



Behavioral adaptation in an adoptive free-ranging female Tibetan macaque

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Abstract

Adoption is an important form of allomaternal care in nonhuman primates, with implications for reproductive output and infant survival. Here, we report a kidnapping that became an adoption of a 3-week-old infant by a mother with her own infant in Tibetan macaques (*Macaca thibetana*). The adoptive mother nursed her “new” infant (allonursing), the first observation of this behavior in the species. The case provided a natural experiment for comparing how a female copes with a heavier burden of care for both her biological infant and another female’s infant, compared to mothers caring for only one infant. Our results showed that the adoptive female spent more time foraging and resting, and less time in group social activity compared to females with a single infant. The adoptive female showed more instances of social bridging. Although the duration of post-bridging grooming received from group members decreased, the frequency of such grooming increased. We discuss this adoption with reference to possible factors involved in the evolution of adoption and allonursing behavior in Tibetan macaques.

Keywords *Macaca thibetana* · Allomaternal care · Allonursing · Activity budget

Introduction

Allomaternal care has been defined as parental care by individuals other than the biological mother. It has been reported in many mammals including carnivores (MacLeod 2015), bats (Wilkinson 1992), ungulates (Zlizer et al. 2020), rodents (Ferrari et al. 2015), and nonhuman primates (Anand et al. 2022). Allomaternal care plays an important role in maximizing reproductive output and infant survival (Xiang et al. 2019, 2023; Ishizuka 2020; Guo et al. 2022; Anand et al. 2022; Tokuyama et al. 2021).

Adoption is one of important form for allomaternal care (Roulin and Heeb 1999). It has been reported in multiple primate species including wild bonnet macaques (*Macaca*

radiata; Anand et al. 2022), Japanese macaques (*Macaca fuscata*; Ishizuka 2020), black and gold howler monkeys (*Alouatta caraya*, Pavé et al. 2010), black-fronted titi monkeys (*Callicebus nigrifrons*, Cäsar and Young 2008), free-ranging red howler monkeys (*Alouatta seniculus*, Agoramorthy and Rudran 1992), and captive rhesus monkey (*Macaca mulatta*; Wood et al. 2021). Studies have shown that adoption can provide substantial benefits to newborn infants in terms of growth and survival in the absence of the newborn’s infant’s biological mother (either disappeared or died, Guo et al. 2022; Ishizuka 2020; Anand et al. 2022; Xiang et al. 2019). The attributes of adoptive individuals may be diverse; for example, adopters may be male or female, immature, mature, or old, and genetically related to adoptees or not. Some adoptive individuals had no newborn infant of their own, and some lasted for a relatively short time (e.g., *Macaca mulatta*, Guo et al. 2022; *Colobus guereza*, Raboin et al. 2021; *Macaca fuscata*, Ishizuka 2020).

An adoptive female currently lactating might provide milk for another female’s newborn (allonursing, Packer et al. 1992; Roulin 2002). Allonursing has been reported in a relatively small number of nonhuman primates (25 species, Packer et al. 1992; Roulin 2002; Hewlett and Winn

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2014; but see Sargeant et al. 2015), and incidence varies from occasionally, to over 10% of total nursing bouts in some species (Packer et al. 1992; but see Sargeant et al. 2015), especially when the infants' mother disappeared prior to weaning. For example, pregnant adoptive females have been reported to nurse other infants for short durations (e.g., 6 days in Nakamichi et al 2010, 29 days in Ishizuka et al. 2020, 44 days in Tanaka 2004).

Here, we report a case of adoption of a newborn infant by a mother with her own infant in Tibetan macaques (*Macaca thibetana*). We observed the adoptive mother nursing adopted infant (allonursing) for the first time in this species. These monkeys live in multi-male, multi-female groups with female philopatry and male dispersal. They are seasonal breeders and normally produce single offspring in the birth season from January to April (Li et al. 2005), but with occasional twins (Xia et al. 2012a, b). This case provided a natural experiment to investigate coping by a female with the heavier burden of caring for both her biological infant and another female's infant compared to the mothers caring for only a single infant. We predicted that the adoptive female would forage and rest more, and socialize less than females with single infants, to conserve energy (prediction 1). We also predicted that the adoptive female would engage in more affiliative interactions by social bridging (a social behavior involving two adults and one infant to strengthen dyadic affiliative relationships between the adults, Jiang et al. 2018) and that she would be groomed more frequently after social bridging, compared to single-infant mothers (prediction 2).

Method

Study site and subjects

The study was conducted at the Mt. Huangshan National Reserve in Anhui Province, China. The study group was the Yulinkeng A1 group (YA1 group). It was provisioned daily with 3–4 kg of corn by reserve staff to maintain their presence at designated tourist-viewing sites between 2004 and 2014, and thus it is habituated to humans (i.e., tolerating proximity < 1 m). In 2015, the tourist-viewing sites were closed, but the group is still provisioned as before. After feeding, the monkeys continue their natural and undisturbed activities in the forest. Demographic data on this population have been collected on a daily basis since 1983, and matrilineal kin relationships are known for all female members of the study group (Li et al. 2020). All members are individually recognizable based on distinctive physical features (e.g., scars, hair color patterns, and facial/body features). During the study period, the YA1 group contained up to 15 adult males (of which 9 immigrated, 1 emigrated to the

YA1 group, and 2 died), 14 adult females, 25 juveniles, and 9 newborn infants (6 males and 3 females). More details of infants can be found in Table 1.

Behavioral data collection

We collected behavioral data from March to June 2022 (55 days in total, mean \pm SE: 13.67 \pm 1.52 days/month; range: 12–15). Following the protocol used by Xia et al. (2012a, b), we followed the group from dawn to dusk, with observations beginning at approximately 07:00–08:00 and ending at 17:00–18:00 each day, depending on the time of year. We collected data from a distance of 5–10 m. We used a digital video camera (model: SONY HDR-CX680) to record the activity of the monkeys.

We used the focal animal sampling and continuous recording to collect data on daily behaviors of all females with infants (data from nine females with infants were used for analysis), including foraging, resting, and social activity. Each focal sampling period was set at 10 min. If the focal monkey could not be followed or was lost from view during the sampling period, another individual was randomly selected (Li et al. 2020). An effort was made to locate and record the behavior of the lost individual during the next 20 min sampling period. Focal sampling yielded a total of 25.18 h of data (mean \pm SE: 2.80 \pm 0.64 h; n = 9; range: 1.32–4.27 total h per monkey).

We defined foraging as behaviors that included ingesting, manipulating or inspecting, or chewing food (Xiang et al. 2010). Resting was defined as remaining stationary, either alone or in proximity to others (Xiang et al. 2010). We classified as social activity behaviors that involved two or more individuals in interactions (excluding agonistic interactions, such as grooming and bridging (Xia et al. 2012a,

Table 1 Information of newborn infants during the study period

Infant ID	Sex	Birth date	Infant's mother		
			ID	Age class	Birth experience
YXH	Male	2022-03-20	YH	Old	Multiparous
YXA	Female	2022-04-30	YCY	Middle adult	Multiparous
YQF	Male	2022-04-25	YXY	Yong adult	Multiparous
TXL	Male	2022-03-03	TH	Old	Multiparous
TQR	Female	2022-04-25	TXX	Middle adult	Multiparous
TDQ	Male	2022-02c20	TQL	Yong adult	Multiparous
TFR	Female	2022-02-27	THY	Middle adult	Multiparous
TFA	Male	2022-04-11	THX	Middle adult	Multiparous
TDD	Male	2022-04-11	TQY	Yong adult	Primiparous

b). We defined bridging as two individuals simultaneously holding or picking up an infant, one pulling on the infant's shoulder, the other pulling its hip upwards, resulting in the infant lying on its back, forming a "bridge" between them (Ogawa 1995; Li et al. 2020). One or both individuals often sucked or touched the infant's penis or genital area while teeth-chattering (Ogawa 1995; Li et al. 2020). We classified grooming as any act in which an individual (groomer) used their hand or mouth to touch, clean, or manipulate the fur of another individual (groomee) for a continuous period of at least 5 s (Berman et al. 2008; Xia et al. 2012a, b).

Data analysis

Data are reported as means \pm SE for the percentage of foraging, resting, and social activity. We calculated the frequency of bridging and post-bridging grooming received as times/h. We calculated the duration of post-bridging grooming received as min/h.

We used a χ^2 test to analyze differences in the adoptive mother's care behaviors toward her biological infant and adopted infant. Following Xia et al. (2012a, b), differences in activity budget (i.e., foraging, resting and social behavior) of the adoptive female and adult females with a single infant were determined by calculating 95% confidence intervals around the means of females with a single infant, and comparing the mean of adoptive female with these. When using confidence intervals, a significant difference is shown when the mean of one group (in this case, the mean of the adoptive female, TQL) falls outside the confidence interval(s) of the other group(s). We used the same to determine differences in bridging engaged in by the adoptive female, females with a single male infant, and females with a single female infant, and to assess differences in grooming after bridging engaged in by adoptive female and adult females with a single infant.

Results

Kidnapping and adoption of a 3-week-old infant by a Tibetan macaque mother

Background: TQL, a young multiparous female in the study group, was born in March 2013. She gave birth in June 2020 (TDY, male) and again in February 2022 (TDQ, male). TH, an old multiparous female, was born in 2003. She gave birth in March 2008 (TXX, female) and 2009 (TXHa, female), June 2011 (TXHu, male), 2012 (TXLo, male) and 2014 (TXF, male), August 2017 (TXJ, male), February 2019 (TXD, female), April 2020 (TXC, male), and March 2022 (TXL, male). TH is TQL's grandmother, but her social rank was lower than TQL. During the study period, TXL (TH's son) was born on March 03, 2022.

The kidnapping took place on March 30, when TXL was 27 days old. TQL with her own infant adopted TH's newborn offspring TXL.

Observation: On March 30 2022, TQL carried and fed her 1-month-old infant, TDQ. TQL approached TH and tried to bridge with her, using TXL three times. However, TH refused each time by turning away, keeping hold of TXL, or blocking with her arms. Suddenly, TQL attacked TH, grabbing and biting her. During the agonistic episode, which lasted 28 s, TQL snatched TXL away from his mother TH, and this kidnapping developed into an adoption (see Fig. 1 left), with TQL caring for the adopted infant and her biological infant simultaneously. At the time of writing (May 23, 2023), both infants were alive, as is TH (personal observation by author SWC). Following the kidnapping/adoption, no behavioral interactions were observed between TXL and his biological mother, although the latter was frequently in proximity to TQL (see Fig. 1 right); nor did TH make any clear attempt to retrieve her infant from the higher-ranking TQL.



Fig. 1 Spontaneous adoption by lactating female. Left: Two infant sucking at the same time; right: TH grooms adoptive female

Care behaviors of the adoptive female toward the two infants

TQL's care behaviors toward her biological infant (nursing: 47.8%; hugging: 14%; carrying: 16%; restraint: 3%; grooming: 4.3%) did not differ significantly from those toward the adopted infant (nursing: 35.19%; hugging: 15%; carrying: 10.8%; restraint: 5.66%; grooming: 1.44%, $\chi^2 = 3.776$, $df = 4$, $P > 0.05$).

Activity budgets of the adoptive female

The adoptive female (TQL) spent a higher proportion of time foraging (0.31) and resting (0.35) than females nursing a single infant (foraging 0.24 ± 0.015 ; resting 0.31 ± 0.01) ($P < 0.05$). In contrast, TQL spent a lower proportion of time engaging in social activity (0.08) than females with single infant (social activity 0.13 ± 0.015 , $P < 0.05$, Fig. 2).

Infant facilitated affiliative relationships of adoptive female

As shown in Fig. 3, TQL engaged in a higher frequency of social bridging (6.89) than females with a single male infant (2.92 ± 0.249) and those with a single female infant (0.54 ± 0.292 , $P < 0.05$). She also received shorter-duration (1.32) but higher-frequency (1.33) of social grooming after social bridging than single-infant females (duration: 2.57 ± 0.502 , $P < 0.05$, frequency: 0.62 ± 0.137 , $P < 0.05$, Fig. 4).

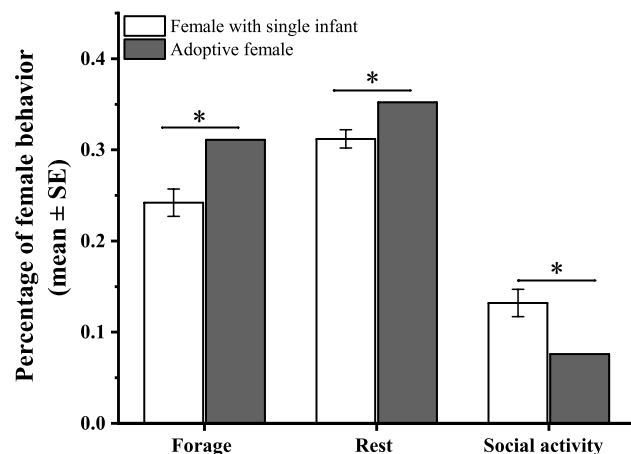


Fig. 2 Activity budgets of adoptive female and females with single infant. Histogram with white background represents activity budget for females with single infant. Histogram with gray background represents activity budget for adoptive female

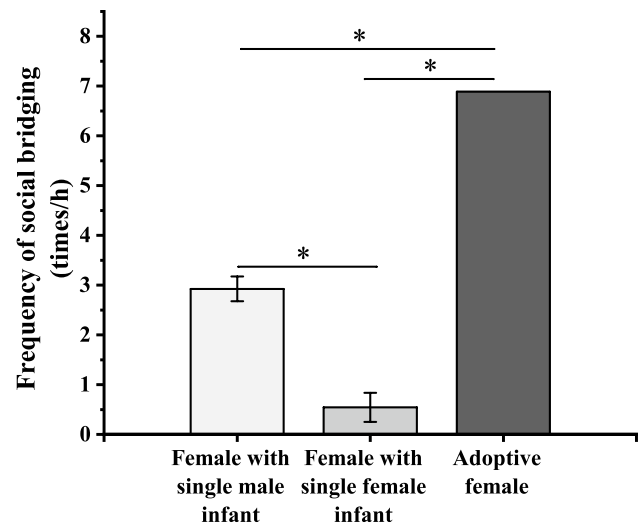


Fig. 3 Frequency of social bridging between adoptive female and females with a single infant (either a male infant or a female infant)

Discussion

To our knowledge, this is the first report of kidnapping resulting in adoption and allonursing in free-ranging Tibetan macaques. A lactating female (TQL, carrying her own infant) kidnapped the infant of her grandmother and adopted it, nursing and caring for two infants simultaneously. Behavioral data showed that after taking on the additional infant her social activity decreased (Prediction 1 was supported), whereas her social bridging and frequency of being groomed after social bridging increased (Prediction 2 was supported), compared to the females with a single infant.

Our observations indicate that in Tibetan macaques a young infant can be successfully adopted by a lactating female even when its biological mother still lives in the group. Adoption following the loss of an infant's biological mother has been reported in captive and free ranging *Macaca mulatta* (Guo et al. 2022), *Macaca fuscata* (Ishizuka 2020), and *Macaca radiata* (Anand et al. 2022). In those cases, the adopter had no newborn infant of their own or did not provide long-term intensive care. By contrast, pregnant females may adopt and nurse other infants for a short duration before giving birth to their own infant or when the adopted infant's mother disappeared before weaning age, as in Japanese macaques (*Macaca fuscata*, Nakamichi et al. 2010; Ishizuka 2020; Tanaka 2004), Yunnan snub-nosed monkeys (*Rhinopithecus bieti*, Ren et al. 2012), and red howler monkeys (*Alouatta seniculus*, Agoramoorthy and Rudran 1992). In wild *Rhinopithecus bieti*, females allow their infant to be held frequently and carried for long durations by other members of the group (Ren et al. 2012). In a case in free-ranging *Colobus angolensis palliatus*, the adoptive female's biological infant died one

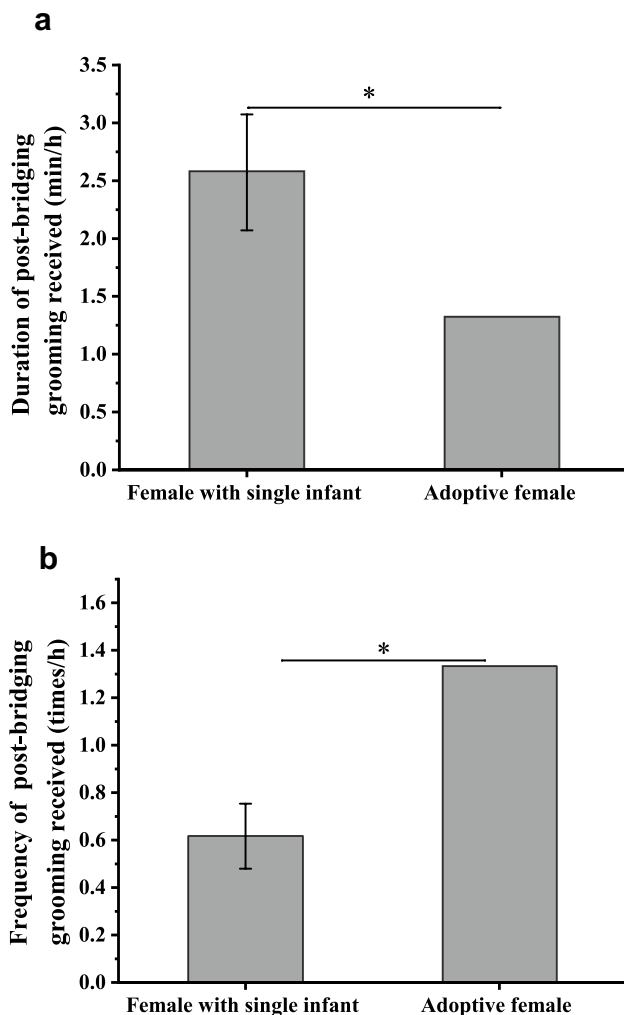


Fig. 4 The difference of post-bridging grooming received duration (left) and frequency (right) of adoptive female and females with single infant. Female with single infant ($n = 7$), adoptive female ($n = 1$)

month after the mother adopted another infant (Dunham and Opere 2016). In the present, rare case, that lactating female adopted an infant and successfully nursed both her own infant and another female's infant simultaneously, in a species in which females are restrict access to their own newborn infants.

Taking on another infants leads to an increased burden for adoptive females. Tibetan macaques in the same study site have produced and successfully raised twins (Xia et al. 2012a, b). It might be argued that the additional food provided to this group through provisioning compensates for the increased costs of raising twins, adoption and allonursing. Our data support the view that females can adapt their activity budget to cope with the increasing burden (prediction 1: the adoptive female showed increased foraging and resting, and decreased social activity compared to females with a single infant).

The question remains: what might be the benefit to the female who increased her maternal burden by kidnapping and nursing a second infant? A potential explanation is that allonursing would invoke reciprocal altruism (see Trivers, 1971; West Eberhard, 1975), with the adoptee providing future social support for the adopter (see reviews in Thierry and Anderson 1986). Lactating females are known to socialize less with other group members (e.g., *Macaca mulatta*, Dunayer et al. 2017; *Macaca thibetana*, Jiang et al. 2018), suggesting that the social value of an infant might depend on the number of newborn infants in the group. Although her overall social activity decreased, the adoptive Tibetan macaque female's frequency of social bridging (a typical form of infant handling) and post-bridging grooming increased. In contrast to a case in wild bonobos (*Pan paniscus*) in which her relationships with other females weakened when a mother's infant died (Cheng et al. 2022), our results might suggest social benefits of having an increased number of infants. Further observations are required to confirm this possibility, and to clarify other reasons for intra-group kidnapping and long-term adoption of an additional infant.

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Data availability Social activity (adoptive female: 0.08, females with single infant: 0.13 ± 0.015 , $p < 0.05$); Social bridging (adoptive female: 6.89, females with single male infant: 2.92 ± 0.249 , females with single female infant: 0.54 ± 0.292 , $p < 0.05$); Post-bridging grooming (adoptive female: 1.33, females with single infant: 0.62 ± 0.137 , $p < 0.05$).

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