Published in final edited form as:

Am J Phys Anthropol. 2012 May ; 148(1): 36–44. doi:10.1002/ajpa.22038.

Handedness in Nature: First Evidence on Manual Laterality on Bimanual Coordinated Tube Task in Wild Primates

Dapeng Zhao^{1,2,*}, William D. Hopkins^{3,4}, and Baoguo Li^{2,*}

¹Tianjin Key Laboratory of Cyto-Genetical and Molecular Regulation, College of Life Sciences, Tianjin Normal University, Tianjin, China

²College of Life Sciences, Northwest University, Xi'an, China

³Department of Psychology, Agnes Scott College, Decatur, GA 30030, USA

⁴Division of Developmental and Cognitive Neuroscience, Yerkes National Primate Research Center, Atlanta, GA 30329, USA

Abstract

Handedness is a defining feature of human manual skill and understanding the origin of manual specialization remains a central topic of inquiry in anthropology and other sciences. In this study, we examined hand preference in a sample of wild primates on a task that requires bimanual coordinated actions (tube task) that has been widely used in captive primates. The Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) is an arboreal Old World monkey species that is endemic to China, and 24 adult individuals from the Qinling Mountains of China were included for the analysis of hand preference in the tube task. All subjects showed strong individual hand preferences and significant group-level left-handedness was found. There were no significant differences between males and females for either direction or strength of hand preference. Strength of hand preferences of adults was significantly greater than juveniles. Use of the index finger to extract the food was the dominant extractive-act. Our findings represent the first evidence of population-level left-handedness in wild Old World monkeys, and broaden our knowledge on evaluating primate hand preference via experimental manipulation in natural conditions.

Keywords

Bimanual coordination; Hand preference; Task complexity

Approximately 90% of humans are right-handed (Porac and Coren, 1981; Annett, 2002). Such an overwhelming right-hand preference at the population level is generally considered a unique evolutionary characteristic of human beings across a variety of cultures and many believe it is associated with the evolution of left cerebral lateralization for manual control and language (Porac and Coren, 1981; Corballis, 1983; Marchant and McGrew, 1998; Corballis, 2002; Raymond and Pontier, 2004). Research on hand preference in nonhuman primates brings essential light to evolutionary origins of human cerebral lateralization and its adaptive value (Fagot and Vaclair, 1991; Bradshaw and Rogers, 1993; Annett, 2002; Vallortigara and Bisazza, 2002; Cashmore et al., 2008). Though evidence of group-level limb biases is weak in nonhuman animals, including primates, there is increasing evidence

*Correspondence to: (1) Dapeng Zhao, Tianjin Key Laboratory of Cyto-Genetical and Molecular Regulation, College of Life Sciences, Tianjin Normal University, Binshui West Road 393, Xiqing District, Tianjin 300387, China. dpzhao@yahoo.cn, skyzdp@mail.tjnu.edu.cn. Tel.: +86-22-23766823, (2) Baoguo Li, College of Life Sciences, Northwest University, Taibai North Road 229, Xi'an 710069, China. baoguali@nwu.edu.cn. Tel.: +86-29-88302418.

of population-level handedness in some primate species (e.g., Byrne and Byrne, 1991; see review by Ward and Hopkins, 1993; Rogers and Andrew, 2002; Vallortigara and Rogers, 2005; Hopkins, 2007a).

There are two continuing issues in the comparative assessment of primate hand preference that require further study. One issue is the matter of methodological inconsistencies across studies. In other words, various tasks are used to assess hand use of nonhuman primates. Most studies on hand preference in wild and captive primates have used relatively simple measures of hand use such as simple reaching (Lehman, 1993; Papademetriou et al., 2005). It is becoming increasingly clear that unimanual tasks, such as simple reaching, may not be the most sensitive for eliciting consistent preferential hand use compared to tasks that require coordinated bimanual actions (Byrne and Byrne, 1991; Vauclair et al., 2005; Hopkins, 2007b). The task complexity theory proposes that strong preferences and group-level biases of manual laterality would be more likely to appear in complex tasks, such as bimanual coordinated tasks compared to less demanding, unimanual tasks (Fagot and Vauclair, 1991). Studies in a number of primate species have provided evidence in support of the task complexity view of primate hand preference (*Cebus apella*: Westergaard and Suomi, 1996; Spinozzi et al., 1998; Lilak and Phillips, 2008; *Cercocebus torquatus*: Blois-Heulin et al., 2006; Laurence et al. 2011; *Cercopithecus c. campbelli*: Chapelain et al. 2006; *Cercopithecus neglectus*: Trouillard and Blois-Heulin, 2005; Schweitzer et al. 2007; *Chlorocebus aethiops*: Harrison and Byrne, 2000; *Gorilla gorilla*: Byrne and Byrne, 1991; *Pan troglodytes*: Colell et al., 1995; *Rhinopithecus roxellana*: Zhao et al. 2010).

Moreover, increasingly, studies are now investigating manual laterality for bimanual coordinated actions in different contexts such as spontaneous or natural behaviors (e.g., bimanual feeding: Hopkins, 1994; Meguerditchian et al., 2010; bimanual grooming: Hopkins et al., 2007; Zhao et al., 2010; bimanual stone handling: Leca et al., 2010) or using experimental tasks (e.g., tube task: Hopkins, 1995; Westergaard and Suomi, 1996; Vauclair et al., 2005; ball task: Schweitzer et al., 2007; box task: Blois-Heulin et al., 2006). It is generally believed that experimental tasks elicit a greater strength of manual laterality than spontaneous tasks (e.g., *Cercopithecus campbelli*: Chapelain et al., 2006; *Cercopithecus neglectus*: Schweitzer et al., 2007). Therefore, considering that the diversity of tasks could cause potential inconsistency of results, choosing more standardized measure of hand use that can be used across different settings is crucial to reliably assess and compare hand preference in nonhuman primate species.

The second critical issue on the comparative assessment of hand preference is the imbalance of data between captive and wild populations of nonhuman primates. The majority of studies on hand preference in nonhuman primates have been conducted in captive living individuals (e.g., Fagot and Vauclair, 1991; Marchant and McGrew, 1991; Hopkins et al., 2011) and some have suggested that being raised by humans during infancy, captive housing conditions and environmental stress may, in essence, influence manual laterality in primates (McGrew and Marchant, 1997, 2001; Palmer, 2003). Since the initial report of population-level handedness in mountain gorillas for bimanual feeding by Byrne and Byrne (1991), there is growing body of evidence reporting population-level handedness in wild nonhuman primates, notably apes (Boesch, 1991; Corp and Byrne, 2004; Lonsdorf and Hopkins, 2005; Peters and Rogers, 2007; Humle and Matsuzawa, 2009). However, in contrast, there are very few studies reporting handedness in wild populations of monkeys (Panger, 1998; Garber et al., 2008; Zhao et al., 2010). Further complicating this issue is the fact that most studies on hand preference in wild primates use different measures (e.g., nut-cracking: Humle and Matsuzawa, 2009; manipulating a dowel: Garber et al. 2008; stone handling: Leca et al., 2010; termite-fishing: Lonsdorf and Hopkins, 2005) than those employed by scientists working in captive settings, though again, this is beginning to change (e.g., simple reaching:

Lilak and Phillips, 2008; bimanual feeding: Hopkins, 1994; Meguerditchian et al. 2010; grooming: Hopkins et al., 2007; tool-use: Hopkins et al., 2009). This makes comparing findings between the two settings very difficult if not impossible.

Hopkins (1995) first introduced “the tube task”, an experimental task that assesses hand use for coordinated bimanual actions. In the tube task, the primate needs to hold a baited tube with one hand and extract the food inside the tube with a finger on the opposite hand (Hopkins, 1995). In contrast to other common measures of hand use, the tube task is a kind of complex task involving bimanual coordination (Hopkins, 1995). The tube task elicits consistent and reliable hand preference at the individual level because it removes the potential influence of situational factors that might influence hand use (Hopkins and Cantalupo, 2005). Moreover, it is relatively simple to administer and therefore can be used with many different primate species. Therefore the tube task is ideally suited as a standard measure of hand preference.

To date, the tube task has been used with a number of primate species including great apes (*Gorilla gorilla*: Hopkins et al., 2003a; Begg-Reid and Schillaci, 2008; Hopkins et al., 2011; *Pan paniscus*: Chapelain and Hogervorst, 2009; Chapelain et al., 2011; *Pan troglodytes*: Hopkins, 1995; Hopkins, 1999a; Hopkins et al., 2001; Hopkins et al., 2003a,b; Hopkins and Cantalupo, 2003; Hopkins et al., 2004; Hopkins et al., 2005; Llorente et al., 2009; Llorente et al., 2011; *Pongo pygmaeus*: Hopkins et al., 2003a), Old World monkeys (*Cercopithecus neglectus*: Schweitzer et al., 2007; *Macaca mulatta*: Westergaard and Suomi, 1996; Westergaard et al., 1997; *Papio anubis*: Vauclair et al., 2005) as well as New World monkeys (*Cebus apella*: Westergaard and Suomi, 1996; Spinozzi et al., 1998; Phillips and Sherwood 2005; Spinozzi et al., 2007; Lilak and Phillips 2008; *Cebus capucinus*: Meunier and Vauclair, 2007). The group-level handedness has been reported in seven nonhuman primates species to date (right-handedness: *Cebus apella*: Spinozzi et al., 1998; *Gorillas gorilla*: Hopkins et al., 2011; *Pan troglodytes*: Hopkins, 1995, 1999a; Hopkins et al., 2001, 2003a,b; 2004, 2005; Llorente et al., 2009, 2011; Hopkins et al., 2011; *Papio anubis*: Vauclair et al., 2005; left-handedness: *Cercopithecus neglectus*: Schweitzer et al., 2007; *Macaca mulatta*: Westergaard et al., 1997, Bennet et al., 2008; *Pongo pygmaeus*: Hopkins et al., 2003a; Hopkins et al., 2011).

One limitation of these studies is that all research on the tube task has been conducted in captive- or semi-naturally living primates (see review by Chapelain and Hogervorst, 2009). Though such settings can offer a more controlled environment for assessing limb preferences in non-human primates, studies of wild or naturalistic populations can potentially provide important insights into how manual laterality is potentially influenced by natural environmental conditions (Hopkins, 2007a). To address this issue, we examined hand preferences for the tube task in a sample of wild primates. The Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) is an arboreal Old World monkey species that is endemic to China, and has, until recently, rarely been studied in laterality research (Zhao et al., 2008a,b,c, Zhao et al., 2010). With regard to bimanual coordination, there are no data to date on the experimental tube task but there is one report on spontaneous bimanual grooming that reported group-level left-handedness in wild *R. roxellana* (Zhao et al., 2010).

There were three main aims of this study in wild *R. roxellana*. First, we sought to examine whether wild *R. roxellana* would show population-level handedness for the tube task. Based on the previous report of group-level left handedness for bimanual grooming in this species (Zhao et al. 2010), we hypothesized that left hand biases would similarly be evident for the tube task.

Second, we aimed to test another prediction that hand preference for the experimental tube task were more biased than that for spontaneous bimanual grooming task based on the hypothetic statement mentioned above, “experimental tasks elicit a greater strength of manual laterality than spontaneous tasks (Chapelain et al., 2006; Schweitzer et al., 2007)”. Third, we aimed to compare the tube task results in this species with previous data from other species on the tube task in order to make an integrated assessment of primate hand preference for bimanual coordinated actions and discuss their differences and similarities from a broad comparative primate perspective.

METHODS

Study site and study species

This study was conducted at the Zhouzhi National Nature Reserve (ZNNR) on the northern slope of the Qinling Mountains, in the Shaanxi province of China. There were two troops of Sichuan snub-nosed monkeys, the East Ridge troop (ERT) and the West Ridge troop (WRT), at the study site. The focal population consists of one-male groups within the WRT, as described in detail by Zhao et al. (2010). Permission of the Zhouzhi National Nature Reserve to conduct this research was obtained before the onset of the study.

We set up one provisioning site at Sanchakou (1646 m above sea level) in Gongnigou valley (33°48′68″N, 108°16′18″E). The field assistants searched for monkeys of the focal population and attracted them to the provisioning site at approximately 9:00 a.m. every day when research was being conducted. Approximately 200g of feed were provided per monkey per day on three occasions (10:00 a.m., 12:00 p.m., and 14:00 p.m. respectively). Compared with the daily total diet of *R. roxellana*, the energy intake of provisioned food is very limited and thus its influence on their natural behavior was minimal. On the whole, the focal group was well-habituated to the presence of observers and had many years of experience as subjects in other naturalistic observational studies. We identified all focal individuals via their physical characteristics and kept a distance of 5–50m from the focal animals during observations.

Data collection

We collected data from September 2010 to January 2011 based on a comprehensive study on asymmetry of limb use in *R. roxellana* (Zhao et al., 2008a,b,c; Zhao et al., 2010). Following the method described by Hopkins (1995), an opaque polyvinyl-chloride (PVC) tube was used in the assessment of hand preferences (Fig.1). In this study, the (PVC) tube was 3 cm in diameter and 10 cm in length. Honey mixed with corn kernels were smeared inside, approximately 2 cm from both ends of the tube. Four PVC tubes were placed on the ground simultaneously so as to minimize individual competition during each test.

We initially chose some individuals as focal subjects only because they performed the tube task on one's own initiative at the earlier stage of the test. If multiple individuals performed the tube task at the same time, we selected the individual with the nearest visible distance from the observer. If more than one individual were the same visible distance from the observer, we selected the individual who had the fewest number of responses. Every effort was made to balance the sampling responses among all subjects, although some of them performed many more responses than others. During our observation, most of data were recorded when monkeys performed the tube task on the ground. Occasionally some subjects took the tube, departed from the place where the tube was placed on, climbed a tree nearby, and then performed the tube task on a branch. All subjects kept the posture of squat when they performed the tube task, either on the ground or on a branch.

We recorded both the frequency and bouts in hand use in the present study. For the frequency in hand use, as described by Hopkins (1995) and Hopkins et al. (2011), we recorded the finger and hand use each time the subject inserted its finger(s) of one hand into the PVC tube and brought corn kernels with honey to its mouth (Fig. 1). The hand used to extract the food was considered as the dominant hand. Data were collected until the subject either dropped the tube or stopped extracting corn kernels for at least 10 seconds. For recording bouts in hand use, as described by Hopkins et al. (2001) and Chapelain and Hogervorst (2009), we defined one bout as each sequence of identical actions and recorded only the first extraction of such sequences. The identification of dominant hand was as same as the frequency recording technology. The new bout in hand use was noted when the subject either dropped the tube, changed the hand grasping the tube, held the tube with both hands or moved to another area to continue feeding. In addition, the digit used (thumb, index finger, middle finger, ring finger, little finger) to extract the food from the tube each time was also recorded. Feeding attempts while using the feet to hold the tube were not considered as responses, based on the method described by Meunier and Vauclair (2007). In order to assess consistency of hand preference on this experimental task, we divided the whole observation period into two periods (the first period: 20 September to 12 November 2010, the second period: 15 November 2010 to January 10 2010). Individuals who performed the tube task a minimum of 15 responses, based on frequency in hand use at each observation period, were included in the analysis of consistency in hand use. A minimum of 30 responses (frequency) was obtained from each subject.

Data analysis

Individual hand preferences were characterized using two methods (Hopkins, 1999b). First, to identify the degree of individual lateral bias, the handedness index (HI), one commonly used index, was calculated for each focal subject following the formula: (right-hand use – left-hand use) / (right-hand use + left-hand use) (Hopkins, 1999b). The HI varied between –1.0 and 1.0. Positive values indicate a bias toward right hand use and negative values indicate a bias toward left hand use. The absolute value (ABS-HI) reflects the strength of the individual-level hand preference. Secondly, *z*-scores were calculated based on the frequency of right and left hand use. The subjects were then categorized as right-handed ($z \geq 1.96$), left-handed ($z \leq -1.96$), or ambipreferent ($-1.96 < z < 1.96$) based on their individual score. Group-level hand preference was analyzed via one-sample tests with individual HI scores and chi-square tests of independence (Hopkins, 1999b, Hopkins et al., 2011).

We used the Spearman correlation test to evaluate the relationship between the number of data points per subject and the HI and ABS-HI as well as the relationship between the HI and ABS-HI when calculated on the basis of bouts and frequencies. We used the Mann-Whitney U-test to evaluate sex/age/task differences in manual laterality. We adopted the Pearson correlation coefficient test to evaluate whether individual preferences were consistent across our two observation periods. Finally, we used analysis of variance (ANOVA) to evaluate the difference of digit use within subjects (Spinozzi et al., 2007). SPSS 16.0 was used to conduct the analyses and a two-tailed test with a level of significance of $p = 0.05$ was adopted for all analyses.

RESULTS

Observations in hand use for the tube task were obtained in twenty-four individuals including 8 males and 16 females. The individual data on left and right hand use are shown in Table 1 and Table 2. For frequency in hand use, the mean number of data points per subject was 62.42 ± 5.74 (range: 31–144) and the mean HI and ABS-HI scores were -0.32 ± 0.15 (range: –1.00–0.97) and 0.73 ± 0.05 (range: 0.27–1.00) respectively. For bouts of hand use, the mean number of data points per subject was 15.21 ± 1.14 (range: 8–30) and the

mean HI and ABS-HI scores were -0.31 ± 0.14 (range: -1.00 - 0.88) and 0.67 ± 0.05 (range: 0.20 - 1.00) respectively.

The number of observations per individual was not significantly correlated with the HI values for frequency ($r = 0.099$, $p = 0.644$) or bouts ($r = 0.084$, $p = 0.695$) in hand use. Similarly, the number of observations was not significantly associated with the ABS-HI scores when calculated on the basis of frequency ($r = 0.084$, $p = 0.697$) or bouts ($r = 0.104$, $p = 0.628$) in hand use. Thus, as has been reported in many other studies, individual differences in the total number of responses did not skew the distribution of handedness values.

Data consistency

There was a significant positive correlation between the HI score of bouts and that of frequencies ($r = 0.991$, $p < 0.001$), as well as between the ABS-HI score of bouts and that of frequencies ($r = 0.938$, $p < 0.001$). This indicates that handedness indices based on bouts and frequencies are sensitive to the same degree of lateral bias in hand use, a finding consistent with many other studies (e.g., Hopkins et al. 2001). Fifteen individuals met the criterion of having at least 15 frequency responses at each observation period in hand use and there was a significant positive correlation (frequency: $r = 0.986$, $p < 0.001$; bout: $r = 0.959$, $p < 0.001$) between HI scores in the two halves of our observation period. In short, individual hand preferences were stable over the observational time periods.

Individual and group-level hand preference

Based on the sign of the HI scores when calculated on the basis of frequency and bouts of hand use, there were 17 left-handed (70.83%) and 7 right-handed (29.71%) individuals (see Table 1, 2). One sample t -tests (frequency: $t_{23} = -2.177$, $p = 0.040$; bout: $t_{23} = -2.317$, $p = 0.030$) as well as a chi-square goodness-of-fit test (both frequency and bout: $X^2_{(1, N = 24)} = 4.167$, $p = 0.041$) revealed a significant group-level left-hand preferences for the tube task. When using z scores as the index for hand preference classification, there were 13 left-handed (54.17%), 4 right-handed (16.67%) and 7 ambiguous handed (29.16%) individuals for the bout data (Table 2). A chi-square goodness-of-fit test showed that there was significantly more left-handed individuals than right-handed individuals for the bout data ($X^2_{(1, N = 17)} = 4.765$, $p = 0.029$).

Digit use

Generally there are five extractive-act categories involved in the tube task. We performed an analysis of variance (ANOVA) on the percentages of responses of each category for each individual, and found a significant difference across categories ($F_{[4, 115]} = 148.414$, $p < 0.001$). The mean percentage for each extractive act were $80.29 \pm 4.16\%$ (mean $\pm$ SE) with the index digit, $11.70 \pm 4.12\%$ with the thumb, $6.20 \pm 1.82\%$ with the index + the thumb, $1.79 \pm 1.14\%$ with the index + the middle, and $0.03 \pm 0.03\%$ with others. A post-hoc analysis using the least significant difference test revealed a significantly higher percentage of responses made with the index finger compared to all other extractive-act categories (all $p < 0.001$).

Age and sex effects

We found no significant difference between adults and juveniles in the direction of hand preference (frequency: $U = 62.50$; $N_1 = 13$; $N_2 = 11$; $p = 0.600$; the mean HI score per subject was -0.27 , $SE = 0.24$ for adults and -0.37 , $SE = 0.17$ for juveniles; bout: $U = 63.50$; $N_1 = 13$; $N_2 = 11$; $p = 0.641$; the mean HI score per subject was -0.28 , $SE = 0.22$ for adults and -0.36 , $SE = 0.15$ for juveniles). However, we found the strength of manual laterality in

adults was significantly higher than that in juveniles (frequency: $U = 28.50$; $N_1 = 13$; $N_2 = 11$; $p = 0.012$; the mean ABS-HI score per subject was 0.85, $SE = 0.06$ for adults and 0.59, $SE = 0.08$ for juveniles; bout: $U = 34.00$; $N_1 = 13$; $N_2 = 11$; $p = 0.029$; the mean ABS-HI score per subject was 0.78, $SE = 0.06$ for adults and 0.44, $SE = 0.13$ for juveniles) (Fig.2). Thus, adults showed stronger hand preferences than juveniles.

We found no significant sex difference either in direction of hand preference (frequency: $U = 60.50$; $N_1 = 8$; $N_2 = 16$; $p = 0.830$; the mean HI score per subject was -0.22 , $SE = 0.29$ for males and -0.37 , $SE = 0.17$ for females; bout: $U = 55.00$; $N_1 = 8$; $N_2 = 16$; $p = 0.580$; the mean HI score per subject was -0.18 , $SE = 0.27$ for males and -0.38 , $SE = 0.15$ for females) or in the strength of hand preference (frequency: $U = 56.50$; $N_1 = 8$; $N_2 = 16$; $p = 0.644$; the mean ABS-HI score per subject was 0.76, $SE = 0.10$ for males and 0.71, $SE = 0.06$ for females; bout: $U = 59.50$; $N_1 = 8$; $N_2 = 16$; $p = 0.782$; the mean ABS-HI score per subject was 0.69, $SE = 0.10$ for males and 0.66, $SE = 0.06$ for females).

Comparison with bimanual grooming task in the same species

Finally, we compared the HI scores for the tube task recorded here with previously published data on hand preference for bimanual grooming in another sample group (Zhao et al., 2010). We found hand preference for the experimental tube task was more biased toward left hand use compared to spontaneous bimanual grooming task for both the direction (frequency: $U = 191.50$; $N_1 = 24$; $N_2 = 26$; $p = 0.019$; the mean HI score was -0.32 , $SE = 0.15$ for the tube task and -0.13 , $SE = 0.04$ for the bimanual grooming; bout: $U = 183.00$; $N_1 = 24$; $N_2 = 26$; $p = 0.012$; the mean HI score was -0.31 , $SE = 0.14$ for the tube task and -0.13 , $SE = 0.04$ for the bimanual grooming) and the strength (frequency: $U = 13.50$; $N_1 = 24$; $N_2 = 26$; $p < 0.001$; the mean ABS-HI score per subject was 0.73, $SE = 0.05$ for the tube task and 0.21, $SE = 0.02$ for the bimanual grooming; bout: $U = 5.50$; $N_1 = 24$; $N_2 = 26$; $p < 0.001$; the mean ABS-HI score per subject was 0.67, $SE = 0.05$ for the tube task and 0.21, $SE = 0.02$ for the bimanual grooming).

DISCUSSION

This is the first study to present data on hand preference for the tube task in a wild primate species. Our study in *R. roxellana*, an arboreal Old World monkey species, revealed several interesting findings. First, group-level left-handedness was found in hand use for the tube task. Second, no significant differences were found between sexes, either in the direction or in the strength of hand preference. Third, the strength of manual laterality for the tube task was significantly stronger in adults than juveniles. Finally, the tube task elicits a stronger degree of hand preference than bimanual grooming.

We recorded both the frequency and bouts in hand use in this study and found that the correlation between the HI measures based on frequency and bouts of hand use was nearly 1.0. This affirms that the two measures quantify the same hand preference and, more importantly, demonstrates that frequency in hand use does not result in skewed distributions of hand preference, as has been suggested by some researchers (McGrew and Marchant, 1997; Cashmore et al., 2008; Cashmore, 2009). Of course, there were more ambiguously-handed subjects when considering hand preference classifications based on bouts of hand use; however, this is not unexpected because of the reduced number of observations for each subject, which makes it more difficult for the z -score to exceed 1.96 or -1.96 .

It has been hypothesized that a) bimanual tasks elicit stronger hand preferences than unimanual tasks and b) that experimental tasks elicit stronger hand preferences than spontaneous tasks. In this study, we compared the hand preferences in *R. roxellana* for an experimental (tube) and spontaneous task (bimanual grooming) task that had the same motor

demands (i.e., both required bimanual actions). As others have reported (Chapelain et al., 2006; Schweitzer et al., 2007), we found that the experimental tube task elicited stronger hand preferences than the spontaneous task. The most parsimonious explanation for this finding is that situational factors likely have little influence in hand use for the tube task compared to grooming. In the case of grooming, the position of the individual being groomed as well as the location of the body part being groomed may influence the hand use by the groomer. These factors are removed in the case of the tube task and likely allow the subjects to more overtly express endogenous preferences for use of the hands.

As a means of placing the results found here within a larger comparative primate perspective, we have plotted the mean HI scores based on frequency data for the snub-nose monkeys with the published HI scores of 9 other species. The results in wild *R. roxellana* are somewhat consistent with those findings in other Old and New World monkeys who are mostly arboreal species, with the exception of capuchin monkeys (Fig.3). It is found that, within apes, orangutans are the most left-handed and gorillas are the most right-handed and these two species are correspondingly the most arboreal and terrestrial ape species (Hopkins et al., 2011). In contrast, chimpanzees and bonobos show more intermediate patterns of hand use and their positional behaviors are more transient than those of the other great apes (Hopkins et al., 2011). Independent of the potential theoretical explanations for the findings reported in Figure 3, we believe the most important aspect of this and other studies is that species can be compared for the same task of evaluating hand preference. As additional data of hand preference accumulate in other species, this will provide an empirical framework for testing more comprehensive theories of the evolution of handedness which are difficult to conduct on a species by species basis.

Current evidence on sex differences in primates hand preference is relatively weak (Fagot and Vauclair, 1993; Springer and Deutsch, 1993; Kimura, 1999; Hopkins, 2007a), and studies reporting sex difference vary between tasks and species (Milliken et al., 1991; Ward and Hopkins, 1993; Spinozzi et al., 1998; Corp and Byrne, 2004; Chapelain et al. 2011). For the tube task, the obvious sex difference is found in one study in *Cebus apella* (Spinozzi et al., 1998, but Spinozzi et al., 2007; Lilak and Phillips, 2008) and one study in *Pan paniscus* (Chapelain et al. 2011, but Chapelain and Hogervorst, 2009) respectively. Wild *R. roxellana* on the tube task did not present significant sex difference, which accords with previous studies on the tube task in other Old World monkeys. In addition, hand preference in *R. roxellana* does not differ between males and females on any spontaneous action in previous reports (Zhao et al., 2008a, 2010). Collectively, the results suggest that the absence of sex difference is one stable characteristic of hand preference in this species, without reference to spontaneous actions or experimental actions.

Increasing evidence has shown that primate manual laterality may increase with age (McGrew and Marchant, 1997). Immature individuals exhibit weaker or less consistent preferences than adults (Vauclair and Fagot, 1987; Milliken et al., 1991; Hopkins, 1994, 1995; Hook and Rogers, 2000; Teixeira, 2008). As the first study examining age differences of hand preference in *R. roxellana*, we found a significant effect of age on the strength of hand preference, but not on the direction of hand preference. Younger individuals were less lateralized than older individuals and these findings partly support the notion that individual hand preference of primates develops with age.

The wild *R. roxellana* preferred to use the index finger on the tube task, which accord with other primate species when performing the same action (e.g. *Cebus apella*: Spinozzi et al., 2007; *Cebus capucinus*: Meunier and Vauclair, 2007; *Cercopithecus neglectus*: Schweitzer et al., 2007; *Pan paniscus*: Chapelain and Hogervorst, 2009; Chapelain et al., 2011; *Pan troglodytes*: Hopkins, 1995; *Papio anubis*: Vauclair et al., 2005). It supports the viewpoint of

Hopkins (1995) that the tube task requires refined movements of distal digits and hands rather than gross or ballistic movements. Distal movements have been shown to require a greater participation of the contralateral hemisphere (Brinkman and Kuypers 1972, in Hopkins 1995).

CONCLUSIONS

We demonstrate the first evidence of left-handedness in Old World monkey species under natural conditions. Our results in *R. roxellana* lend further support to task complexity theory raised by Fagot and Vauclair (1991). Our findings highlight the importance of applying the tube task as a standard measure of primate manual laterality, and warrant further investigation with more samples in this species as well as in other primate species under wild conditions. In addition, this study broadens our knowledge on evaluating primate hand preference via experimental manipulation in natural conditions.

Acknowledgments

Our study adhered to the animal care regulations and national laws in China. We are grateful to the staff of Zhouzhi National Nature Reserve for permission and logistical support.

Grant sponsor: Natural Science Foundation of China; **Grant numbers:** 30970444

Grant sponsor: NIH; **Grant numbers:** NS-42867, HD-56232, HD-60563

LITERATURE CITED

- Annett, M. Handedness and brain asymmetry: the right shift theory. Hove: Psychology Press; 2002.
- Begg-Reid C, Schillaci M. Infant cradling in a captive mother gorilla. *Zoo Biol.* 2008; 27:420–426. [PubMed: 19360636]
- Bennett AJ, Suomi SJ, Hopkins WD. Effects of early adverse experiences on behavioural lateralisation in rhesus monkeys (*Macaca mulatta*). *Laterality.* 2008; 13:282–292. [PubMed: 18449842]
- Blois-Heulin C, Guitton JS, Nedellec-Bienvenue D, Ropars L, Vallet E. Hand preference in unimanual and bimanual tasks and postural effect on manual laterality in captive red-capped mangabeys (*Cercocebus torquatus torquatus*). *Am J Primatol.* 2006; 68:429–444. [PubMed: 16541442]
- Boesch C. Handedness in wild chimpanzees. *Int J Primatol.* 1991; 6:541–558.
- Bradshaw, J.; Rogers, LJ. The evolution of lateral asymmetries, language, tool use and intellect. San Diego: Academic Press; 1993.
- Brinkman C, Kuypers HGJM. Split-brain monkeys: cerebral control of ipsilateral and contralateral arm, hand and finger movements. *Science.* 1972; 176:536–539. [PubMed: 4624322]
- Byrne RW, Byrne JM. Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla gorilla berengei*). *Cortex.* 1991; 27:521–536. [PubMed: 1782788]
- Cashmore L. Can hominin “handedness” be accurately assessed? *Ann Hum Biol.* 2009; 36:624–641. [PubMed: 19626485]
- Cashmore L, Uomini N, Chapelain AS. The evolution of handedness in humans and great apes: a review and current issues. *J Anthropol Sci.* 2008; 86:7–35. [PubMed: 19934467]
- Chapelain AS, Bec P, Blois-Heulin C. Manual laterality in Campbell’s monkeys (*Cercopithecus c. campbelli*) in spontaneous and experimental actions. *Behav Brain Res.* 2006; 173:237–245. [PubMed: 16919818]
- Chapelain AS, Hogervorst E. Hand preferences for bimanual coordination in 29 bonobos (*Pan paniscus*). *Behav Brain Res.* 2009; 196:15–29. [PubMed: 18692095]
- Chapelain AS, Hogervorst E, Mbonzo P, Hopkins WD. Hand preferences for bimanual coordination in 77 bonobos (*Pan paniscus*): replication and extension. *Int J Primatol.* 2011; 32:491–510.
- Colell M, Segarra MD, Sabatier-Pi J. Manual laterality in chimpanzees (*Pan troglodytes*) in complex tasks. *J Comp Psychol.* 1995; 109:298–307. [PubMed: 7554826]

- Corballis, MC. Human laterality. New York: Academic Press; 1983.
- Corballis, MC. From hand to mouth: the origins of language. Princeton: Princeton University Press; 2002.
- Corp N, Byrne RW. Sex difference in chimpanzee handedness. *Am J Phys Anthropol.* 2004; 123:62–68. [PubMed: 14669237]
- Fagot J, Vauclair J. Handedness and bimanual coordination in the lowland gorilla. *Brain Behav Evol.* 1988; 12:89–95. [PubMed: 3179697]
- Fagot J, Vauclair J. Manual laterality in nonhuman primates: a distinction between handedness and manual specialization. *Psychol Bull.* 1991; 109:76–89. [PubMed: 2006230]
- Garber PA, Gomes DF, Bicca-Marques JC. Experimental field study of hand preference in wild black-horned (*Cebus nigritus*) and white-faced (*Cebus capucinus*): evidence for individual and species differences. *Anim Cogn.* 2008; 11:401–411. [PubMed: 18183435]
- Harrison KE, Byrne RW. Hand preferences in unimanual and bimanual feeding by wild vervet monkeys (*Cercopithecus aethiops*). *J Comp Psychol.* 2000; 114:13–21. [PubMed: 10739308]
- Hausmann M, Kirk IJ, Corballis MC. Influence of task complexity on manual asymmetries. *Cortex.* 2004; 40:103–110. [PubMed: 15070005]
- Hook MA, Rogers LJ. Development of hand preferences in marmosets (*Callithrix jacchus*) and effects of aging. *J Comp Psychol.* 2000; 114:263–271. [PubMed: 10994842]
- Hopkins WD. Hand preferences for bimanual feeding in 140 captive chimpanzees (*Pan troglodytes*): rearing and ontogenetic determinants. *Dev Psychobiol.* 1994; 27:395–407. [PubMed: 8001728]
- Hopkins WD. Hand preferences for a coordinated bimanual task in 110 chimpanzees (*Pan troglodytes*): cross-sectional analysis. *J Comp Psychol.* 1995; 109:291–297. [PubMed: 7554825]
- Hopkins WD. Heritability of hand preference in chimpanzees (*Pan troglodytes*): evidence from a partial interspecies cross-fostering study. *J Comp Psychol.* 1999a; 113:307–313. [PubMed: 10497796]
- Hopkins WD. On the other hand: statistical issues in the assessment and interpretation of hand preference data in nonhuman primates. *Int J Primatol.* 1999b; 20:851–866.
- Hopkins, WD. The evolution of hemispheric specialization in primates. San Diego: Academic Press; 2007a.
- Hopkins, WD. Hemispheric specialization in chimpanzees: evolution of hand and brain. In: Shackelford, T.; Keenan, JP.; Platek, SM., editors. *Evolutionary cognitive neuroscience*. Boston: MIT Press; 2007b. p. 99–120.
- Hopkins WD, Fernandez-Carriba S, Wesley MJ, Hostetter A, Pilcher D, Poss S. The use of bouts and frequencies in the evaluation of hand preference for a coordinated bimanual task in chimpanzees (*Pan troglodytes*): an empirical study comparing two different indices of laterality. *J Comp Psychol.* 2001; 115:294–299. [PubMed: 11594498]
- Hopkins WD, Cantalupo C. Does variation in sample size explain individual differences in hand preferences of chimpanzees (*Pan troglodytes*)? An empirical study and reply to Palmer (2002). *Am J Phys Anthropol.* 2003:878–881.
- Hopkins WD, Cantalupo C. Individual and setting differences in the hand preferences of chimpanzees (*Pan troglodytes*): a critical analysis and some alternative explanations. *Laterality.* 2005; 10:65–80. [PubMed: 15841824]
- Hopkins WD, Stoinski TS, Lukas KE, Ross SR, Wesley MJ. Comparative assessment of handedness for a coordinated bimanual task in chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*). *J Comp Psychol.* 2003a; 117:302–308. [PubMed: 14498806]
- Hopkins WD, Hook M, Braccini S, Schapiro SJ. Population-level right handedness for a coordinated bimanual task in chimpanzees: replication and extension in a second colony of apes. *Int J Primatol.* 2003b; 24:677–689. [PubMed: 18159222]
- Hopkins WD, Wesley MJ, Izard MK, Hook M, Schapiro SJ. Chimpanzees (*Pan troglodytes*) are predominantly right-handed: replication in three populations of apes. *Behav Neurosci.* 2004; 118:659–663. [PubMed: 15174946]
- Hopkins WD, Cantalupo C, Freeman H, Russell J, Kachin M, Nelson E. Chimpanzees are right-handed when recording bouts of hand use. *Laterality.* 2005; 10:121–130. [PubMed: 15849030]

- Hopkins WD, Russell JL, Remkus M, Freeman H, Schapiro SJ. Handedness and grooming in *Pan troglodytes*: comparative analysis between findings in captive and wild individual. *Int J Primatol*. 2007; 28:1315–1326.
- Hopkins WD, Russell JL, Schaeffer JA, Gardner M, Schapiro SJ. Handedness for tool use in captive chimpanzees (*Pan troglodytes*): sex differences, performance, heritability and comparison to the wild. *Behaviour*. 2009; 146:1463–1483. [PubMed: 20221316]
- Hopkins WD, Phillips KA, Bania A, Calcutt SE, Gardner M, Russell JL, Schaeffer J, Lonsdorf EV, Ross SR, Schapiro SJ. Hand preferences for coordinated bimanual actions in 777 great apes: implications for the evolution of handedness in hominids. *J Hum Evol*. 2011; 60:605–611. [PubMed: 21334723]
- Humle T, Matsuzawa T. Laterality in hand use across four tool use behaviors among the wild chimpanzees of Bossou, Guinea, West Africa. *Am J Primatol*. 2009; 71:40–48. [PubMed: 18942096]
- Kimura, D. Sex and cognition. Cambridge: MIT Press; 1999.
- Laurence A, Wallez C, Blois-Heulin C. Task complexity, posture, age, sex: Which is the main factor influencing manual laterality in captive *Cercocebus torquatus torquatus*? Laterality. 2011
- Leca JB, Gunst N, Huffman MA. Principles and levels of laterality in unimanual and bimanual stone handling patterns by Japanese macaques. *J Hum Evol*. 2010; 58:155–165. [PubMed: 19931886]
- Lehman, RAW. Manual preference in prosimians, monkeys, and apes. In: Ward, JP.; Hopkins, WD., editors. *Primate laterality: current behavioral evidence of primate asymmetries*. New York: Springer-Verlag; 1993. p. 107-124.
- Lilak AL, Phillips KA. Consistency of hand preference across low-level and high-level tasks in capuchin monkeys (*Cebus apella*). *Am J Primatol*. 2008; 70:254–260. [PubMed: 17894405]
- Llorente M, Mosquera M, Fabre M. Manual laterality for simple reaching and bimanual coordinated task in naturalistic housed *Pan troglodytes*. *Int J Primatol*. 2009; 30:183–197.
- Llorente M, Riba D, Palou L, Carrasco L, Mosquera M, Colell M, Feliu O. Population-level right-handedness for a coordinated bimanual task in naturalistic housed chimpanzees: replication and extension in 114 animals from Zambia and Spain. *Am J Primatol*. 2011; 73:281–290. [PubMed: 20954250]
- Lonsdorf EV, Hopkins WD. Wild chimpanzees show population level handedness for tool use. *Proc Natl Acad Sci USA*. 2005; 102:12634–12638. [PubMed: 16105943]
- Marchant LF, McGrew WC. Laterality of function in apes: a meta-analysis of methods. *J Hum Evol*. 1991; 21:425–438.
- Marchant LF, McGrew WC. Human handedness: an ethological perspective. *Hum Evol*. 1998; 13:221–228.
- McGrew WC, Marchant LF. On the other hand: current issues in and meta-analysis of behavioral laterality of hand function in primates. *Yearb Phys Anthropol*. 1997; 40:201–232.
- McGrew WC, Marchant LF. Ethological study of manual laterality in the chimpanzees of Mahale Mountains, Tanzania. *Behaviour*. 2001; 138:329–358.
- Meguerditchian A, Calcutt SE, Lonsdorf EV, Ross SR, Hopkins WD. Brief communication: captive gorillas are right-handed for bimanual feeding. *Am J Phys Anthropol*. 2010; 141:638–645. [PubMed: 20033918]
- Meunier H, Vauclair J. Hand preferences on unimanual and bimanual tasks in white-faced capuchins (*Cebus capucinus*). *Am J Primatol*. 2007; 69:1064–1069. [PubMed: 17407149]
- Milliken GW, Stafford DK, Dodson DL, Pinger CD, Ward JP. Analyses of feeding lateralization in the small-eared bushbaby (*Otolemur garnettii*): a comparison with the ring-tailed lemur (*Lemur catta*). *J Comp Psychol*. 1991; 105:274–285. [PubMed: 1935006]
- Palmer AR. Reply to Hopkins and Cantalupo: Chimpanzees' right-handedness reconsidered: sampling issues and date presentation. *Am J Phys Anthropol*. 2003; 121:382–384.
- Panger MA. Hand preference in free-ranging white-throated capuchins (*Cebus capucinus*) in Costa Rica. *Int J Primatol*. 1998; 19:133–163.
- Papademetriou E, Sheu CF, Michel GF. A meta-analysis of primate hand preferences for reaching and other hand-use measures. *J Comp Psychol*. 2005; 119:33–48. [PubMed: 15740428]

- Peters HH, Rogers LJ. Limb use and preferences in wild orangutans during feeding and locomotor behavior. *Am J Primatol.* 2007; 69:1–15.
- Phillips KA, Sherwood CC. Primary motor cortex asymmetry is correlated with handedness in capuchin monkeys (*Cebus apella*). *Behav Neurosci.* 2005; 119:1701–1704. [PubMed: 16420175]
- Porac, C.; Coren, S. Lateral preferences and human behavior. New York: Springer; 1981.
- Raymond M, Pontier D. Is there geographical variation in human handedness? *Laterality.* 2004; 9:35–52. [PubMed: 15382729]
- Rogers, LJ.; Andrew, RJ. Comparative vertebrate lateralization. Cambridge: Cambridge University Press; 2002.
- Schmitt V, Melchisedech S, Hammerschmidt K, Fischer J. Hand preferences in Barbary macaques (*Macaca sylvanus*). *Laterality.* 2008; 13:143–157. [PubMed: 18302057]
- Schweitzer C, Bec P, Blois-Heulin C. Does the complexity of the task influence manual laterality in De Brazza's monkeys (*Cercopithecus neglectus*)? *Ethology.* 2007; 113:983–994.
- Swinnen SP, Wenderoth N. Two hands, one brain: cognitive neuroscience of bimanual skill. *Trends in Cogn Sci.* 2004; 8:18–25. [PubMed: 14697399]
- Spinozzi G, Castorina MG, Truppa V. Hand preferences in unimanual and coordinated-bimanual tasks by tufted capuchin monkeys (*Cebus apella*). *J Comp Psychol.* 1998; 112:183–191.
- Spinozzi G, Laganà T, Truppa V. Hand use by tufted capuchins (*Cebus apella*) to extract a small food item from a tube: digit movements, hand preference, and performance. *Am J Primatol.* 2007; 69:336–352. [PubMed: 17146792]
- Springer, SP.; Deutsch, G. Left brain, right brain. New York: Freeman; 1993.
- Teixeira LA. Categories of manual asymmetry and their variation with advancing age. *Cortex.* 2008; 44:707–716. [PubMed: 18472040]
- Trouillard E, Blois-Heulin C. Manual laterality and task complexity in De Brazza's monkey (*Cercopithecus neglectus*). *Laterality.* 2005; 10:7–27. [PubMed: 15841820]
- Vallortigara, G.; Bisazza, A. How ancient is brain lateralization?. In: Rogers, LJ.; Andrew, JR., editors. Comparative vertebrate lateralization. Cambridge: Cambridge University Press; 2002. p. 9-69.
- Vallortigara G, Rogers LJ. Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behav Brain Sci.* 2005; 28:575–589. [PubMed: 16209828]
- Vauclair J, Fagot J. Spontaneous hand usage and handedness in a troop of baboons. *Cortex.* 1987; 23:265–274. [PubMed: 3608520]
- Vauclair J, Meguerditchian A, Hopkins WD. Hand preference for unimanual and coordinated bimanual tasks in baboons (*Papio anubis*). *Cogn Brain Res.* 2005; 25:210–216.
- Ward, JP.; Hopkins, WD. Primate laterality: current behavioural evidence of primate asymmetries. New York: Springer-Verlag; 1993.
- Westergaard GC, Suomi SJ. Hand preference for a bimanual task in tufted capuchins (*Cebus apella*) and rhesus macaques (*Macaca mulatta*). *J Comp Psychol.* 1996; 110:406–411. [PubMed: 8956511]
- Westergaard GC, Champoux M, Suomi SJ. Hand preference in infant rhesus macaques (*Macaca mulatta*). *Child Dev.* 1997; 68:387–393. [PubMed: 9249955]
- Zhao DP, Ji WH, Watanabe K, Li BG. Hand preference during unimanual and bimanual reaching actions in Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). *Am J Primatol.* 2008a; 70:500–504. [PubMed: 18080318]
- Zhao DP, Li BG, Watanabe K. First evidence on foot preference during locomotion in Old World monkeys: a study of quadrupedal and bipedal actions in Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). *Primates.* 2008b; 49:260–264. [PubMed: 18685923]
- Zhao DP, Gao X, Li BG, Watanabe K. First wild evidence of neonate nipple preference and maternal cradling laterality in Old World monkeys: a preliminary study from *Rhinopithecus roxellana*. *Behav Process.* 2008c; 77:364–368.
- Zhao DP, Gao X, Li BG. Hand preference for spontaneously unimanual and bimanual coordinated tasks in wild Sichuan snub-nosed monkeys: implication for hemispheric specialization. *Behav Brain Res.* 2010; 208:85–89. [PubMed: 19914301]

Fig. 1.

An adult female *R. roxellana* performing the tube task on a branch (A color version of this figure may be viewed in the online issue, which is available at <http://onlinelibrary.wiley.com/>.)

Fig. 2.

Age differences of hand preference in *R. roxellana*

a. based on frequency data

b. based on bout data

* indicates significant difference between adults and juveniles ($p < 0.05$)

Fig. 3.

The mean HI score based on frequency data for 10 nonhuman primate species that has been tested on the tube task

* indicates significant population-level handedness based on combined published data from each species.

Handedness data for each species came from the following sources: Great apes from Hopkins et al. (2011) and Llorente et al. (2011), rhesus monkeys from Bennett et al (2008), Barbary macaques from Schmitt et al. (2008), baboons from Vauclair et al. (2005), De Brazza monkeys from Schweitzer et al. (2007), and capuchin monkeys from Lilak and Phillips (2008), Meunier and Vauclair (2007) and Spinozzi et al. (1998).

Samples sizes for each species were: chimpanzees (n = 536), bonobos (n = 118), gorillas (n = 76), orangutans (n = 44), De Brazza (n = 12), rhesus (n = 74), Barbary (n = 28), baboon (n = 104) and capuchins (n = 54).

Note: The tube task has been administered in several other studies within the rhesus and capuchin monkey species but individual data were not available in the published papers, so they were not included in these analyses.

Table 1

Frequency data on hand preference for the tube task in wild *R. roxellana*

No	Animal ID	Age class	Gender	L ¹	R ²	Percentage ³	HI	ABS-HI
1	bbe	Adult	male	23	47	67.14	0.34	0.34
2	bb-j140	Juvenile	female	28	13	68.29	-0.37	0.37
3	bb-j40	Juvenile	female	33	13	71.74	-0.43	0.43
4	bzt-j250	Juvenile	female	14	27	65.85	0.32	0.32
5	eq	Adult	male	39	0	100.00	-1.00	1.00
6	ff	Adult	female	129	2	98.47	-0.97	0.97
7	fg-j30	Juvenile	female	118	26	81.94	-0.64	0.64
8	fhtp	Adult	female	27	4	87.10	-0.74	0.74
9	fp-j20	Juvenile	female	43	12	78.18	-0.56	0.56
10	hm-3	Juvenile	female	23	10	69.70	-0.39	0.39
11	hto	Adult	male	66	3	95.65	-0.91	0.91
12	huj-4	Juvenile	male	47	27	63.51	-0.27	0.27
13	jba	Adult	male	65	0	100.00	-1.00	1.00
14	jb-j20	Juvenile	female	54	4	93.10	-0.86	0.86
15	jdi	Adult	female	10	43	81.13	0.62	0.62
16	jgu	Adult	female	82	0	100.00	-1.00	1.00
17	lm-3	Juvenile	male	6	80	93.02	0.86	0.86
18	rx-j30	Juvenile	female	36	0	100.00	-1.00	1.00
19	rx-j41	Juvenile	male	34	5	87.18	-0.74	0.74
20	sd	Adult	female	66	12	84.62	-0.69	0.69
21	thu	Adult	female	2	56	96.55	0.93	0.93
22	wxf2	Adult	female	3	46	93.88	0.88	0.88
23	xh	Adult	male	1	69	98.57	0.97	0.97
24	yli	Adult	female	50	0	100.00	-1.00	1.00

¹L: The number of responses made with the left hand

²R: The number of responses made with the right hand

³Percentage: The percentage of use of the preferred hand

Table 2

Bout data on hand preference for the tube task in wild *R. roxellana*

No	Animal ID	Age class	Gender	L ¹	R ²	Percentage ³	HI	ABS-HI	z-score	Category ⁴
1	bbe	Adult	male	5	10	66.67	0.33	0.33	1.29	Ambiguous-handed
2	bb-j140	Juvenile	female	11	3	78.57	-0.57	0.57	-2.14	Left-handed
3	bb-j40	Juvenile	female	8	4	66.67	-0.33	0.33	-1.15	Ambiguous-handed
4	bzt-j250	Juvenile	female	4	6	60.00	0.20	0.20	0.63	Ambiguous-handed
5	eq	Adult	male	8	0	100.00	-1.00	1.00	-2.83	Left-handed
6	ff	Adult	female	25	1	96.15	-0.92	0.92	-4.71	Left-handed
7	fg-j30	Juvenile	female	25	5	83.33	-0.67	0.67	-3.65	Left-handed
8	fhtp	Adult	female	7	1	87.50	-0.75	0.75	-2.12	Left-handed
9	fp-j20	Juvenile	female	14	5	73.68	-0.47	0.47	-2.06	Left-handed
10	hm-3	Juvenile	female	9	4	69.23	-0.38	0.38	-1.39	Ambiguous-handed
11	hto	Adult	male	11	2	84.62	-0.69	0.69	-2.50	Left-handed
12	huj-4	Juvenile	male	11	7	61.11	-0.22	0.22	-0.94	Ambiguous-handed
13	jba	Adult	male	16	0	100.00	-1.00	1.00	-4.00	Left-handed
14	jb-j20	Juvenile	female	14	2	88.00	-0.75	0.75	-3.00	Left-handed
15	jdi	Adult	female	3	8	73.00	0.45	0.45	1.51	Ambiguous-handed
16	jgu	Adult	female	18	0	100.00	-1.00	1.00	-4.24	Left-handed
17	lm-3	Juvenile	male	2	22	92.00	0.83	0.83	4.08	Right-handed
18	rx-j30	Juvenile	female	8	0	100.00	-1.00	1.00	-2.83	Left-handed
19	rx-j41	Juvenile	male	7	2	78.00	-0.56	0.56	-1.67	Ambiguous-handed
20	sd	Adult	female	12	4	75.00	-0.50	0.50	-2.00	Left-handed
21	thu	Adult	female	2	15	88.00	0.76	0.76	3.15	Right-handed
22	wxf2	Adult	female	1	12	92.00	0.85	0.85	3.05	Right-handed
23	xh	Adult	male	1	16	94.00	0.88	0.88	3.64	Right-handed
24	yli	Adult	female	14	0	100.00	-1.00	1.00	-3.74	Left-handed

¹L: The number of responses made with the left hand

²R: The number of responses made with the right hand

³Percentage: The percentage of use of the preferred hand

⁴Category of hand preference based on the index of the z-score