First wild evidence of neonate nipple preference and maternal cradling laterality in Old World monkeys: A preliminary study from *Rhinopithecus roxellana*

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Abstract

Although captive or free-ranging settings offer a more controlled environment for assessing non-human primate laterality, research on wild populations provides evidence of how laterality is affected by natural environmental conditions and, thus may yield potential insights into the evolution of laterality. This study of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) constitutes the first report on asymmetric patterns of early mother–infant interactions among Old World monkeys in the wild. It was found that neonate nipple preference and maternal cradling laterality are both evident on the individual level. Although there is no significant group-level preference direction, the group preference strength on both measures is evident. Moreover, neonate nipple preference is not significantly correlated with maternal cradling laterality on either LBI scores or the direction (LBI scores: \( r = 0.174, p = 0.632 \); direction: \( r = 0.624, p = 0.054 \)). Taken together, it is possible to suggest that wild *R. roxellana* show independent orientation laterality from the first week of life.

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1. Introduction

Lateralized behavior has been studied as an observable measure of cerebral functional asymmetry for many years and interest in the evolutionary origins of lateralized behavior in humans has prompted recent research into laterality in non-human primates (Corballis, 1997; Papademetriou et al., 2005). For non-human primates, limb laterality is thought to be largely determined by environmental factors such as maternal cradling laterality (Hopkins, 2004). Asymmetry in the early mother–infant interaction (mainly focus on nipple preference and maternal cradling laterality) of non-human primates is evident based on current research results. Such kind of asymmetry may have a bearing on the development of handedness in their offspring (for a review, see Hopkins, 2004). There is a growing body of evidence for asymmetries in early mother–infant interactions in non-human primates as well as in humans: women, for example, show universal left-sided biases in cradling infants (Damerose and Vauclair, 2002). Current research shows a left-side bias in nipple preference and maternal cradling in apes, notably in chimpanzees, gorillas and bonobos (Manning and Chamberlain, 1990, 1991; Hopkins et al., 1993; Nishida, 1993; Dienske et al., 1995; Hopkins, 2004; Hopkins and Lathouwers, 2006). Old World monkeys, New World monkeys and prosimians have been subject to less study as concerns population-level asymmetries in early mother–infant interactions, but left- or right-side individual biases are clearly apparent (Damerose and Vauclair, 2002).

Among Old World monkeys, research has been conducted in captive (e.g., Damerose and Hopkins, 2002) and free-ranging conditions (e.g., Jaffe et al., 2006), but almost entirely in Cercopithecinae (*Macaca fuscata*: Haraiwa, 1981; Nakamichi, 1983; Tanaka, 1989; Ōta et al., 1991; *Macaca mulatta*: Hinde et al., 1964; Deets and Harlow, 1970; Lindburg, 1971; Tomaszczyki et al., 1998; Jaffe et al., 2006; *Macaca nemestrina*: Erwin et al., 1975; *Papio anubis*: Damerose and Hopkins, 2002; *Semnopithecus entellus*: Winkler and Prestel, 1989). Although

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Table 1
Focal mother–infant dyads and LBI scores in this study

<table>
<thead>
<tr>
<th>No.</th>
<th>Mother ID</th>
<th>Infant ID</th>
<th>Infant sex</th>
<th>Neonate nipple preference</th>
<th>Maternal cradling laterality</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>L</td>
<td>R</td>
</tr>
<tr>
<td>1</td>
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<td>YuChui</td>
<td>Female</td>
<td>19</td>
<td>6</td>
</tr>
<tr>
<td>2</td>
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<td>YuDian</td>
<td>Male</td>
<td>2</td>
<td>7</td>
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<tr>
<td>3</td>
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<td>YuHei</td>
<td>Female</td>
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<td>6</td>
</tr>
<tr>
<td>4</td>
<td>TaoHua</td>
<td>YuHua</td>
<td>Male</td>
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<td>9</td>
</tr>
<tr>
<td>5</td>
<td>DanHuang</td>
<td>YuHuang</td>
<td>Female</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td>HeiJin</td>
<td>YuJin</td>
<td>Male</td>
<td>4</td>
<td>8</td>
</tr>
<tr>
<td>7</td>
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<td>YuMao</td>
<td>Male</td>
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<td>3</td>
</tr>
<tr>
<td>8</td>
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<td>YuMei</td>
<td>Male</td>
<td>0</td>
<td>13</td>
</tr>
<tr>
<td>9</td>
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<td>YuXian</td>
<td>Female</td>
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<td>0</td>
</tr>
<tr>
<td>10</td>
<td>HeiZuan</td>
<td>YuZuan</td>
<td>Female</td>
<td>24</td>
<td>8</td>
</tr>
</tbody>
</table>

captive and free-ranging settings could offer a more controlled environment for assessing limb preferences, studies of wild or naturalistic populations can potentially provide important insights into how limb laterality is affected by natural environmental conditions and so into the evolution of laterality. To date several hypotheses have been proposed to explain maternal cradling laterality: that the fetus becomes imprinted to the heartbeat of its mother, and left-side cradling has a soothing effect on the infant because it allows the infant to be close to the heart (Salk, 1973); that the cradling bias may be determined by the head-turning preferences of the infant (Ginsburg et al., 1979), which in turn may result from neural asymmetries related to handedness (Michel, 1981) or the different tactile sensitivities of the right and left female breast (Kaplan-Solms and Saling, 1988; Saling and Cooke, 1984); that left-side cradling had to do with the hemispheric specialization of emotions, and the mother could better monitor her infant’s emotional state when holding on the left side rather than on the right (Manning and Chamberlain, 1991; Vauclair and Donnot, 2005).

In this study, our aim is to assess whether wild Sichuan snub-nosed monkeys (Rhinopithecus roxellana) show any evidence of neonate nipple preference and maternal cradling laterality, and to investigate the effect of maternal cradling on neonate nipple preference in this Colobine monkey.

2. Methods

2.1. Study site and species

The study site is located in Yuhuangmiao area, Zhouzhi National Nature Reserve, in the Qinling Mountains of China (Li et al., 2000; Zhao et al., 2005, 2008). Two polygynous troops of Sichuan snub-nosed monkey (R. roxellana), the east ridge troop (ERT) and the west ridge troop (WRT), are present at the study site (Li and Zhao, 2007). The WRT includes one all-male group as well as the focal group which consists of one-male units (OMU) (Zhang et al., 2006). The subjects of the study were 10 R. roxellana mother–infant dyads (Table 1) in the focal group. Of the infants observed in this study, six were females and four males.

2.2. Food provisioning

Provisioning of the study group was started on October 24, 2001. A 15 m × 30 m provisioning site is established at Sanchakou (1646 m above sea level) in Gongnigou valley (33°48′68″N, 108°16′18″E). The monkeys were herded towards provisioning sites at approximately 9:00 h every day where the research was conducted (Zhang et al., 2006; Zhao et al., 2008). Approximately 200 g of feed were provided per monkey per day on three occasions. To reduce any effect of provisioning on behavioral data collection, observations began only when the monkeys moved into the adjacent trees and resumed their normal activities after feeding at the provisioned area. A distance of 5–50 m was kept between the observer and the focal animals during the observation. All individuals could be identified by individual physical peculiarities (Zhang et al., 2006; Li and Zhao, 2007).

2.3. Data collection

The study was conducted from March to April 2007. Throughout the first week of the infant’s life, each mother–infant pair was observed twice (on the 2nd day and the 6th day respectively) in a 1-h observation session. During the observation sessions, two observers, D.P. Zhao and X. Gao, watched each focal dyad simultaneously and collected the data using a check sheet.

The data on neonate nipple preference and maternal cradling laterality were collected by a scan-sampling technique with 60-s intervals (Altmann, 1974; Martin and Bateson, 1993). Any or all contact with the nipple by the infant was considered as suckling behavior because it was difficult to discern the difference between non-feeding nipple contact and actual suckling because of the constraints presented by the natural environment (e.g., Tanaka, 1997). As a result, neonate nipple preference was defined as contact between neonate’s mouth and mother’s nipple. Nipple side was recorded from the mother’s perspective (i.e., the mother’s left or the mother’s right). Maternal cradling laterality was defined as the mother holding the offspring with either her left or her right hand. It was recorded only when the infant was held ventrally by the mother when she was in a sitting posture (e.g., Tomaszycki et al., 1998).
A total of 60 scan samples were completed for each observation session. For each sampling point, the observers scanned the focal mother–infant dyad, noting whether each infant was nursing from the mother’s left nipple, or right nipple, or not nursing. It was also noted whether the mother was cradling her infant with the left arm, the right arm, or both arms, or not cradling. If the infant nursed or was cradled for several successive 60-s intervals, each scan was considered a separate instance. If the infant or mother was not engaged in any of the operationally defined measures of lateral bias, observers recorded it as “no behavior”. If the nipple or cradling position was not clearly visible (e.g., the mother was in a huddle with other monkeys), or if the two observers did not agree on the score to be assigned, the sampling point was skipped, as recommended by Tomaszycki et al. (1998); this amounted to 6 cases in total.

2.4. Data analysis

For the scan-sampling procedure, we summed the total frequency of left- and right-sided responses for two observation sessions for each measure of lateral bias. To assess the presence of a group bias in nipple preference and maternal cradling, the scores for each subject were totaled for the whole observation. Based on these totals, the lateral bias index (LBI) was calculated by subtracting the number of left-sided observations (L) from the number of right-sided observations (R) and dividing by the total number of observations, i.e. \( \frac{R - L}{R + L} \). The LBI scores ranged from \(-1\) to \(1\) with positive values reflecting a right-side bias and negative values a left-side bias. The absolute value of the LBI score (referred to as ABS-LBI) reflected the magnitude of asymmetry for each measure, as in Jaffe et al. (2006).

We conducted a single-sample t-test on mean LBI scores to test for a group-level preference for a particular nipple (either left or right). We used the single sample t-test with absolute mean LBI scores to test for group-level strength of preference. We tested for any sex effect on the direction and strength of neonate nipple preference by means of a Mann–Whitney U-test. Correlation between LBI scores of neonate nipple preference and maternal cradling was assessed with a Pearson Product-Moment correlation coefficient. Correlation between the direction (1: right preference; \(-1\): left preference; 0: no preference) of neonate nipple preference and maternal cradling was also measured by a Pearson correlation test. All statistical tests were two-tailed and \(p < 0.05\) was chosen as the level of significance.

3. Results

3.1. Neonate nipple preference

In total, 157 neonate nipple preference events were recorded from 10 mother–infant dyads. The mean number of data points per focal neonate is 16 (S.D. = 9). The mean LBI score and mean ABS-LBI score for neonate nipple preference were 0.06 (S.D. = 0.62) and 0.50 (S.D. = 0.33), respectively. Based on the LBI score, five infants were classified as having left-side nipple preference (Fig. 1), four as having right-side preferences and one as having no preference on an individual level (Table 1). No significant group-level preference \((t(9) = -0.329, p = 0.750)\) was found whereas there was a significant group-level strength of preference \((t(9) = 4.859, p = 0.001)\) in the neonate nipple preference of wild \(R.\) roxellana.

One female neonate exhibited ambiguous nipple preference, five females showed left nipple preference, and four males displayed right nipple preference on the individual level. The difference between the sexes in direction of neonate nipple preference was significant \((U = 0; N_1 = 4; N_2 = 6; p = 0.011)\), the mean LBI score per subject was 0.55, S.D. = 0.33 for males and -0.47, S.D. = 0.35 for females), whereas there was no difference in its strength \((U = 10.50; N_1 = 4; N_2 = 6; p = 0.748)\), the mean ABS-LBI score per subject was 0.55, S.D. = 0.33 for males and 0.47, S.D. = 0.35 for females).

3.2. Maternal cradling laterality

A total of 486 maternal cradling events were recorded from 10 mother–infant dyads. The mean number of data points per focal mother is 49 (S.D. = 31). The mean LBI score and mean ABS-LBI score in the maternal cradling laterality were 0.14
(S.D. = 0.33) and 0.27 (S.D. = 0.22), respectively. Based on the LBI score, three mothers were classified as having left-side maternal cradling preference (Fig. 1), seven as having right-side preferences. No significant group-level preference (t(9) = 1.369, p = 0.204) was found whereas there was a significant group-level strength of preference (t(9) = 3.819, p = 0.004) in maternal cradling laterality of wild *R. roxellana*.

For this study, neither LBI scores nor the direction of neonate nipple preference showed any significant correlation with maternal cradling laterality (LBI scores: r = 0.174, p = 0.632; direction: r = 0.624, p = 0.054).

4. Discussion

To our knowledge, this is the first wild study to report asymmetry on early mother–infant interactions among Old World monkeys. For wild *R. roxellana*, our study results demonstrate that on the individual level, not only neonate nipple preference but also maternal cradling laterality are evident for both preference direction and strength (i.e., ABS-LBI). The lack of maternal cradling laterality on the group level is in accordance with results on captive or free-ranging Old World monkeys (Hopkins, 2004). Nipple preference of wild *R. roxellana* emerges in the first week of life; it is earlier than in Rhesus monkeys (*Macaca mulatta*), where it appears after 2 weeks of age (Hinde et al., 1964; Deets and Harlow, 1970; Lindburg, 1971; Tanaka, 1989; but see Jaffe et al., 2006). The difference between them may be due to interspecific differences in infant vision development: considering that nipple preference in wild *R. roxellana* is not correlated with maternal cradling laterality, it is possible to suggest that this species develops independent orientation laterality in the first week of life.

Although we failed to find group-level directional asymmetries, our results are consistent with findings on other Old World monkey species by Haraiwa (1981), Tanaka (1989) and Jaffe et al. (2006), but inconsistent with those findings of Tomaszyczik et al. (1998) and Damerose and Hopkins (2002), who report a population-level left preference, and of Lindburg (1971), who reports a population-level right preference. Furthermore, we found a significant sex difference in neonate nipple preference in wild *R. roxellana*, which is contrary to some other findings in Old World monkeys (e.g., Tomaszyczik et al., 1998; Jaffe et al., 2006).

Beside the possible effect of differing sample sizes, these discrepancies may result from three main differences in methodology between the studies. Firstly, the living settings are different: our study was conducted on wild primate groups, while others have been conducted on captive (Lindburg, 1971; Haraiwa, 1981; Tomaszyczik et al., 1998; Damerose and Hopkins, 2002) or free-ranging groups (Tanaka, 1989; Jaffe et al., 2006). Secondly, different species have been studied (e.g., macaques, baboons, and langurs), and it is possible that not all Old World primates have the same mechanism for expressing nipple preference. The final factor is that various data collection methods have been used in different studies, and this may affect the results; we employed a scan-sampling method, while others used a focal sampling technique.

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In conclusion, this study provides the first evidence on neonate nipple preference and maternal cradling laterality in an Old World monkey in the wild although we could not make strong generalizations. Such a study needs to be realized at least during the first month of life of the infants to control for the robustness of the preference throughout development. Given the discrepancies among different studies of Old World monkeys, further investigations using larger sample sizes and comparable methodologies are needed. Future investigation should also attempt to relate developmental influence on infant nipple preference and its relationship with maternal cradling laterality.

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