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Original Article

Adoptions of unrelated infants in wild Taihangshan macaques (*Macaca mulatta tcheliensis*), Jiyuan, north China

Mengya Han[a,b], Yanyan Zhou[a,b], Yuwei Wang[a,b], Tongtong Luo[a,b], Jundong Tian[a,b], and Jiqi Lu[a,b,*]

[a]School of Life Sciences, Zhengzhou University, No. 100 Kexue Road, Gaoxin District, Zhengzhou 450001, China
[b]Institute of Biodiversity and Ecology, Zhengzhou University, No. 100 Kexue Road, Gaoxin District, Zhengzhou 450001, China

[*]Address correspondence to Jiqi Lu. E-mail: lujq@zzu.edu.cn
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Abstract

Infant-care behavior, a range of caring behaviors by parental or alloparental individuals towards infants unable to live independently, plays a significant role in the survival of infants and the continuation of the species in non-human primates. During a behavioral ecological study of Taihangshan macaques, we observed 2 cases of infant adoptions by unrelated adult females. In case 1, a multiparous female adopted a lost infant from a neighboring group, with the infant being snatched back by her biological mother 35 days after the adoption. This is the first report of cross-group adoption in *Macaca*. In case 2, a nulliparous adult female, who had been once adopted by her elder sister, adopted an orphan from her group for 36 days. We describe the details of adoptions in Taihangshan macaques and explore possible reasons for adoptions to contribute to understanding the evolution of infant-care behavior and altruistic behavior of adoption in primates.

Key words: adoption, altruism, female, learning to mother, Taihangshan macaque (*Macaca mulatta tcheliensis*).

Adoption, the primary care (nursing, carrying, grooming, cradling, and protection) of orphaned or abandoned infants for an extended period by allomaternal individuals, is a specific and costly type of alloparental behavior (Thierry and Anderson 1986; Tokuyama et al. 2021). This behavior has been reported in several wild and captive non-human primates (NHPs) (Thierry and Anderson 1986; Maestripieri 2001; Rossi et al. 2020; Anand et al. 2022). Although there are published cases of adult males, subadults, and juveniles adopting weaned infants and young juveniles (Hrdy 1976; Gould 2000; Boesch et al. 2010), adult females often perform the role of adopters, caring for more dependent infants by carrying, grooming, and nursing (Thierry and Anderson 1986).

NHPs usually form stable groups and use visual, auditory, and olfactory cues to recognize group members from out-group individuals (Rendall et al. 1996; Murai et al. 2011; Habbershon et al. 2013; Briseño-Jaramillo et al. 2014; Henkel et al. 2015). Amongst the published works, most cases of adoption behavior in NHPs have been observed within groups (Thierry and Anderson 1986; Wroblewski 2008; Chaves et al. 2020; Anand et al. 2022). Adoptions of out-group infants by NHPs have been reported only in 4 species: red howler monkeys (*Alouatta arctoidea*) (Agoramoorthy and Rudran 1992), black-fronted titi monkeys (*Callicebus nigrifrons*) (Casar and Young 2008), Angolan black and white colobus monkeys (*Colobus angolensis palliates*) (Dunham and Opere 2016), and bonobos (*Pan paniscus*) (Tokuyama et al. 2021). Apart from reports of wild capuchin monkeys (*Cebus libidinosus*) (Izar et al. 2006) and captive spider monkeys (*Ateles geoffroyi*) (Estrada 1982), cases of cross-species adoption are much rarer in NHPs.

Researchers have proposed several theories to explain adoption behavior based on analysis of behavioral costs, benefits, and motivations (Thierry and Anderson 1986; Gould 2000; Boesch et al. 2010; Tokuyama et al. 2021; Anand et al. 2022). Several adaptive explanations include 1) Kin selection theory (Hamilton 1964): Adopters will direct altruistic behavior (including adoption) toward related infants, enhancing their survival chances and increasing their own inclusive fitness (Eberhard 1975; Thierry and Anderson 1986). For example, in wild populations of Taihangshan macaques (*Macaca mulatta tcheliensis*), an orphan was adopted by her sister (Guo et al. 2023); 2) "Learning to mother" hypothesis (Lancaster 1971): This hypothesis applies to adoption by juvenile or nulliparous females, that is, females without reproductive experiences may learn the skills necessary for raising infants by adopting someone else's infants, which provides them with experience in maternal behavior, and thereby improves their reproductive success in the future (Hrdy 1976; Riedman 1982). For example, in vervet monkeys (*Cercopithecus aethiops*), females with more experience in caring for and carrying infants during adolescence ultimately had higher survival rates of their firstborn offspring (Fairbanks 1990); 3) Reciprocal altruism (Anand et al. 2022): Adoptions independent of kin relationships can be considered reciprocal altruism (Silk 1990; Boesch et al. 2010; Xu et al. 2014; Franklin and Volk 2016).

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Adopters can also benefit from adopting unrelated individuals, for example, having an adoptee may increase their reputation within the group (Riedman 1982; Thierry and Anderson 1986; Silk 1987; Fehr and Fischbacher 2003; Goody 2021) and improve their existing social relationships within the group (Tokuyama et al. 2021), and the adoptee may become a future social ally (Boesch et al. 2010; Tokuyama et al. 2021); 4) Preexisting social bonds (Tokuyama et al. 2021; Anand et al. 2022): When an orphan has no close maternal relatives in its group, it is usually adopted by an unrelated individual with close social bonds to the deceased mother (Boesch et al. 2010; Samuni et al. 2019). For example, in wild bonnet macaques (*M. radiata*), adoptions were facilitated by preexisting social bonds of the deceased mother (Anand et al. 2022). Adoption may also be considered non-adaptive, indicating that the adopters are drawn to the infants and have a strong interest in them (Quiatt 1979; Riedman 1982; Thierry and Anderson 1986; Clutton-Brock 1991).

The Taihangshan macaque (*Macaca mulatta thceliensis*) is a subspecies of rhesus macaque endemic to China, with their wild populations currently distributed only in the southern Mt. Taihangshan area, north China (Lu et al. 2007; Lu 2020). During field investigations on their behavioral ecology, we observed 2 cases of infant adoptions by unrelated adult females. We report those cases here. We aim to enrich the understanding of the social ecology of Taihangshan macaques and increase the knowledge of NHPs behavioral ecology.

Materials and Methods

Study site

The study site is located in the Wulongkou area (35°12′49″ N, 112°41′25″ E) of the Taihangshan Macaque National Nature Reserve (TMNNR) (34°54′–35°42′ N, 112°02′–113°45′ E), Jiyuan, north China (Song and Qu 1996; Lu et al. 2007; Tian et al. 2017). This area is characterized by a highly seasonal pattern of temperature and rainfall, resulting in hot and wet summers and dry and cold winters, with an average annual temperature of 14.3 °C and an annual precipitation of 695 mm (Hu et al. 2004; Guo et al. 2020).

Target group

There were 5 groups of Taihangshan macaques inhabiting the Wulongkou area, named WLK-1A, WLK-1B, WLK-2, WLK-3, and WLK-4. Troops WLK-1A and WLK-1B were the 2 groups generated by the 2017 fission of the previous Troop WLK-1. Taihangshan macaques in this area have free access to natural food resources (e.g., young plant leaves, buds, and wild fruits) and a small supplementary diet consisting of maize, wheat, peanuts, and carrots (Guo et al. 2020). Like many species of macaques, Taihangshan macaques are strictly seasonal breeders, with the mating period from September to December and the parturition period from March to June (Tian et al. 2013; Lu 2020).

Troop WLK-1A consisted of 9 adult males, 34 adult females, 2 subadults, 24 juveniles, and 14 infants. All individuals in this group were identified and named according to their morphological characteristics (length and color of body coat and body scars) and behavioral traits (aggressiveness and degree of activeness) (Tian et al. 2011). During a behavioral ecological study on Troop WLK-1A from September 2021 to July 2023, 2 cases of infant adoptions by unrelated adult females were observed, and we recorded the details of this rare behavior.

Behavioral observations and genetic analyses

On 4 July 2022, an unfamiliar infant (named JX) occurred in Troop WLK-1A and was subsequently adopted by HM, a multiparous female within the group. On 12 February 2023, a 9-month-old male infant GG from Troop WLK-1A was adopted by QB, a nulliparous female within the group. In both cases, we recorded the maternal behaviors that the adoptive mothers provided to the adoptees, such as carrying, grooming, and cradling, using focal animal sampling (Altmann 1974), and the social interactions between the adoptees and group members other than their adoptive mothers ad libitum.

To identify the genetic relationship between adoptive mothers and adoptees, we collected fecal samples of adoptive mothers, adoptees, biological mothers, and 23 other individuals (including 15 adult females and 8 adult males). We selected 10 microsatellite loci to genotype them (Guo 2021; Guo et al. 2023). Three independent PCRs were performed for each locus of each sample to eliminate microsatellite locus genotyping errors. Allele frequency analysis was performed via CERVUS 3.0 (Marshall et al. 1998; Kalinowski et al. 2007) based on all sampled individuals ($N = 29$) to calculate the number of different alleles, observed heterozygosity (H_o), expected heterozygosity (H_e), polymorphic information content (PIC), Hardy-Weinberg equilibrium (HWE), null allele frequency, and combined exclusion probability (CEP) of the 10 loci (Supplementary Table S1). Maternity analysis of adoptees was performed using CERVUS 3.0, with a reliable result when the calculated LOD value (the logarithm of the likelihood ratio) is positive with a confidence level of 80% or more. Furthermore, the relatedness values between adoptees and adopters were calculated by ML-Relate (Queller and Goodnight 1989; Kalinowski et al. 2006), with the theoretical value of 0.5 for parent-offspring/full-sibling kin-relationship, and 0.25 and 0.125 for second- and third-degree kin-relationship respectively (Blouin et al. 1996; de Ruiter and Geffen 1998; Bryant et al. 2016). In actual populations, the relatedness values calculated based on microsatellites usually fluctuate around the theoretical values, so in this study, the mean value of 0.1875 for the second-degree relatedness (0.25) and the third-degree relatedness (0.125) was used as the threshold for distinguishing between relatedness and unrelatedness (Blouin et al. 1996; Csilléry et al. 2006).

Results

Case 1

This adoption case occurred cross-group. HM, a multiparous female from Troop WLK-1A, adopted JX, an about 1-month-old female infant from the neighboring group (Troop WLK-3).

At 17:41 on 4 July 2022, an unfamiliar female infant JX was first seen in Troop WLK-1A. Since newborn infants of this group in 2022 were recorded, we concluded that JX was not born in this group and presumed that she might be from a neighboring group and wandered off and then came to our study group. A review of previous video recordings for other groups revealed that JX had been present in Troop WLK-1B on the morning of 4 July while she was tightly hugging the right hind leg of LMM, an adult female within the group (Figure 1A). LMM gave birth to a male infant on 3 May 2022 and displayed evasive behavior toward JX. When JX was first seen in the Troup WLK-1A at 17:41 on 4 July, she was resting in the arms of a subadult female XKA, and XKA was grooming her (Figure 1B). Subsequently,

Figure 1 Adoption of JX of Taihangshan macaque in Wulongkou area, Jiyuan, China. (A) JX hugging the right hind leg of LMM tightly, whose biological offspring (infant) was suckling from her; (B) XKA grooming JX on the left side of the picture, while XB grooming HM and SS grooming XH on the right side; (C) XB cradling JX; (D) XKA cradling JX while HM grooming SS on the right side; (E) JX suckling from HM; (F) An adult female JJ hugging JX; (G) HM carrying JX dorsally; (H) Biological mother JE holding JX tightly while JX howling and struggling in JE's arms; (I) JE holding her newborn infant JX on 1 June 2022; (J) JX resting in JE's arms while holding JE's nipple in her mouth; (K) Weak JX feeding; and (L) JE and deceased JX.

XKA's juvenile sister SS also groomed JX, whereas XKA' and SS' mother HM sat nearby and appeared unconcerned about JX. Afterward, an adult female XB and a juvenile female JT successively cradled or carried JX (Figure 1C). At 19:42, XKA and SS were seen cradling and playing with JX (Figure 1D). Meanwhile, HM was attracted to JX for the first time. HM inspected and cradled JX and then carried her to the sleeping site. HM had given birth to a male infant XH on 3 May 2021 but had not given birth in 2022. On 5 July, HM was seen cradling JX in her arms and has adopted JX since then. At 19:06 on 7 July, JX was observed suckling from HM (Figure 1E).

The following month, HM was JX's primary caregiver, showing maternal behaviors such as nursing, cradling, examination, carrying, grooming, and protecting, which made JX have good physical health and mental state. Meanwhile, group members other than the adoptive mother also tolerated JX's presence. JX was frequently observed playing with other infants within the group, and most adult, subadult, and juvenile females, including the α-female, displayed allomaternal care such as inspecting, cradling, smelling, touching, and grooming JX (Figure 1F). No males within the group were observed to show allomaternal care (male-infant care) toward JX, and group members were rarely observed to attack JX. Notably, on 9 July, the α-female XT was observed cradling JX, while JX was suckling from her. However, JX was not tolerated by XT for too long before being pushed away from her and was then carried away by HM.

On the morning of 8 August, HM was still seen cradling, carrying, nursing, and grooming JX (Figure 1G). At 18:56, Troops WLK-1A and WLK-3 were foraging in the same area with light rain falling. Suddenly, JE, an adult female from Troop WLK-3, with the help of 2 other females, snatched JX in the bordering area between the 2 groups. As JX howled, HM immediately rushed to scramble for her, but JE quickly ran back to her group with JX in her arms, which initiated a fierce fight between the 2 groups. JX howled and struggled in JE's arms, trying to get back to HM, but JE consistently pulled and tugged on JX, making it difficult for her to escape (Figure 1H). HM looked at the snatched JX and let out a growl. Eventually, JE carried JX away with her group and disappeared into the rainy night. A review of the newborn infants' birth records for Troop WLK-3 in 2022 revealed that JE had given birth to a female infant on 1 June (Figure 1I).

Based on the above-mentioned observations, we suspected that JX was JE's biological offspring, and she was lost to Troop WLK-1A and then adopted by HM. The results of maternity analysis showed that the LOD and Δ values between JX and JE were both positive with a confidence level of 95%, whereas the LOD value between JX and HM was negative (Table 1). Furthermore, the relatedness value between JX and JE was 0.5000, while that between JX and HM was 0.1656 and less than the threshold (0.1875) for distinguishing between relatedness and unrelatedness (Table 2). These results demonstrated that JX was the biological offspring of JE, and HM was unrelated to JX.

Table 1. The results of maternity analysis

Offspring	Candidate mother	Pair loci compared	Pair loci mismatching	Pair LOD score	Pair Delta (Δ)	Pair confidence
JX	JE	10	0	4.82	4.50	*
JX	HM	10	4	−13.10	0.00	
GG	HH	10	0	4.41	4.41	*
GG	QB	10	4	−12.42	0.00	

Note: * means Pair LOD score is significant with a 95% confidence interval.

Table 2. The pairwise relatedness of individuals

Offspring	Candidate mother	Relatedness
JX	JE	0.5000
JX	HM	0.1656
GG	HH	0.5000
GG	QB	0.1157

Note: The mean value of 0.1875 for the second-degree relatedness (0.25) and the third-degree relatedness (0.125) was used as the threshold for distinguishing between relatedness and unrelatedness.

On 9 August, we located and followed up Troop WLK-3, observing JX resting in JE's arms all day and occasionally holding JE's nipple (Figure 1J). On 10 August, JX was in a poor mental state, while JE still held JX tightly and restricted her free movement until 11 August. Over the next 2 days, JX was observed to be thin and weak, slow-moving, with a different status from other infants. JX had been struggling to feed, and she would break away and continue to feed when JE and other individuals cradled her (Figure 1K). During the following more than 1 month, JX continued to get weaker. At 18:00 on 4 October, we found JX dead (Figure 1L). JE carried the carcass of JX for 3 days before abandoning her. Afterward, HM gave birth to a male infant on 2 April 2023, and JE gave birth to a female infant on 9 May 2023.

Case 2

This adoption case occurred within Troop WLK-1A. QB, a nulliparous and 5-year-old adult female, adopted orphans XHH and GG on 12 February 2023. The 2 orphans were brothers, with XHH about 1 year and 9 months old and GG about 9 months old.

HH, the mother of XHH and GG, died on 12 February 2023 due to poor health (Figure 2A). XHH and GG were then temporarily cared for by QB (Figure 2B). XHH also died a few days later due to his poor health. After continued observation, we were certain QB adopted GG (Figure 2C). During the adoption, QB was the primary caregiver of GG, and the main maternal behaviors included cradling, grooming, carrying, protecting, and sharing food (Figure 2D; Figure 2E). A juvenile female XLB and QB's elder sister PP were also sometimes observed cradling and grooming GG. However, GG died on 20 March 2023 due to continued deterioration in his health (Figure 2F). QB carried the carcass of GG for 2 days before abandoning him.

The results of maternity analysis showed that the LOD and Δ values between GG and HH were both positive with a confidence level of 95%, whereas the LOD value between GG and QB was negative (Table 1). Furthermore, the relatedness value between GG and HH was 0.5000, while that between GG and QB was 0.1157 and less than the threshold (0.1875) for distinguishing between relatedness and unrelatedness (Table 2). These results showed that GG was the biological offspring of HH and QB was unrelated to GG.

Discussion

This study is the first report of 2 cases of infant adoptions by unrelated adult females in wild Taihangshan macaques. Case 1 was the adoption of an approximately 1-month-old female infant from Troop WLK-3 by a multiparous female from Troop WLK-1A, the first reported cross-group adoption in *Macaca*. Case 2 was the adoption of an approximately 9-month-old orphaned male by a nulliparous adult female in Troop WLK-1A. The adopter of case 2 was once an adoptee in our previous report (Guo et al. 2023).

It is usually assumed that adoption, especially cross-group adoption, is likely to occur in species with high social tolerance (Anand et al. 2022). The activity ranges of the 5 groups in our study site overlap, and groups may meet each other sometimes, but Taihangshan macaques, as a group-living animal, have a strong sense of territoriality, and there is a clear line of demarcation between groups. Moreover, among *Macaca* species, rhesus macaque (*M. mulatta*) is categorized into the least tolerant clade among the 4-grade scale clades regarding social tolerance (Thierry 2022). Since rhesus macaques could recognize group and out-group members via olfactory cues alone (Henkel et al. 2015), the adult female HM in case 1 likely recognized that JX was from another group but ultimately adopted her, and group members also accepted her presence. Our results provide evidence for higher social tolerance of out-group immature individuals in Taihangshan macaques than is expected based on the species' social style.

In Taihangshan macaques, the weaning process for infants begins at 3 months of age and is completed by 7–14 months of age (Guo et al. 2023). Thus, in case 1, JX, about 1 month-old, could not survive unless she was adopted. The final adopter, HM, initially showed no interest in JX, but rather, XKA and SS, HM's offspring, and other females within the group exhibited the most infant care. Similar phenomena have been observed in chimpanzees (*P. troglodytes*) (Thunstrom et al. 2013). This suggests that the final adopter does not necessarily show maternal interest initially and that there can be flexibility in maternal behavior in adult female Taihangshan macaques. Maternal behaviors, such as nursing, cradling, examination, carrying, grooming, and protecting, were provided to JX during the adoption by HM. Because HM's offspring born in 2021 was approximately 14 months old and not fully weaned before adopting JX, she still had milk available to nurse JX. JX's good health during the adoption

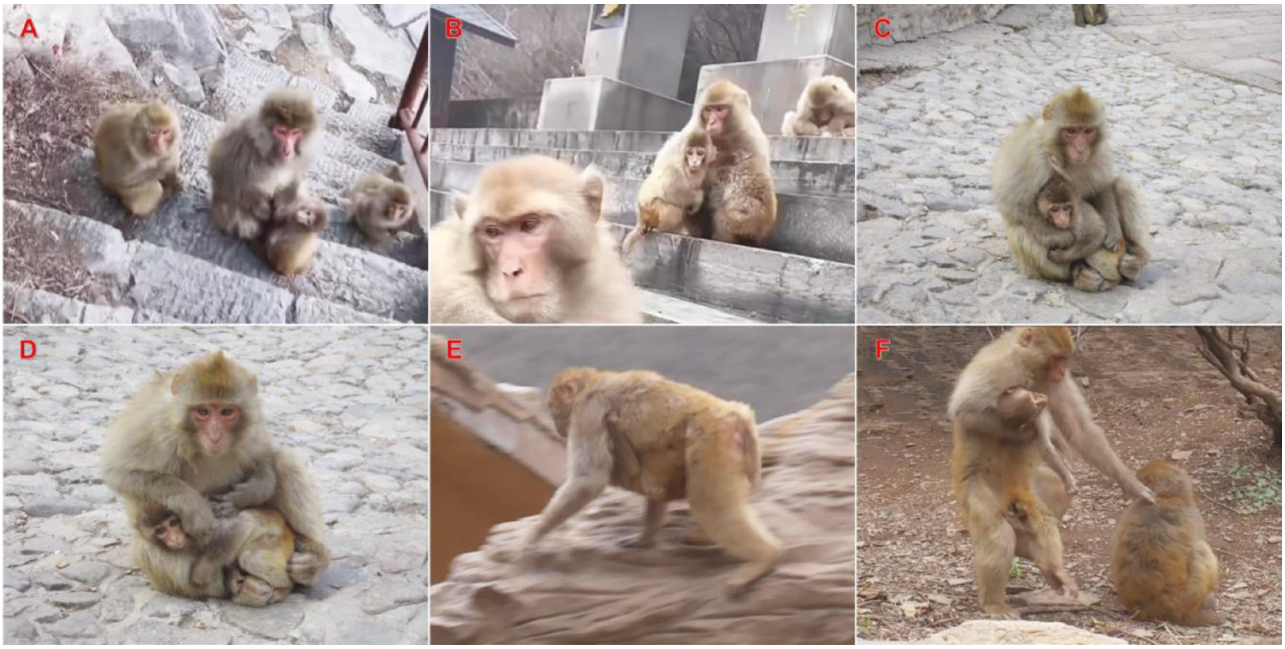

Figure 2 Adoption of GG of Taihangshan macaque in Wulongkou area, Jiyuan, China. (A) GG (second from right), his weak mother HH (second from left), his elder brother XHH (first from right), and the nulliparous adult female QB (first from left) resting together before the death of HH; (B) QB hugging GG and XHH; (C) QB hugging GG; (D) QB grooming GG; (E) QB carrying GG ventrally; (F) QB carrying deceased GG.

reinforces the fact that HM could indeed provide adequate and nutritious milk for JX. But after being snatched back by JE, her biological mother, JX's health deteriorated, and she eventually died of weakness and malnutrition, despite often holding JE's nipple in her mouth or endeavoring to feed on her own. We suggest that JE, the biological mother, had no milk available and that JX's nipple contact may only have occurred to seek comfort (comfort nursing), not obtain milk (Bădescu et al. 2016; Tokuyama et al. 2021).

In case 2, QB, the adoptive mother, as a nulliparous female, showed caring behaviors, such as cradling, grooming, carrying, protecting, and sharing food, toward GG, the adoptee. GG was about 9 months old and could feed himself without being totally dependent on milk. His brother XHH and mother HH all died because of poor health, and he was also in poor health before being adopted. His health continued to deteriorate during the adoption, and he eventually died after 36 days of adoption.

Regular allomaternal nursing has been reported in several platyrrhine monkeys (O'Brien and Robinson 1991; Williams et al. 2005; Baldovino and Di Bitetti 2007; Sargeant et al. 2015), colobine monkeys (Xiang et al. 2019), and some human societies (Hewlett and Winn 2014), but it is not common in cercopithecin monkeys. In case 1, we observed XT, a lactating α-female, cradling JX but pushing her away when JX suckled from her. This phenomenon has been reported in other populations of rhesus macaques, where caregivers usually do not tolerate sucking behavior by alien offspring for too long (Breuggeman 1973). A possible explanation for allomaternal nursing behavior, that is, a lactating female nursing an alien offspring, is the misdirected parental care hypothesis, whereby lactating females inadvertently nurse the alien offspring because they do not notice that allosucklers are not their own, or because allosucklers steal their milk (Roulin 2002). It was observed in this case that the allomaternal nursing behavior could be "milk theft" by JX, as the behavior was stopped immediately upon detection by XT, who refused to allow JX to nurse.

Published works demonstrated that primate mothers can recognize their offspring by visual, olfactory, or vocal cues from a few hours after delivery to 3 to 4 weeks postpartum (Maestripieri 2001). In case 1, JX was snatched back by JE, her biological mother, 35 days after adoption, indicating that female Taihangshan macaques can still accurately recognize their offspring 35 days after separation from them. However, after being snatched back by JE, JX howled and struggled incessantly. This seems to indicate that JX was already unfamiliar with her biological mother or that JX's recognition skills had not fully developed because of her young age when separated from her biological mother.

Kin selection is the primary mechanism for the evolution of adoption behavior (Eberhard 1975; Riedman 1982; Thierry and Anderson 1986). Our genetic analyses showed that the adoptive mothers were unrelated to the adoptees in both cases. Thus, kin selection theory does not seem to explain the 2 observed cases of adoptions in Taihangshan macaques. *Macaca* species, including Taihangshan macaque, exhibit multi-male and multi-female social structure based on matrilineal units, with males leaving the group when they reach sexual maturity and females remaining in the group throughout their lives and forming matrilineal units with their matrilineal relatives (Lu 2020). Guo et al. (2023) reported the case of an orphaned Taihangshan macaque adopted by her elder sister. Thus, adoption behaviors may take different forms even in the same species, which requires attention in future studies.

The "Learning to mother" hypothesis applies to juvenile or nulliparous females, that is, juvenile or nulliparous females can gain valuable infant-care experience before giving birth to their own offspring (Lancaster 1971). In case 2, QB had been involved in mating activity for the first time in the winter of 2021 and became pregnant, but aborted on 26 April 2022, so QB, the adoptive mother, was a nulliparous female.

Therefore, we suggest that QB adopted the unrelated orphan within the group most likely to gain infant-care experience and thus improve the survival rate of her firstborn offspring. In addition, QB had been an orphan at 6 months of age and was adopted by her elder sister PP (Guo et al. 2023), and she initiated allomaternal care more frequently towards infants within the group compared to other nulliparous females of near age (personal observation, unpublished data). Whether the early experience of being adopted leads to a stronger desire to initiate allomaternal care or even adopt infants compared to other individuals needs to be explored by adding more cases and then conducting a detailed and systematic study.

Infant adoptions by unrelated individuals may be a form of reciprocal altruism (Boesch et al. 2010; Anand et al. 2022). Adoptees can benefit from the provision of carrying, grooming, emotional support, and social learning opportunities by their adoptive mothers (Tokuyama et al. 2021), while adopters may also benefit from adoption. Some researchers have found that primates, including humans, who adopted infants boost their reputation in the group (Riedman 1982; Thierry and Anderson 1986; Silk 1987; Fehr and Fischbacher 2003). In NHPs, young infants can easily attract the attention of other females (Alley 1980; Silk 1999; Boose et al. 2018), which may provide an opportunity for the adoptive mothers to strengthen social bonds with other females. In addition, the adoptee may become a future social ally of the adoptive mother. Boesch et al. (2010) suggested reciprocal altruism as a possible explanation for adoption in chimpanzees (*P. troglodytes verus*) at Taï National Park, Côte d'Ivoire. He argued that a long-term benefit of adopting male infants was that the males may grow up to be allies. In Taihangshan macaques' society based on matrilineal units, adoptive mothers adopt female infants, who will stay with adopters when they grow up and become close social allies. Therefore, in case 1, the adoptive mother may adopt the out-group female infant to gain a future social ally. Due to the death of the adoptee in case 1, the question of whether the adoptive mother will benefit from adoption and topics related to reciprocal altruism are subject to future data accumulation.

Preexisting social bonds can be also a proximate explanation for adoption (Tokuyama et al. 2021; Anand et al. 2022). In case 1, the adoptive mother and the adoptee belonged to different groups and thus had no preexisting social bonds. In case 2, although the adoptee's adoptive and biological mothers were in the same group, we observed that the biological mother belonged to a different matrilineal unit from the adoptive mother during her lifetime and had little social interaction with the adoptive mother. Therefore, preexisting social bonds is an unlikely explanation for the 2 adoption cases in our study.

In some cases, adoption may also be a manifestation of a strong interest in the infants due to their attractiveness, that is, adoption is altruistically and emotionally driven and cannot be explained solely in terms of the benefits gained by the adoptive mother. For example, in humans, chimpanzees, and bonobos, it has been found that adoption behavior may be provoked by adopters' emotions, altruism, and strong attraction to infants (Silk 1990; Boesch et al. 2010; Franklin and Volk 2016; Samuni et al. 2019; Tokuyama et al. 2021). Therefore, we argue that the cross-group adoption in case 1 may also stem wholly or partially from the adopter's strong attraction to the infant, altruism, and high social tolerance for out-group immature individuals.

In summary, this study reported 2 cases of infant adoptions by unrelated adult females in Taihangshan macaques. The adoption behavior in case 1 may stem wholly or partially from the adopter's strong attraction to the infant, altruism, and high social tolerance for out-group immature individuals, and that in case 2 supports the "learning to mother" hypothesis. Our findings contribute to a deeper understanding of adoption and altruistic behavior in primates.

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Authors' Contributions

M.Y.H. contributed to behavior observations, data collection, data analysis, and manuscript writing. Y.Y.Z. contributed to data analysis and editing. Y.W.W. contributed to data analysis. T.T.L. contributed to data collection. J.D.T. provided valuable insights and suggestions on the manuscript. J.Q.L. was responsible for project design, project coordination, and manuscript communication.

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Conflict of Interest Statement

The authors declare no conflict of interest.

Ethics Statement

Data collection adhered to Chinese legal requirements and complied with protocols approved by the National Forestry and Grassland Administration, China. The project has been approved by all required state and local administration departments. Data collection did not affect the living conditions of the monkeys. This study has been approved by the Ethics Committee of Life Sciences of Zhengzhou University.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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