-adult female from group AF, in the twelve seconds preceding the successful transfer from AFT234. However, both of those transfers were unsuccessful (BO2T3 did not obtain any food).

Observation 6

The sixth observation occurred 15 seconds after the fifth one. AFT1234, AFT0C and AFT234 from group AF were foraging at the platform, and BO2T3, from group BO2, was eating the transferred piece of banana nearby, when BO2T13, an adult male (1 year and 7 months old) from group BO2 approached the substrate. AFT0C was getting food out of the substrate, when BO2T13 reached from below and grabbed the piece of banana before AFT0C could put it in its mouth. BO2T13 left the area immediately after having obtained food.

In the first three observations the individual who initially had the food stopped resisting before the second individual obtained the food. In each of these transfers the individual who initially had the food was male and the individual who obtained it was female. Two of the donor males were adults (> 18 months old), and one was a subadult (between 10 and 18 months old), while all three of the receiver females were subadults. In the fourth observation, where the food was transferred from a sub-adult female to an adult male, the adult male received the food despite the sub-adult female resisting at the point of transfer. In the last two observations, in which the food was transferred from an adult female to a sub-adult female (fifth observation), and from an adult male to another adult male (sixth observation), the transfer of food took place quickly, and I was unable to see whether there was any resistance during the transfer.

Discussion

The six observations clearly show that sharing food with strangers is not a uniquely human or great ape characteristic. As with bonobos, it is possible that this sharing between members of different groups show a new level of tolerance in golden lion tamarins (Fruth &

Hohmann, 2018). However, unlike bonobos, the food resources that were transferred between the golden lion tamarins were easily monopolisable by just one individual, and unlike Fruth & Hohmann (2018), I do not think that our data helps explain the emergence of social norms in human societies. Although sharing between groups might have played an important role in human evolution, I suggest, like Westergaard & Suomi (1997), that such sharing between groups evolved independently in different primate linages.

Although food transfers between different groups in golden lion tamarins could be indicative of a new level of social tolerance in this species, it is important to note that golden lion tamarins are highly territorial, with intergroup interactions usually being aggressive (French & Inglett, 1989; Peres, 1989; Ruiz-Miranda et al., 2002). During dispersal events, resident golden lion tamarins are also aggressive toward immigrants (Baker & Dietz, 1996), so the six observations of social tolerance reported herein are particularly surprising, and inconsistent with previously suggested functions of food transfer in this species. In golden lion tamarins, food transfers have mainly been studied in the context of providing nutrition or information to juveniles, or nutrition to pregnant females. Here I suggest that food transfers may be used to create and/or strengthen social bonds with non-group members.

Subordinate golden lion tamarins have two main reproductive options: 1) wait for a breeding opportunity in their natal group, while caring for the young of the breeding pair, or 2) emigrate to explore their own breeding opportunities (Romano et al., 2019). Both male and female golden lion tamarins disperse from their natal group, and settle in the first available breeding position or unoccupied area that they encounter, but males tend to disperse more frequently than females, and are more successful when dispersing (Baker & Dietz, 1996; Dietz & Baker, 1993; Moraes et al., 2018; Romano et al., 2019). Furthermore, males and females use different strategies to emigrate: males are more likely to immigrate into established groups compared to females who are more likely to form new groups (Romano et al., 2019), and females are also more likely to inherit their natal territory than males (Baker & Dietz, 1996). Food transfers between individuals of different groups could therefore be used to create a social bond prior to immigration, which could either facilitate acceptance and reduce aggression when immigrating to a new group, or enable individuals to find social partners to form a new group with. Food sharing with individuals from a

different group, particularly with individuals of a different sex, might enable future immigrants to assess their likelihood of being integrated into a new group, or of finding a mate. In fact, by 2016, only 4 of the 11 individuals which took part in the food transfers described here were still in their group. The 7 others disappeared, but it is not known whether they died, became satellites or went to a groups that is not monitored by the Associação Mico-Leão-Dourado. Miller et al. (2003) found evidence that scent markings are not used for territorial defence in golden lion tamarins, but might be used as a way to communicate information for mate selection, extra-group copulation and or attracting immigration partners. Food transfers could similarly be used to decrease aggression in order to communicate information beyond the group.

Romano et al. (2019) found that conspecific attraction, where individuals leave their natal group because they are attracted by potential extra-group mates and/or emigrating group mates, characterises emigration for both male and female golden lion tamarins. Food transfers might be a way to assess potential extra-group mate quality or acceptance, and Hankerson & Dietz (2014) suggest that males in particular might be prospecting neighbouring groups for breeding opportunities. Hence food transfers might be particularly useful for males deciding where and when to immigrate to reduce the probability of eviction. Romano et al. (2019) also found evidence for parallel dispersal (emigration with peers or close kin) in golden lion tamarins. Since females are more likely to start new groups compared to males, female might evaluate potential mates or social partners with whom to form a new group through those intergroup food transfers.

Four out of the six observations reported herein were food transfers between individuals of different sex: in three observations (number 1,2,3) the food went from a male to a female, while in one observation (number 4) it went from a female to a male. Those four observations might be a way for individuals to assess quality of potential mate prior to dispersing. This would support the sexual selection hypothesis, which postulate the occurrence of competition for being chosen as a mate (West-Eberhard, 1983). However, two of the observations took place between same-sex individuals: in observation 5 the food went from a female to a female and in observation 6 the food went from a male to a male. It is possible that instead of helping choose between a potential mate, those food transfer events also help individuals select future social partner prior to dispersing. Overall, I suggest

that the food transfers to members of a different group may be a way to create a social bond with those individuals, especially prior to dispersal. Further data is required to assess which of these roles is more likely to have a primary role in driving food transfers between adults of different groups.

One limitation of the observations reported here is that they were conducted during an experiment where food items were provided to golden lion tamarin groups, so it is possible that an increase in food availability induced an atypical level of tolerance towards non-group members, resulting in the observed food transfers. However, I think it unlikely that the increase in food availability created this high level of tolerance, because half of the observations (number 3, 5, and 6) were conducted during the fruiting season, where plenty of food were available – so much so that it was sometimes difficult to have the groups interested in the fruits in the experiments as they were more interested in the fruits in the trees. Furthermore, some experiments in captivity suggest that food transfers are less likely when food is abundant (e.g.: Price & Feistner, 1993) because it is easier to acquire food personally instead of getting it from another individual.

Conclusions

Most previous work on food transfers in golden lion tamarins has focussed on transfers from adults to young, aiming to determine whether they function to provide nutrition, information or both (Price & Feistner, 1993; Rapaport, 1999; Troisi, 2017; Troisi et al., *In prep*). Until now, adult-adult food transfers had only reported in captive or reintroduced individuals (Ruiz-Miranda et al., 1999). Here there not only is evidence for adult-adult food transfers in the wild, but also for food transfers between individuals of different groups, which is inconsistent with previously suggested functions of food transfers. I suggest an additional function of food transfers in wild golden lion tamarins: to create and/or strengthen social bonds outside of the family group, which could be particularly useful for tamarins prior to immigrating to a new group or founding a new group with individuals from other groups.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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Table 1: Summary of the successful transfers between groups (Obs = observation, in order listed in the report). Locations include Fazenda Afetiva-Jorge (FAJ) and Poco das Antas Biological Reserve (PDA). Adults are >18 months old and sub-adults are between 9 and 18 months old.

Obs	Location	Date	Individual who initially had the food (donor)	Donor group	Donor sex	Donor age class	Individual who obtained the food (receiver)	Receiver group	Receiver sex	Receiver age class	Resistance during transfer	Resistance at point of transfer
1	FAJ	1/2/2014	AF2T3	AF2	Male	Sub-adult	SuperT3	Super	Female	Sub-adult	Yes	No
2	FAJ	1/2/2014	AF2T1	AF2	Male	Adult	SuperT13	Super	Female	Sub-adult	Yes	No
3	PDA	6/9/2014	BO2T13	BO2	Male	Adult	AFT3	AF	Female	Sub-adult	No	No
4	FAJ	19/2/2014	AF2T34	AF2	Female	Sub-adult	SuperT0C	Super	Male	Adult	Yes	Yes
5	PDA	14/9/2014	AFT234	AF	Female	Adult	BO2T3	BO2	Female	Sub-adult	NA	NA
6	PDA	14/9/2014	AFT0C	AF	Male	Adult	BO2T13	BO2	Male	Adult	NA	NA

Figure 1: **A)** Photo of the food-transfer experiment; **B)** Photo from the food-offering call experiment