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ORIGINAL ARTICLE

Successful adoption of an orphan infant in a wild group of brown howler monkeys

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Abstract

The rarity of infant adoption in wild primates compromises our understanding of its consequences for the participating individuals. We report the first case of successful infant adoption in a wild group of brown howler monkeys (*Alouatta guariba clamitans*). We evaluated the potential costs of the behavior for the adoptive mother by comparing her activity budget and diet before and after the adoption. On 18 June 2013, a domestic dog killed the mother of a 2-month-old male infant (Victorio) as she attempted to cross a canopy gap. Victorio was immediately rescued from her belly by a researcher and released in a climber near another infant-carrying female (Sofia, his likely grandmother). Sofia recovered him 2 min later. She carried and breastfed both infants during the next 4 weeks, when her own infant disappeared. We monitored Victorio until he reached adulthood in March 2018. Sofia fed more (mainly on immature leaves) when she nursed only Victorio than when nursing only her own or both infants. Assuming that the disappearance of Sofia's own infant was unrelated to the adoption of Victorio, we conclude that his successful adoption may contribute to Sofia's inclusive fitness if he sires his own infants.

Keywords Allomaternal care · Inclusive fitness · Kin selection · Predation · Dog attack

Introduction

Adoption of a nutritionally dependent infant is an extreme case of alloparental care (Riedman 1982). It can occur when the providing parent dies, fails to care for, or abandons the immature individual, or when another individual kidnaps it, normally after losing their own offspring (Riedman 1982; Thierry and Anderson 1986; Kouba et al. 2017). Adoption occurs mostly in family groups of social mammals in which youngsters remain with their parents for one or more years, until they reach dispersal age or adulthood, or in other small groups characterized by high levels of kinship (Riedman 1982; Thierry and Anderson 1986). Given that the feeding of dependent infant mammals is eminently a lactating mother's responsibility, cases of adoption in mammals often involve other females (Riedman 1982; Clutton-Brock 1991).

Mammalian adoptions fit the predictions of kin-selection theory when the inclusive fitness of the adoptive parent increases as a result of the survival of an adopted kin infant (i.e., a form of altruism influenced by relatedness between individuals: Foster et al. 2016). In the absence of inclusive fitness benefits, the adoption can still benefit the adoptive parent by providing the opportunity to practice parenting skills (Riedman 1982). When neither inclusive fitness nor experience benefits can be identified, adoption is considered a nonadaptive behavior triggered by females' general attraction toward infants (Riedman 1982; Clutton-Brock 1991). However, our understanding of this phenomenon is still incomplete, given the scarcity of detailed long-term studies and the scarcity of reports of adoption in some vertebrate groups, including wild nonhuman primates.

Adoption of infants has been recorded in all major primate radiations (Agoramoorthy and Rudran 1992; Riedman 1982; Dunham and Opere 2016). Among New World monkeys, adoption has been witnessed in howler monkeys in

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Central (e.g., *Alouatta palliata*: Clarke and Glander 1981; *A. pigra*: Schneider et al. 1999) and South America (e.g., *A. arctoidea*: Agoramoorthy and Rudran 1992; *A. caraya*: Pavé et al. 2010; *A. seniculus*: Izawa 1989), in spider monkeys (*Ateles geoffroyi*: Estrada and Paterson 1980), and in titi monkeys (*Callicebus nigrifrons*: Cäsar and Young 2008). Most of these studies reported a nursing female adopting a dependent orphan infant and her increased nutritional demands resulting from the need to nurse and carry 'twins'. However, none of them evaluated the consequences for the adoptive mother's activity budget and foraging, or the adoptee's survival until adulthood, which requires long-term monitoring (Riedman 1982; Thierry and Anderson 1986).

Free-ranging primate populations living in anthropogenic landscapes create opportunities for adoption because all group members are vulnerable to threats that are uncommon in pristine habitats (e.g., electrocution, road kills, dog attacks or capture by people). This is the case for brown howler monkey (*Alouatta guariba clamitans*) groups inhabiting conserved or altered habitats (e.g., plantations or agroforests) near human settlements, where deaths of adults from the aforementioned causes (Printes 1999; Buss 2012) leave orphaned infants and juveniles.

Here, we present the first report of successful adoption (i.e., survival of the adoptee until adulthood) of an infant male brown howler monkey by an infant-carrying, nursing adult female in a free-ranging group. Specifically, we describe the process of adoption of the infant after the death of his mother, the development of his plant-based diet after adoption, and his survival until adulthood. We also compare the adoptive mother's activity budget and diet with those of the group's adult male during three infant caregiving stages (hereafter ICS): when she was caring for her own infant (ICS_a), both infants (ICS_b), and only the adoptee (ICS_c). Given the high nutritional demands of nursing and infant-carrying for primates (Link et al. 2006; Dias et al. 2017), we expected that the adoptive mother would increase her feeding post-adoption compared to the pre-adoption stage to be able to rear two infants. We also expected increased consumption of plant items rich in energy and protein, such as fruits and immature leaves (Righini et al. 2017), as the infants grew older.

Methods

Study site and group

This study was conducted from April 2013 to March 2018 in a 4.1-ha Atlantic forest fragment within a 20-ha agroecological farm (Sítio Chachá; 30°12′28″S, 51°05′53″W, 40 m a.s.l.) in Porto Alegre, state of Rio Grande do Sul, Brazil. The anthropogenic matrix surrounding the fragment is a complex mosaic of scattered plantations of *Eucalyptus citriodora*, *Pinus taeda* and *Cycas revoluta*, agricultural fields, pastures, small human settlements, and unpaved roads. Two domestic dogs lived in Sítio Chachá. Like most rural properties in the region, an unknown number of stray dogs often also visited this area.

At the beginning of the case reported here (June 2013), the howler monkey group contained five individuals (one adult male and two adult females with their 2-month-old dependent male infants). Although we did not perform DNA analyses to determine the relatedness between the two adult females (hereafter Sofia and Rosalia), we believe that they were, respectively, mother and daughter, for the following two reasons. First, in 2011 the group was composed of four individuals: an adult male, an adult female with body size and pelage similar to Sofia, a subadult female, and an infant male named Pipo (who died of unknown causes in 2013). Second, no immigration occurred from 2011 to February 2019, when we stopped monitoring the group. Two male infants were born around the second (Aureliano) and third (Victorio) weeks of April 2013. Victorio was distinguishable from Aureliano by his reddish forelock and more brownish pelage. However, we were unable to distinguish them in most observations during June 2013 because they were similar in size and their faces were normally turned toward Sofia's belly, and because of poor light conditions.

Author V.M. monitored the study group on a monthly basis from December 2012 to January 2014. Within the study fragment, the howlers sometimes covered short distances on the ground (up to around 50 m) during movements between isolated portions of their home range, to exploit *Ficus cestrifolia* and *Psidium guajava* fruits. At least two other howler groups inhabited neighboring forest patches, but home range overlap was negligible.

Field observations

We recorded data before and soon after the death of Rosalia and the adoption of Victorio by Sofia; to do so we used the ad libitum method (Altmann 1974) with the aid of high-resolution 10×42 binoculars. V.M. and D.C. then recorded the behavior of Rosalia and the infant(s) on a monthly basis from June 2013 to January 2014 using instantaneous scan sampling (Altmann 1974) with 5-min sampling units at 15-min intervals. We recorded the infants' location on Sofia's body (ventral, dorsal or lateral) and each individual's behavior (feeding, resting, moving or socializing) in each scan. We also recorded the plant species exploited and the food items ingested when Victorio started to feed on plants.

We followed the study group for 293 h distributed over 29 sampling days from April 2013 to January 2014, obtaining 3763 behavioral records in 1172 scan samples. We could not compare parental care devoted to each infant due

to the aforementioned problems in identifying them in the first period after adoption. Finally, O.M.C. assessed Victorio's physical condition and his interaction with Sofia via 10-min monthly focal observations of both individuals for about 123 h between November 2014 and February 2015, November 2016 and February 2017, and October 2017 and March 2018. Both Victorio and Sofia were alive and apparently healthy when we stopped monitoring them in February 2019. The main datasets used to run the analyses described below are available in Chaves et al. (2019).

Data analysis

We used generalized linear mixed models (GLMM) to compare Sofia's frequency of feeding, resting, and moving, and her frequency of feeding on leaves and fruits during the three ICSs ($n_a = 8$ sampling days, 254 scans; $n_b = 3$ days, 113 scans; $n_c = 20$ days, 854 scans). We also compared her patterns with those of the adult male, to assess whether any changes in her behaviors resulted from environmental factors that also affected him. If not, we could conclude that her behavioral changes were likely related to the different energetic demands of raising one younger infant, then two infants simultaneously, and then a single older infant.

We ran the analyses using the function 'lmer' of the R package lme4 (Bates et al. 2015). We set a Poisson distribution with log link-function for the error distribution as recommended for count dependent variables (Crawley 2012). We used the bootstrapping approach over the R 'sample' function to set a standardized number of 20 scan sampling units for each ICS to control for asymmetry in sampling effort. We specified the main behavioral state or the food item, the ICS, and their interactions as fixed factors and the days' ID as a random factor to account for repeated measures during the same sampling days.

We used a likelihood ratio test over the 'lrtest' function of R package epiDisplay (Chongsuvivatwong 2015) to assess the significance of the whole model compared with the corresponding null model. We identified differences between ICSs using post hoc contrasts with the function 'glht' of the R package multcomp (Hothorn et al. 2008), with P values adjusted using the Tukey method. We performed all statistical analyses in R v.3.3.2 (R Core Team 2018), setting the statistical significance threshold at $P \leq 0.05$.

Results

Description of Victorio's adoption

We describe the process of Victorio's adoption during the three stages and also report observations during the post-adoption period (Table 1). Both infants were ca. 2 months old during the two first adoption stages, and Victorio was 3 to 9 months old in the third stage.

ICS_a began at 15:55 on 18 June 2013, when a domestic dog killed the adult female Rosalia, and the 2-month-old orphan Victorio was rescued and placed in a climber (Table 1; Fig. 1a, b). Immediately, the adult male moved near Victorio. He vocalized lightly, but did not touch the infant.

Victorio climbed Sofia's back at the beginning of ICS_b at 16:14, and the latter displayed clearly maternal care toward him (Table 1, Fig. 1c–e). During the next 2 days, ventral carrying was Sofia's predominant carrying style for both infants (>94% of carrying records in both cases, Fig. 1d, e). Although poor visibility prevented the confirmation of nursing during this stage, Victorio appeared to readily accept Sofia's care. After ICS_a, the adult male showed no specific interest in Victorio, and they did not interact.

Sofia continued to provide maternal care to Victorio and her own infant throughout ICS_b (Table 1). Distress vocalizations by Victorio gradually decreased the day after his adoption. On 20 June 2013, both infants climbed onto Sofia's back and explored the environment, although they did not leave her body.

On 15 July 2013, we found that Aureliano had disappeared and that Victorio was the only infant in the group. We were unable to determine the cause of Aureliano's disappearance (likely death), because the group had not been followed during the previous several days. We detected no wounds on either Victorio or Sofia that might have suggested receipt of aggression. Victorio showed no sign of discomfort with his adoptive mother during the next month (Table 1). On 31 July 2013, the ca. 4-month-old Victorio began to feed on plant items, and his dietary range had increased to at least 27 species by January 2014 (Table S1).

Victorio started to gradually feed more and move independently during the post-adoption stage, when he was ca. 8-months old (Table 1). When carried by his adoptive mother, his position was mostly dorsal (53%, ventral = 44%, lateral = 3%). He survived to adulthood in his natal group, where he was a subordinate male in January 2018 (Table 1). We conclude that the adoption was successful. O.M.C. observed him smelling his adoptive mother's genitals on nine occasions in February and March 2018, but no mating attempt was recorded.

Sofia's and the adult male's activity budgets and diets

Between June 2013 and January 2014, Sofia devoted most of her time (mean ± SD percentage of total scan sampling records) to resting (53 ± 9%), followed by feeding (35 ± 9%), moving (11 ± 5%), and socializing and other activities (1 ± 2%). Corresponding percentages for the adult male were

Table 1 Description of the main events of the processes of Victorio's adoption and development over the 5-year study period

Date	Hour	Stage/event	Description
		I: Pre-adoption	
18 June 2013	15:55	Dog attack	A dog attacks Rosalia (carrying Victorio on her back) when she tries to jump across a canopy gap
	16:02	Rosalia's death	Rosalia dies, and the researcher V.M. rescues Victorio from her back
		II: Early adoption	
18 June 2013	16:13	Victorio's return to the group	After confirming that Victorio is not injured, V.M. and D.C. place him in a climber (17 m in height) near the trees where the group rests
	16:14	Victorio's rescue	Victorio's distress calling (lasting ca. 2 min) attracts Sofia's attention. She moves toward Victorio and turns her back to him
	16:45	Allomaternal care	Sofia carries both Victorio and Aureliano on her back for ca. 1 h. She quickly grooms or inspects Victorio's body. Both infants move to a suckling position
19–22 June 2013		Intense caregiving	Sofia carries, grooms, and nurses Victorio many times every day
		III: Advanced adoption	
15 July 2013		Aureliano's disappearance	Upon returning to the study site 24 days later, V.M. observes that Aureliano is missing. Sofia carries only Victorio
Late July 2013		Environmental exploration	Victorio handles plant items near Sofia during periods of <2 min
Late July–Sep 2013		Victorio-Sofia integration	Sofia and Victorio continue displaying typical mother–infant behaviors
		Beginning of independence	Victorio is observed feeding on young leaves for the first time on 31 July. He occasionally ingests young leaves and small ripe fruits, but he still sucks frequently and depends on Sofia to move between trees
		IV: Post-adoption	
Oct 2013–Jan 2014		Plant feeding	Victorio feeds on small ripe fruits, young leaves, and other plant items of 22+ plant species (Table S1). He sucks occasionally
Nov 2014–Feb 2015		Victorio's independence	Victorio feeds and travels independently, and most of the time he does not stay in body contact with Sofia
Nov 2016–Feb 2017		Juvenile-subadult transition	The color of Victorio's pelage begins to change from dark brown to reddish brown
Jan–Mar 2018		Adulthood	Victorio's body size and reddish-brown pelage are similar to those of the alpha adult male. He smells his adoptive mother's genitals occasionally

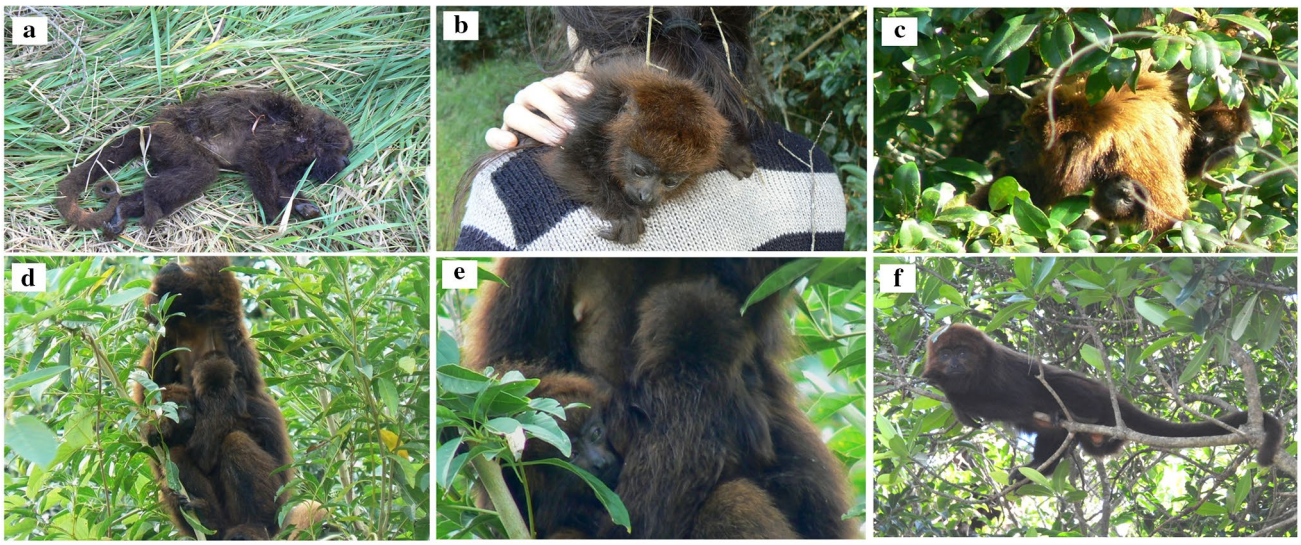

Fig. 1 Victorio before and after his adoption by the lactating female Sofia. **a** Victorio's mother's corpse after the dog attack. **b** Victorio rescued by V.M. in June 2013. **c**, **d** Adoptive mother Sofia carrying Victorio and her own son Aureliano. **e** Sofia nursing one infant. **f** Victorio at the age of 3.9 years in February 2017

57 (±8%), 31 (±8%), and 11 (±5%). The amount of time spent by both Sofia and the adult male in their main diurnal activities differed across ICSs (GLMM: AIC = 1971, χ^2 = 1731, *df* = 17, $P < 0.0001$), but we detected only one difference between the individuals: Sofia spent more time feeding during ICS_c than the adult male (Tukey contrast test: $P < 0.01$; Fig. 2). We found a similar pattern of variation when we analyzed the activities of each individual separately (Fig. S1).

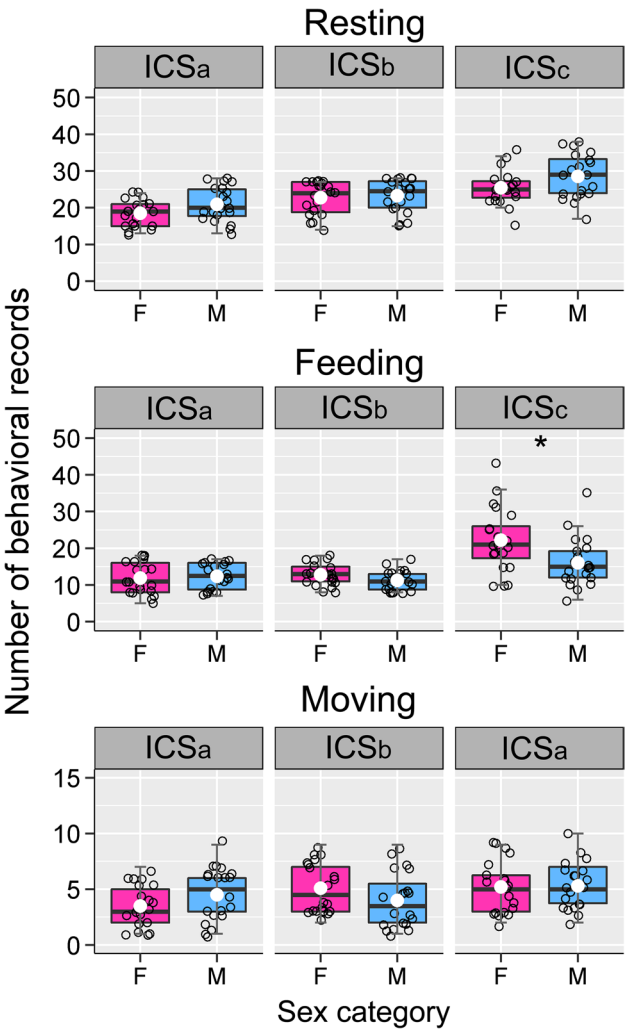

Fig. 2 Number of instantaneous scan records devoted to resting, feeding, and moving by the adoptive mother Sofia (F) and the group's adult male (M) during each infant caregiving stage: own infant Aureliano only (ICS_a), both infants (ICS_b), and adoptee Victorio only (ICS_c). The black line within each box represents the median, the large white circle represents the mean, the box represents the first and third quartiles (interquartile range [IQR]), and the whiskers represent the IQR multiplied by 1.5. Dots represent the data for each sampling day ($N = 20$ sampling days in each case). Pink bars represent the adult female, and blue bars the adult male. Asterisks indicate significant differences ($P < 0.05$) between the individuals

Similarly, the frequency of feeding on leaves and/or fruits by Sofia and the adult male differed among ICSs (GLMM: AIC = 1618, χ^2 = 309, *df* = 23, $P < 0.0001$, Fig. 3) but not between the individuals (Tukey contrast test: $P > 0.05$ in all cases; Fig. 3), despite Sofia's higher consumption of immature leaves and ripe fruits during ICS_c than ICS_a and ICS_b (Fig. S2).

Discussion

This is the first reported case of successful adoption of a dependent infant brown howler monkey by an infant-carrying, nursing female. Despite the absence of independent immature individuals in the study group, our observation is compatible with the view that adult female primates, particularly lactating or pregnant ones, are prone to adopt orphan immature individuals (Thierry and Anderson 1986; Pavé et al. 2010). In addition to the hormonal stimulus of lactation as a proximate trigger for adoption (Thierry and Anderson 1986), our observation is compatible with the kin-selection perspective (West-Eberhard 1975; Riedman 1982). The deceased and the adoptive mothers were probably daughter and mother, respectively; therefore, Victorio is likely Sofia's grandson.

Maternal skills training (Riedman 1982; Thierry and Anderson 1986) and social support gain (West-Eberhard 1975) are weaker explanations of the described case, because Sofia was an experienced multiparous female and the only mature individual in the group other than the adult male. However, she would only obtain an increase in inclusive fitness, as suggested in other howler monkey studies (*A. arctoidea*: Agoramoorthy and Rudran 1992; *A. caraya*: Pavé et al. 2010), if the death of her son Aureliano was unrelated to Victorio's adoption (e.g., accident, disease, or predation). If the adoption triggered Aureliano's death, as suggested in a case reported in *Colobus angolensis* (Dunham and Opere 2016), the adoption would be nonadaptive. Although we do not know Aureliano's fate, he is likely to have died, because a dependent infant cannot survive by itself.

Although Aureliano's disappearance occurred during a period of almost a month in which we were not monitoring the group, we did not observe any evidence that Sofia was incapable of rearing two same-age infants simultaneously, a phenomenon reported in black-and-gold howler monkeys (Pavé et al. 2010; see also Bicca-Marques and Calegaro-Marques 1994). Compatible with increased energetic and nutritional demands of nursing and carrying a growing infant, Sofia showed increased feeding during ICS_c. However, the fact that the adult male also showed a slight increase in feeding during this stage weakens this interpretation.

Contrary to our prediction, we found that Sofia's consumption of leaves and fruits did not differ from that of the

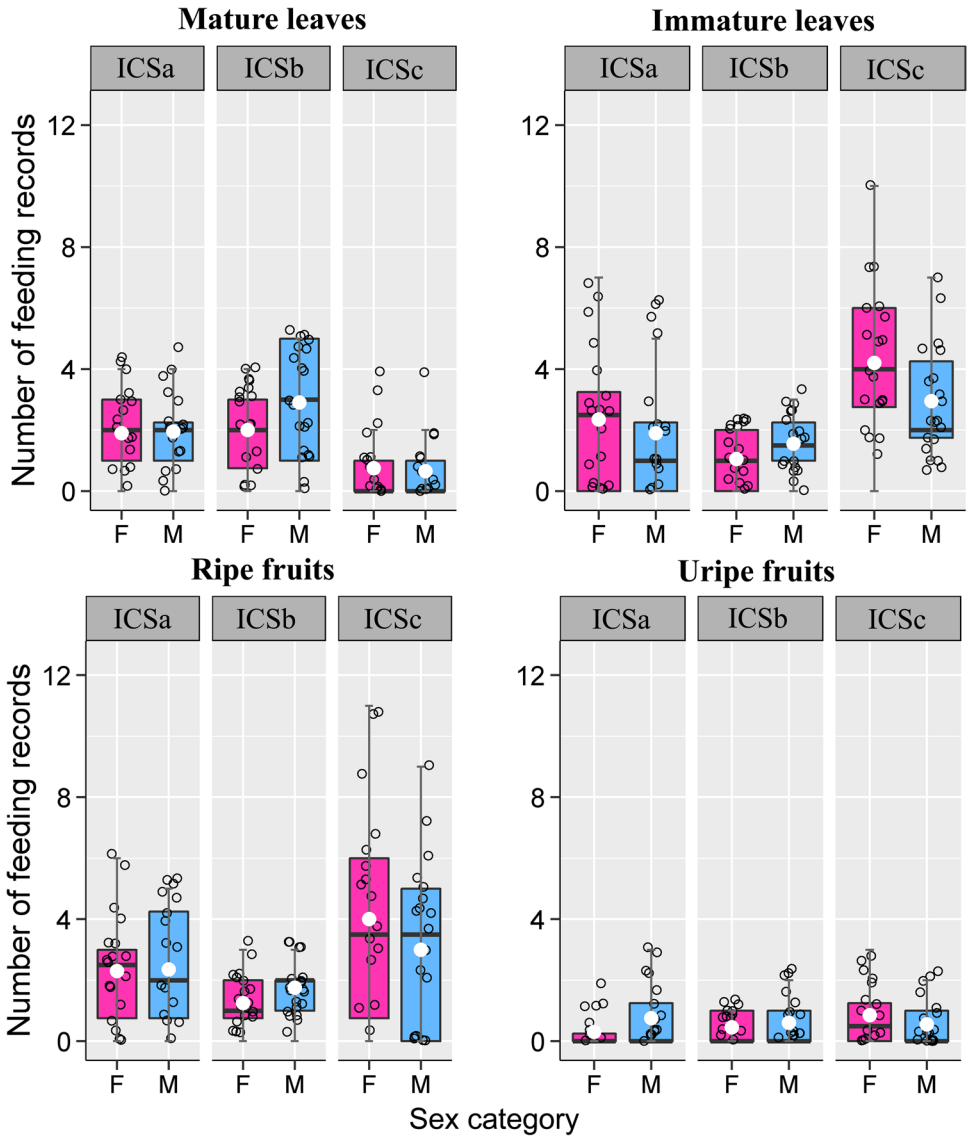

Fig. 3 Number of records of feeding on the main plant items by the adoptive mother Sofia (F) and the group's adult male (M) during each ICS. Additional details as in Fig. 2

adult male in all ICSs. Therefore, we cannot argue that she needed to increase her intake of protein- and energy-rich foods to satisfy her potentially higher nutritional demands of either raising two infants simultaneously or one growing one (Coley and Barone 1996; Righini et al. 2017). In fact, it is likely that the plant consumption pattern of both adults was simply due to the greater availability of immature leaves and lower availability of ripe fruits during some months of ICS_c (i.e., July–September 2013: see Chaves and Bicca-Marques 2016).

From the infant's perspective, Victorio's likely close kinship with Sofia may have played an important role in the success of his adoption. The failure of a relocation attempt (witnessed by O.M.C.) on 14 April 2018 of a ca. 2-month-old orphan male brown howler (Tito), whose mother died (unknown cause) in another population more than 5 km from the study group, is compatible with our hypothesis. Upon his release on a tree near the prospective adoptive group, an adult female ventrally carrying a ca. 4-month-old infant approached Tito and allowed him to climb her back. She carried and groomed him. However, Tito left the female's back 35 min later and climbed into the crown of a *Ficus cestrifolia* tree about 20 m away. He remained isolated there even though the entire group did not move away from him for about 40 min, and the same female attempted to rescue him again at least twice. The group eventually left the area, leaving Tito behind. The infant was recovered by the personnel responsible for the attempted relocation and sent to a local wildlife rescue center. Therefore, the success of an adoption, even of young infants, depends on the willingness of both the adoptive mother and the orphan, and some degree of familiarity between them may be critical.

Overall, Victorio's development followed the typical pattern for howler monkeys. His dependence on Sofia decreased

around the fifth and sixth months (Baldwin and Baldwin 1973; Podgaiski and Jardim 2009), when he also began to ingest plant foods (particularly fruits and immature leaves). All plant items eaten by Victorio were also eaten by Sofia and the adult male (V.M., pers. obs.) and are common foods in the diet of six other brown howler groups in the region (Chaves and Bicca-Marques 2016).

In conclusion, we recommend that management strategies for orphan infant howler monkeys, and perhaps other primates, target nearby groups as prospective adoptive groups, rather than attempting translocation to populations of unrelated individuals. This advice may become more important as habitat encroachment continues to bring non-human primates into increasingly dangerous contact with humans (Estrada et al. 2017, 2018), likely increasing the need for effective orphan infant management in anthropogenic landscapes.

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