

# Do Foster Mothers from Socially Hierarchical Primate Species “Selfishly” Adopt Orphans?

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## Abstract

Adoption, a particular type of alloparental care in which primary caretaking of an infant is transferred to a previously unrelated adult, has been shown to increase the likelihood of infant survival. Alloparental care and adoption behavior have been analyzed in over 120 mammalian and 150 avian species and have been especially observed in 'K-selected' species, defined by long periods of development, comparatively few progeny, and long life spans (e.g., seals, elephants, primates). Primate species feature extremely K-selected traits; however, primate non-kinship adoptions have been shown to be individually “selfish” in nature, as reflected by maternal skill improvement among juvenile and nulliparous females, reciprocal altruism among parous females, and exploitation by low-ranking males. Moreover, species-typical social structure also affects female primate fostering behavior. Here we demonstrate that adult parous female cynomolgus monkeys (*Macaca fascicularis*), in the absence of their social group, display exclusive adoption of their own biological offspring by failing to adopt non-kin orphan infants independent of the physical presence of their infant kin or maternal status. These findings support the hypothesis that adult parous females from socially hierarchical primate species that do not stand to gain from reciprocal altruistic effects are genetically restrictive in their adoption behaviors.

**Keywords:** adoption, alloparental, altruism; cynomolgus, macaque, monkey, primate

## Introduction

Adoption, a particular type of alloparental care in which primary caretaking of an infant is transferred to a previously unrelated adult, has been shown to increase the likelihood of infant survival[1] Alloparental care and adoption behavior has been analyzed in over 120 mammalian and 150 avian species and has been especially observed in 'K-selected' species defined, in part, by long periods of development, comparatively few progeny, and long life spans (e.g., seals, elephants, primates). [2]More specifically, alloparental care and adoption behavior is most frequently observed in K-selected species which also display the following characteristics: (1) small groups

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with tight kinship bonds, (2) familial groups in which the young remain for one to two years following weaning or after reaching reproductive maturity, and (3) highly social or cooperative group structures[2]

Primate species feature extremely K-selected traits, such as neoteny, low fecundity, relatively long life span, and prolonged periods of offspring dependency.[2] As predicted by Hamilton's Rule of 'inclusive fitness,' primate kinship adoptions involving closely related individuals are consistent with kin-selection theory[1,3] However, primate non-kinship adoptions have been shown to be individually “selfish” in nature, as reflected by maternal skill improvement among juvenile and nulliparous females, reciprocal altruism among parous females, and exploitation by low-ranking males.[1,4] Moreover, species-typical social structure also affects female primate fostering behavior.[5] On the negative side, primate foster mothers have also been shown to mistreat non-kin infants.[4] Similarly, stemming from the medieval fairy tale notion of “the wicked stepmother” combined with modern reports of neglect and maltreatment and lower rates of permanency and positive child perceptions in non-kinship foster placements,[6,7,8,9] neglect and maltreatment in the human child-non-kin foster mother dyad has been a subject of scientific interest with no definitive sociobiological conclusions.[10,11] Thus, primate foster mothers display complex non-kinship adoption behavior that requires further investigation.

To better assess this phenomenon, the adult parous female cynomolgus monkey (*Macaca fascicularis*) was chosen as a non-human primate 'foster mother' model for this study on the basis of several factors: (1) widespread use as an experimental animal model in behavioral studies,[12] (2) high degrees of genetic and phenotypic homology with the human,[13] (3) similar female reproductive physiology to the human (e.g., distinct menarche and menopause, monthly menstrual cycles, uniparous births) [14](4) similar parenting behaviors to the human (e.g., nursing, embracing, carrying, protecting, grooming) [15,16]and (5) adult parous females were selected to rule out maternal skill improvement effects previously observed in juvenile and nulliparous female primates and exploitation effects previously observed in males[1,4]One previous study has examined adoption behavior in the adult, parous female cynomolgus monkey; adoption rates were affected by the postbirth stage of the foster mother, but not by the orphan's age or sex[17] However, the previous study was conducted on individually-reared subjects and may not represent the more natural behavior of socially-reared subjects employed here.

## **Materials and Methods**

All animal work, in experimental cage, was conducted according to relevant national and international guidelines. In accordance with the recommendations of the Weatherall report, “The use of non-human primates in research,” the following statement has been included to document the details of animal welfare and the steps

taken to ameliorate suffering in all work involving non-human primates. This study was performed in strict accordance with the recommendations in the “Guide for the Care and Use of Laboratory Animals” of the Institute of Neuroscience at Chongqing Medical University (Approval No.: 20100031). State regulators and the Committee on Ethics of Animal Experimentation at Chongqing Medical University approved the protocols for this cognitive test prior to implementation.

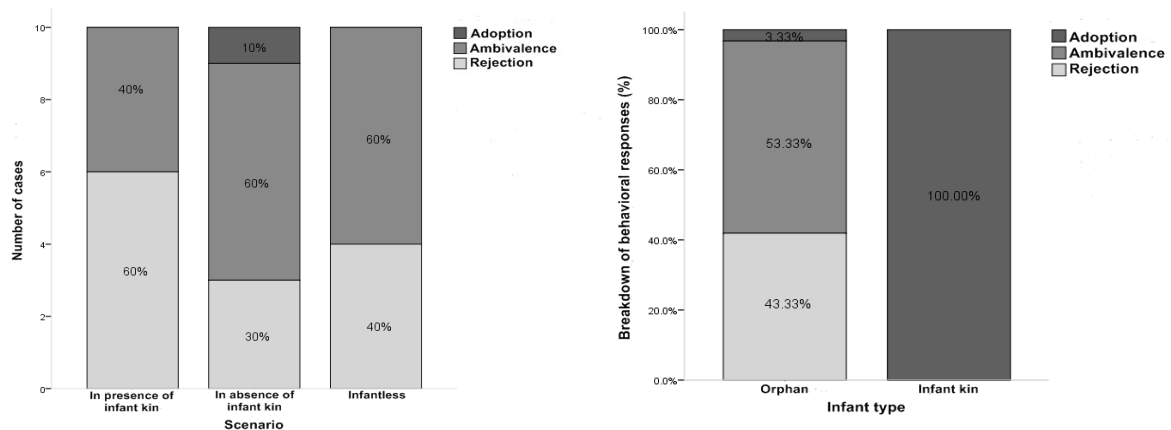
From 1007 healthy, adult, parous female cynomolgus monkeys, 40 'foster mother' candidates were selected by random seed sampling; 14 had infant kin at the time of selection. As infants older than six months must be placed into groups, only orphan candidates between two and five months of age were selected. Subjects were transferred to single cages measuring 80×80×100 cm (one subject per cage) in August 2012. Each cage was placed 100 cm above the ground for cleaning and cross-infection avoidance. After one month of observation, preliminary experimentation was performed to evaluate safety and control. To prevent injury, we halted the experiment whenever the infants were about to be attacked. In the rare case of injury, infants were removed and did not rejoin until recovery. No infant suffered fatal or disabling injuries. Infants were not separated from their mothers for more than two hours and were returned to their mothers upon completion. The total experimental duration was capped at three days to minimize psychological impact.

After the preliminary experiments, only 10 orphans met the conditions. To equalize the number of pairs, 10 foster mothers who had not experienced separation from their infant kin over the past two months along with 10 infantless foster mothers were randomly selected from the 40-subject pool. The 20 foster mothers were subjected to three scenarios: (1) 'in presence of infant kin' in which a non-kin infant ('orphan') was introduced to a foster mother in the presence of her own biological infant ('infant kin') (n=10), (2) 'in absence of infant kin' in which an orphan was introduced to a foster mother in the absence of her infant kin (same group as scenario [1]), and (3) 'infantless' in which an orphan was introduced to an infantless foster mother (n=10). We measured the foster mothers' behavioral responses to the orphan on the basis of three categories: (1) adoption (e.g., nursing, embracing, carrying, protecting, grooming), (2) ambivalence (e.g., no physical interaction, indiscriminately engaging or repelling), and (3) rejection (e.g., failure to approach, threatening, attacking, biting, snatching food from orphan). Behavioral responses in the three scenarios were video-recorded. After 15 min, the feeder offered food. After an additional 15 min, recording was terminated. After the infant kin was returned ('absence of infant' scenario), we recorded for another 15 min. Chi-square analysis was used to compare the constituent ratio of the behavioral responses (Stata version 12.0). P-values of <0.05 were deemed significant. For more detail on the testing facility and ethical treatment of the macaque subjects, please refer to our previous publication[18].

## Results

Foster mothers, in the presence of their own offspring, universally adopted their infant kin and failed to adopt orphans (Fig. 1, 'in presence of infant kin'). These observations suggested non-adoption of orphans; however, these findings may have been due to the physical presence of the infant kin. Therefore, we observed the behavioral responses of the same group of foster mothers to the orphans in the absence of their infant kin; similarly, the foster mothers (with one exception\*) failed to adopt the orphans albeit with a shift favoring ambivalence over rejection (Fig. 1, 'in absence of infant kin'). (\*Note: In order to exclude the effects of milk-rising in the foregoing exceptional case, the experiment was immediately repeated post-ablactation. This foster mother rejected the orphan, consistent with the trend.) Upon return of their own offspring, all foster mothers adopted their infant kin. Pooling all observations, there was a significant difference in the behavioral responses of foster mothers to infant kin vs. orphans ( $\chi^2 = 29.7190$ ,  $df = 4$ ,  $P = 0.000$ , Fig. 2).

The foregoing observations indicated that foster mothers in the process of rearing their infant kin failed to adopt orphans; however, these findings may have been due to the foster mothers' maternal status. Therefore, we observed the behavioral responses of a group of infantless foster mothers to the orphans. These infantless foster mothers also failed to adopt the orphans (Fig. 1, 'infantless'). Moreover, no significant differences were found between the foster mothers' behavioral responses across all three scenarios ( $\chi^2 = 3.7746$ ,  $df = 4$ ,  $P = 0.437$ ).



**Fig 1**

**Fig 1 Behavioral responses of foster mothers to orphans by scenario.** Behavioral responses were categorized as adoption, ambivalence, or rejection. Foster mothers failed to adopt orphans independent of the physical presence of their infant kin or their maternal status. No significant differences were found between the foster mothers' behavioral responses across all three scenarios ( $\chi^2 = 3.7746$ ,  $df = 4$ ,  $P = 0.437$ ).

**Fig 2**

**Fig 2 Breakdown of behavioral responses by infant type.** Behavioral responses were categorized as adoption, ambivalence, or rejection. There was a significant difference in the behavioral responses of foster mothers to infant kin vs. orphans ( $\chi^2 = 29.7190$ ,  $df = 4$ ,  $P = 0.000$ ).

## Discussion

In order to assess adoption behavior, we relied upon two independent dimensions that have been previously used to assess the parenting style of macaque mothers: maternal protectiveness and rejection [19,20]. Here, behavioral responses associated with high maternal protectiveness and low maternal rejection ('adoption' behaviors) were used as indicators of adoption, and behavioral responses associated with low maternal protectiveness ('ambivalence' behaviors) and high maternal rejection ('rejection' behaviors) were used as indicators of non-adoption.

Our findings demonstrate that foster mothers consistently adopted their infant kin and failed to adopt non-kin orphans independent of the physical presence of their infant kin or their maternal status. The infantless foster mothers' failure to adopt non-kin orphans is especially suggestive of genetically restrictive adoption behavior in female cynomolgus monkeys, as these females did not have a competing maternal bond with an infant kin. Through the selection of healthy, parous adult females that were separated from their social group, we ruled out maternal skill improvement, exploitation, and reciprocal altruism as factors under investigation, leaving species-typical social structural effects. According to the adaptive hypothesis, low-ranking mothers from despotic species characterized by strict female dominance hierarchies may be reluctant to surrender their infants to other females because of their inability to retrieve them [5]. In contrast, in more egalitarian primate species, mothers appear more permissive of alloparental behavior as a result of their higher confidence in infant retrieval [5]. As female cynomolgus monkeys display a strict female dominance hierarchy [21] the failure to adopt non-kin orphans may be influenced by this species-typical social structure, as adoption of a non-kin orphan belonging to

an absent higher-ranking female may result in retaliatory aggression toward the foster mother. Our findings are consistent with previous studies showing non-adoption in five other macaque species; only one study, conducted under captive experimentally-induced conditions, demonstrated adoption behavior in the rhesus macaque<sup>2</sup>. Interestingly, our findings parallel past human societal groupings with strict female dominance hierarchies, such as the imperial harems of the Ottoman Empire and the Chinese Han Dynasty. Lower-ranking concubines did not assume caretaking of the royal scion without the consent of the alpha-female (e.g., Queen Mother, Empress Dowager) [22,23,24,25].

In conclusion, our findings support the hypothesis that adult parous females from socially hierarchical primate species that do not stand to gain from reciprocal altruistic effects are genetically restrictive in their adoption behaviors. As this study had a small number of subjects and observations were conducted over short sessions, a larger investigation conducted over longer durations of exposure is needed to examine whether the foster mothers' behavioral responses towards the orphans vary with time. Further study involving aunts and/or older female siblings of the orphans would also be of interest.

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