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Hand preference by black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) in captivity: Influence of tasks and sexes

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Task complexity (Fagot & Vauclair 1991), bimanual complementary role differentiation (Uomini 2009), and the obligate use of a particular hemisphere (Rogers, 2009) have been proposed to explain why hand preferences in non-human primates are often influenced by tasks. We examined how tasks (reaching, carrying, extractive foraging, and object manipulation) and gender influenced hand preference in 11 adult black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) out of a total of 13 known adult captive individuals of this species. A logistic regression was used to analyse 2556 bouts of binary left- vs right- hand use data. The explanatory variables are tasks, gender, and the interaction of tasks and gender. Hand preference is influenced by the task, in that subjects used the right hand significantly more often for extractive foraging and object manipulation than for reaching and carrying. We also found a significant interaction of sex and task: males used the left hand significantly more often than females for reaching and carrying, respectively, but not for extractive foraging or object manipulation. This is the first study on hand preference in *R. bieti*. As predicted,

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the hand preference in *R. bieti* is not a fixed property of the species or sexes but depends on the task.

Keywords: Handedness; Reaching; Object manipulation; Gender difference; Bimanual task.

Humans are predominantly right-handed across a variety of behaviours (Corballis, 2003; Papademetriou, Sheu, & Michel, 2005; Toga & Thompson, 2003). This phenomenon is called handedness, which has been a central issue in human evolution (Corballis, 2003; Damerose & Vauclair, 2002; Harris, 2000; Kelly, 2001; Lazenby, 2002). Evaluation of hand laterality, as with other phenomena reflecting hemispheric specialisation of function, in current living non-human primates helps scientists to understand the origins of handedness in human (Uomini, 2009) or more generally to understand the hemispheric specialisation among vertebrates from the viewpoints of both evolutionary biology and neuropsychology (MacNeilage, Rogers, & Vallortigara, 2009; Vallortigara & Rogers, 2005; Vallortigara, Rogers, & Bisazza, 1999).

Hand preference in non-human primates is often task specific (McGrew & Marchant, 1997a). Categories of behaviour that subjects perform are referred to as “tasks”. Degree of task complexity (Fagot & Vauclair, 1991) and bimanual complementary role differentiation (Uomini, 2009) have been proposed as task-specific factors affecting hand preference. Fagot and Vauclair (1991) argued that low-level tasks, e.g., reaching for food and other routine actions, comprise grossly regulated, familiar, practised, simple activities requiring undemanding cognitive processes, and lead to symmetrical hand use patterns in the non-human primate population. High-level tasks, e.g., precise object manipulation, comprise novel, fine-tuned motor acts that are demanding both spatio-temporally and in terms of complex cognition, and lead to asymmetrical hand use patterns in the non-human primate population. In the bimanual complementary role differentiation model, one hand executes high-frequency tasks (involving finer temporal and spatial resolution) while the other hand performs low-frequency tasks (such as supporting an object) (Uomini, 2009). Both Fagot and Vauclair’s model and the bimanual complementary role differentiation model dichotomise tasks, but McGrew and Marchant (1997a) emphasised that task complexity should be a graded continuum. Empirical studies also suggest that species vary in the task specificity of their handedness (Hook & Rogers, 2008). Rather than determining the degree of task complexity per se in all species in Fagot & Vauclair’s theory, the third theory hypothesizes that the task demand for the obligate use of one hemisphere, which is related to hand/paw preference, is species-specific, i.e., the same task may demand

different use of one hemisphere in different species and thus results in different hand preference in different species. To localise the obligate use of the processing specialisation of one hemisphere, we further suggest using measurements independent of the hand preference data but from non-invasive neurological methods. Such neurological methods include the Wada procedure (Wada & Rasmussen, 1960), transcranial magnetic stimulation (Schluter, Rushworth, Passingham, & Mills, 1998), and functional brain imaging (Ries et al., 2004) if technologically feasible.

Sex influences paw preference in dogs (Quaranta, Siniscalchi, Frate, & Vallortigara, 2004) and cats (Wells & Millsopp, 2009) and hand preference in non-human primates (Ward, Milliken, & Stafford, 1993). A delay of left-hemisphere growth due to elevated testosterone level *in utero* in males (Toga & Thompson, 2003) and the absence of the right-shift genotype (Geschwind, Miller, DeCarli, & Carmelli, 2002) has been proposed to explain the greater incidence of left-handedness in human males.

The genus of snub-nosed monkeys (*Rhinopithecus*, Colobinae, Cercopithecidae), which comprises four endangered species (IUCN 2008 Red List), has been subject to little study on lateral preferences (McGrew & Marchant, 1997a). Neuroanatomical asymmetry in sulcus principalis was found in *R. roxellana* and *R. bieti* (Ma, Cai, & Tian, 1992). Only *R. roxellana* (Liang & Zhang, 1998; Ma, Tian, & Deng, 1988; Zhao, Gao, & Li, 2010; Zhao, Gao, Li, & Watanabe, 2008a; Zhao, Ji, Watanabe, & Li, 2008b; Zhao, Li, & Watanabe, 2008c) were studied on lateral preference. The theory of task complexity was supported in *R. roxellana* (Zhao et al., 2010). *R. bieti* is the most sexually dimorphic (Jablonski & Pan, 1995) species within the genus. It is closely related to *R. roxellana* (Jablonski, 1998) and difficult to observe due to the physical conditions of the habitat of *R. bieti* in the wild (Xiao, Ding, Cui, Zhou, & Zhao, 2003).

This study, which includes all known adult captive *R. bieti* in the world (Long, Craig, Zhong, & Xiao, 1996) except two from the Beijing Zoo, evaluates the effects of tasks and gender on hand preference of (1) reaching for food, (2) carrying, (3) extractive foraging, and (4) object manipulation in *R. bieti*. We expected that hand preference would be task specific, based on the fact that task specificity had been observed in its close relative *R. roxellana* as well as in other non-human primates.

METHOD

Subjects and housing

Table 1 provides subject information and housing groupings for the 11 subjects studied (6 females and 5 males). All the subjects originated from the Gemorong wild group (Long et al., 1996). Each animal in Kunming

Institute of Zoology (KIZ), Yunnan, China has an identity number according to its birth order. In the daytime animals in KIZ were kept in two outdoor cages (each 66 m² × 4 m height). In the daytime animals in Kunming Zoo (KZ), Yunnan, China, were kept in two outdoor grid cages (each 140 m² × 4 m). All animals were sampled, but only adults (>2 years old) were analysed on the grounds of homogeneous, completed maturation (McGrew & Marchant, 1997a, p. 209). All subjects were naïve to any experiments. All subjects, who had been observed by the observer of this study since September 2004 (6 months prior to data collection), were habituated to the observer.

Data collection

Data on hand preference were collected using focal animal and ad libitum sampling techniques (Altmann, 1974) between February 21st and April 30th 2005. Each focal session was 10 minutes long. Efforts were made to ensure that samples were evenly distributed throughout the day and 10 minutes/session × 28 sessions = 280 minutes focal time were collected equally for each sub-adult or adult subject. If the focal animal was out of sight, ad libitum sampling of another individual was made until one more un-sampled subject of the schedule appeared, and the previous record of the focal animal was also treated ad libitum. All occurrences of the following defined hand use behaviours were recorded continuously by event sampling.

TABLE 1
Subjects: Captive *Rhinopithecus bieti*, excluding four aged ≤2 yrs

Subgroup	Identity ¹ (age or year of birth)	Mother/father
Kunming Institute of Zoology (KIZ)-Cage A	f1 (>15yrs)	Wild born
	f2 (>15yrs)	Wild born
	m5 (>15yrs)	Wild born
	f22 (2001)	f2/m5
KIZ-Cage B	m16 (1997)	f1/m5
	m18 (1999)	f3/m5
	f17 (1998)	f4/m5
	f19 (1999)	f2/m5
Kunming Zoo (KZ) Cage A	m1 ² (1997)	f2 or f3/m5
	f (>15yrs)	Wild born
KZ Cage B	m2 ³ (about 1989)	Wild born

¹f, female; m, male. Of KIZ subjects, Arabic numerals in the identity indicate birth order.

²Transferred from KIZ in 1999, and his mother should be f2 or f3. ³Supposed to be about 4 years old in 1992 on arrival at KZ.

Definition of behaviours

When there are repeated or consecutive behavioural responses in performing the same task, each response is an event, whose direction (left vs right) can potentially be affected by the previous event (Hopkins, 1999; McGrew & Marchant, 1997a) and thus not independent of each other. To define relatively independent data points we use “bout” as the unit of independent behavioural responses. The independence of data points (bouts) is safeguarded by the behavioural criterion: each lateralised action was preceded by a non-lateralised action (Harrison & Byrne, 2000) as detailed in the following definition of tasks.

Reaching. This occurred when subjects extended the forelimb towards an attached or detached food item to pick the food item up (Panger, 1998). Food items included pieces of shoots, grasses, leaves, fruits, and whole cherry tomatoes on the ground or in the baskets, and balls of artificial food (Ji et al., 1998) from a right-handed zoo keeper’s hand one at a time, in KIZ and KZ. *R. bieti* did not use opposable grips (cf. Spinozzi, Truppa, & Lagana, 2004) to pick up food items in our study. To preclude hand use bias from the fact that one hand had already held an object, both hands of the subject needed to be empty at the beginning of a reach. To avoid enlarged sample size, continuous pickings-up of food items with only finger movements within one arm extension movement were counted as one bout.

Carrying. This occurred when a subject transported an object in either hand for \geq one metre. After a subject moved for \geq one metre, the bout ended if the subject stopped moving, changed hand, manipulated the object bimanually, or ate the object. Instances of carrying with the mouth and carrying two objects with both hands (two objects) were omitted. Subjects were never observed to carry one object using two hands. Adult and sub-adult subjects carried food with quadrupedal posture.

Extractive foraging. This occurred when subjects used the dominant hand to take seeds, stones, and anything inedible out of fruits, while the subordinate hand held the same fruit. Extractive foraging on the same fruit was counted as one bout no matter how many repeated diggings-out or pickings-out of seeds or stones of the held fruit, or peeling of the fruit pericarp, occurred. However, if the subjects began to feed or hold the fruit with both hands, or dropped it, the bout ended.

Object manipulation. This occurred when subjects manipulated a non-food object with the manipulative hand through the metal cage grids while

the supportive hand kept the balance of the subject's extended or posturally adjusted body. The objects manipulated were the cage parts, the plants growing outside the cage, or naturally formed icicles hanging from the cage roof. Object manipulation is distinct from the other tasks because subjects had to get the objects through the holes of the cage grids, which required the subjects to support their body weight via the non-object-manipulating hand.

Each time a subject touched, dug, grasped, or otherwise manipulated an object was coded as an event. When the subject continued using one hand to manipulate an object, no matter how many events occurred, it was counted as one bout. If a fixed object became loose during manipulation, and the subject then pounded or rubbed the obtained object against a substrate to make noise and perhaps raise the attention of peers, the sequence of events was still scored as the same bout. However, if the subject changed hand a new bout began. The bout ended if the subject changed the supportive hand, or if the subject neither manipulated the object nor looked at the object for more than 3 seconds. Object manipulation of *R. bieti* was spontaneous without intentional provision of raw material, problems posed by humans, or human demonstration.

Data processing

For each individual, the handedness index (HI) and z -score were calculated. $HI = (\#R - \#L) / (\#R + \#L)$, in which $\#L$ is the number of left-handed bouts and $\#R$ is the number of right-handed bouts. A binomial z -score based on the frequency of right- and left-hand bouts was calculated to classify each subject as right-handed ($z > 1.96$), left-handed ($z < -1.96$), or non-preferent (i.e., non-bias or ambilateral) ($-1.96 \leq z \leq 1.96$) (Hopkins, 1999; Parnell, 2001; Westergaard, Lussier, & Higley, 2001).

To examine the influence of tasks and gender on hand preference we utilised two analyses; one of mean HI values within each task, the other a logistic regression calculated in SPSS 16.0. The logistic regression was applied to the binary dependent behavioural measurement: the left vs the right hand. In a logistic regression the dependent variable should be dichotomous but no assumptions are made about the distributions of the explanatory variables (Cohen, Cohen, West, & Aiken, 2003). The mixed factorial design of the logistic regression model did not treat data from the same subject as though they were independent (i.e., no pooling fallacy). Instead, the correlation of data within subject was treated by coding subject variability as described by Keppel and Zedeck (2006) for mixed factorial designs (pp. 308–311). Tasks (reaching, carrying, extractive foraging, and object manipulation), sexes (male and female), interaction of tasks and

sexes, and the vectors for coding subject variability were entered simultaneously into the model. All tests were two-tailed with the alpha set at 0.05.

RESULTS

A total of 2585 bouts of behaviours from all the sub-adult and adult subjects were recorded. Since a minimum of six cases are needed to produce a statistically significant result (Binomial test, $p < .05$, two-tailed), as recommended by McGrew and Marchant (1997a), analysis was limited to data with more than five bouts of behaviours for a task and for each subject (i.e., the number of total bouts in a cell of Table 2 must be greater than five for the data in this cell to be included in the analysis). Thus 2556 bouts of behaviours comprised the data set for analysis excluding categories with fewer than 6 bouts.

Hand preference at the individual level

Table 2 shows the number of right vs left responses, HI values, and z -scores for each task (in a column) and each individual (each row). The individual level of hand preference was revealed according to individual's z -scores. A total of 8 out of 11 subjects showed significant hand preference for reaching in either direction, 2 out of 6 subjects showed significant hand preference for carrying, 2 out of 6 subjects showed significant hand preference for extractive foraging, and 1 out of 5 subjects showed significant hand preference for object manipulation.

To test the reliability, for each task we ran the Spearman Correlation (Harrison & Byrne, 2000, p. 16) between the degree of hand use (absolute value of z -score and HI value and absolute value of HI value, in addition) and sample size (number of bouts per subject). There was no significant correlation in any task with regard to any measure of hand use (Table 3).

We further modified Palmer's (2002, pp. 194–196) test on the influence of sample size and hand use by dividing the existing reaching data of each individual into four groups, each of 25%, 50%, 75%, and 100% of the original sample size for reaching data. The group that was 100% of its original size is the original data set, and the estimated HI value for each monkey is the original HI value for each monkey. For the group that was 75% of the original size, we randomly selected 75% of the original data without replacement and calculated a HI value for this particular small sample. This process was iterated 100 times, and produced 100 HI values for each smaller sample. The mean of the 100 HI values thus gained estimated

TABLE 2
Hand preferences in 11 subjects: Captive *R. bieti*

Subjects	Handedness ¹	Reaching	Carrying ²	Extractive foraging	Object manipulation
f1	R/(R+L)	86/138	2/3	8/9	1/1
	HI	0.246		0.778	
	z-score	2.89**		2.33**	
f2	R/(R+L)	70/141	14/23	4/4	
	HI	-0.007	0.217		
	z-score	-0.08	1.04		
m5	R/(R+L)	34/93	6/19	10/10	
	HI	-0.269	-0.368	1.000	
	z-score	-2.59**	-1.61	3.16***	
m16	R/(R+L)	85/170	5/17	5/5	3/4
	HI	0.000	-0.412		
	z-score	0.00	-1.70		
f17	R/(R+L)	136/186	3/4	5/10	17/24
	HI	0.462		0.000	0.417
	z-score	6.31***		0.00	2.04*
m18	R/(R+L)	93/196	4/16	12/18	27/45
	HI	-0.051	-0.500	0.333	0.200
	z-score	-0.71	-2.00*	1.41	1.34
f19	R/(R+L)	116/161	13/25	3/6	15/27
	HI	0.441	0.040	0.000	0.111
	z-score	5.60***	0.20	0.00	0.58
f22	R/(R+L)	172/303	20/28	9/15	27/45
	HI	0.135	0.429	0.200	0.200
	z-score	2.36*	2.27*	0.77	1.34
m1	R/(R+L)	78/191	11/19	4/2	6/9
	HI	-0.183	0.158		0.333
	z-score	-2.53*	0.69		1.00
f	R/(R+L)	257/438	8/11	4/4	
	HI	0.174	0.455		
	z-score	3.63***	1.51		
m2	R/(R+L)	39/150	5/13	2/2	
	HI	-0.480	-0.231		
	z-score	-5.88***	-0.83		

¹R, raw number of right-hand bouts; L, raw number of left-hand bouts; (R+L): raw total number of bouts; *Handedness Index (HI)* = $\frac{R-L}{R+L}$; zp: binomial z-score and p-value (*, $p < .05$; **, $p < .01$; ***, $p < .001$). ²Struck through = $n \leq 5$ per individual; blank = no record.

the HI value of that particular monkey if the sample size had been reduced to 75% of its original size. Similarly, we estimated the HI values of reaching data if sample size had been reduced to 50% and 25% of its original size for each monkey. Then we ran a one-way ANOVA with the groups as explanatory variable and the estimated HI value as the response variable.

TABLE 3
Spearman rank correlation between number of bouts and measurement of hand preference

Task	N	HI		Absolute value of HI		Absolute value of z-score	
		Coefficient	Sig.	Coefficient	Sig.	Coefficient	Sig.
Reaching	11	0.218	0.519	-0.300	0.370	-0.064	0.853
Carrying	9	0.226	0.559	-0.460	0.213	-0.017	0.966
Extractive foraging	6	0.191	0.717	0.191	0.717	0.191	0.717
Object manipulation	5	-0.579	0.306	-0.579	0.306	0.158	0.800

The estimated HI values were not significantly different across groups, $F(3, 40) < 0.001$, $p > .999$.

The influence of tasks and sexes on the hand preference

Table 4 shows the results of the logistic regression. A significant main effect of tasks and a significant interaction of sexes by tasks were found. Gender itself did not significantly influence the choice of the left vs right hand (Wald $\chi^2 = 0.064$, $df = 1$, $p = .801$). The Hosmer and Lemeshow Test and Nagelkerke R-squared showed that the overall logistic regression model was a good fit of the observed data.

TABLE 4
Logistic regression model for predicting left- vs right-hand response ($n = 2556$)

Significant variables	Wald χ^2	df	Sig.
Tasks	16.554	3	0.001
Reaching-object manipulation	5.018	1	0.025
Carrying-object manipulation	5.190	1	0.023
Interaction of sexes and tasks	13.919	3	0.003
Sexes by reaching	4.494	1	0.034
Sexes by carrying	5.646	1	0.017
Overall model statistics	χ^2	df	Sig.
Hosmer and Lemeshow Test	1.386	7	0.986 ^a
Nagelkerke R-squared	0.077		

^aThe logistic regression model's prediction fits the observed data very well. Significance for Hosmer and Lemeshow Test greater than 0.05 is desired.

The influence of tasks. From Table 4, the significant difference of the predicted probability of a left- vs right-hand response between reaching and object manipulation and the significant difference between carrying and object manipulation was responsible for the main effect of the tasks on which hand was chosen. There was no significant difference between extractive foraging and object manipulation (Wald $\chi^2 = 2.908$, $df = 1$, $p = .088$). The proportions of the observed bouts of right-hand use out of total bouts were 0.538 ($n = 2167$), 0.503 ($n = 171$), 0.691 ($n = 68$), and 0.613 ($n = 150$) for reaching, carrying, extractive foraging, and object manipulation, respectively. That is, subjects used the right hand more often for extractive foraging and object manipulation than for reaching and carrying.

The deviations of the left- vs right-hand use for each task were accessed by a one-sample t -test against zero. Subjects showed symmetrical use of hands for reaching (mean HI = 0.04, $n = 11$, $t = 0.49$, $p = .636$) and carrying (mean HI = -0.02, $n = 9$, $t = -0.19$, $p = .851$). Subjects used the right hand significantly more often (H_a : mean HI $\neq 0$) than equal left- and right-hand use (H_0 : mean HI = 0) for object manipulation (mean HI = 0.25, $n = 5$, $t = 4.64$, $p = .010$). Subjects used the right hand more often than equal left- and right-hand use for extractive foraging but the test narrowly missed significance (mean HI = 0.39, $n = 6$, $t = 2.27$, $p = .073$). There was no significant difference for the strength of hand preference (the absolute value of HI) across tasks (Kruskal-Wallis test), $\chi^2(3, N = 31) = 1.207$, $p = .75$.

The interaction of sexes by tasks. The sexes differed significantly at reaching and carrying, in that females used the right hand more while males used the left hand more, but the sexes did not differ at extractive foraging or object manipulation (see Table 4). For reaching, the proportion of observed bouts of right-hand use out of total bouts for females as a whole was 0.612 ($n = 1367$), and 0.411 ($n = 800$) for males. For carrying, the proportion of observed bouts of right-hand use out of total bouts for females was 0.632 ($n = 87$), and 0.369 ($n = 84$) for males.

For each task the difference between the mean HI in males and females was evaluated by two independent sample t -test. The sexes also did not differ at extractive foraging or object manipulation. The sexes differed significantly at reaching (mean HI for 5 males = -0.20, mean HI for 6 females = 0.24, $t = 3.89$, $p = .004$) and carrying (mean HI for 5 males = -0.27, mean HI for 4 females = 0.29, $t = 3.55$, $p = .009$).

DISCUSSION

This is the first study to document hand preference in *R. bieti*. We found that hand preference in *R. bieti* was task specific. Hand preference for object

manipulation was significantly more asymmetric (towards the right) than reaching and carrying, respectively; it was not significantly different from extractive foraging. Finally, for reaching and carrying females preferred the right hand significantly more than males.

Reliability

We discuss the reliability of the results with regard to the variation in the number of bouts per subject per task. Due to the limited total number of captive *R. bieti* on earth and the uneven occurrences of behaviour within each task, many bouts were collected for reaching, but not for the other tasks in our study. The uneven occurrences of behaviour within different tasks reflect the nature of different tasks. A routine action, such as reaching for food (Fagot & Vauclair, 1991, p. 81), happens more frequently than other actions for subjects exhibiting their own behavioural repertoire than for subjects in a controlled experimental setting. In general, the more natural the setting, the more valid the results are likely to be (McGrew & Marchant, 1997a). On the other hand, the rare occurrences of carrying, extractive foraging, and object manipulation reduced the possibility for data points in those tasks to be inflated because of temporal and spatial scarcity (McGrew & Marchant, 1997a) in addition to our pre-defined behavioural criterion.

However, the variation in the number of bouts per subject per task can potentially be problematic if the effect size is dependent on sample size (Palmer, 2002). When there are more subjects in future field studies, it will be important to keep (the variation of) the sample sizes relatively uniform across tasks. When the sample size varies across tasks, it is very important that the mean should be independent of the sample size, which is one of the four properties of the funnel plot (Palmer, 2002). We demonstrated empirically that, in our particular study, HI values are not affected by the sample size. First, we did a test of reliability following Harrison and Byrne (2000). We found the correlation between hand use and sample size was not significant. It is desirable that there is no significant correlation between the frequency of hand use and the measure of lateral bias (Hopkins, 1999). Second, we re-sampled the reaching data and calculated the mean HI value using a variety of sample sizes, and there was no significant influence of sample size on the mean HI value. Third, further analyses were based on both HI values and a logistic regression to avoid any particular statistical method biasing the results. The results from the two lines of analyses agreed with each other. Thus we consider our results—based on an overall large data set which we were best able to collect under the data-collection constraints at the time—were not likely to be empirically biased by variations of sample size across tasks.

Effects of task complexity on hand preference

Both task complexity (high- vs low-level tasks) based on cognitive demand (Fagot & Vauclair, 1991) and bimanual complimentary role differentiation (high- vs low-frequency tasks) based on kinetics (Uomini, 2009) have positive contributions to explain the task-specific hand preference of *R. bieti* in our sample. Our discussion is organised at the task level instead of the factor level, based on the view that the two factors can be seen as a set of independent variables that have a common functional role (Cohen et al., 2003, pp. 163–170) in the hand preference. The high-frequency tasks involving finer temporal and spatial resolution, which right-handers use the right hand to perform in the bimanual complementary role differentiation model, have similar functions of asymmetric hand use pattern as the high-level tasks demanding both spatio-temporally and in terms of complex cognition in Fagot and Vauclair's model.

The lack of hand preference for reaching in this sample of *R. bieti* as a whole agreed with Fagot and Vauclair's (1991) prediction of no hand preference for reaching for a group. Low-level tasks are the grossly regulated routine acts of daily life, and reaching is a given in the low-level tasks (Fagot & Vauclair, 1991). In our study reaching for vegetarian food items did not involve precise grips, so it was grossly regulated but not fine-tuned. There was no “visually guided reaching” (MacNeilage, Studdert-Kennedy, & Lindblom, 1987) in a ballistic motion for fast-moving insects. It was one of the most routine daily actions in the subjects' life. Our result also agreed with a statistical meta-analysis that found no preference for reaching in langurs (lacking data from snub-nosed monkeys) (Table 9 in Papademetriou et al., 2005) and with results from unimanual reaching for food in *R. roxellana* (Zhao et al., 2008b). This concordance is reminiscent of the phylogenetic closeness of those langur species. The snub-nosed monkeys (or the snub-nosed langurs) (*Rhinopithecus spp*) are closely related to douc langurs (*Pygathrix spp*) (Jablonski, 1998; Li, Wei, Huang, Pan, & de Ruiter, 2004) and/or common langurs (*Presbytis spp*) (Disotell, 2000; Wang et al., 1995); *R. bieti* and *R. roxellana* are closely related to each other (Jablonski, 1998).

There have been few studies on hand preference in carrying in non-human primates, so the discussion extends to distally related species. Lack of hand preference for carrying for this sample as a whole disagreed with results from captive bonobos, which had a significant left lateral bias in carrying objects, food, and infants (Hopkins, Bennett, Bales, Lee, & Ward, 1993; Hopkins & de Waal, 1995). The discrepancy resulted from differentiation in items carried because the bonobo study included bonobos carrying infants, but our study excluded monkeys carrying infants. Since infant carrying was reported to be left biased in most primates (for review see Damerose &

Vauclair, 2002), a left bias is more likely to be found in a study that involved infant carrying, such as the bonobo study, than in a study that excludes infant carrying, such as ours. For carrying, our results from a quadrupedal locomotor pattern in *R. bieti* were not comparable with results from capuchin monkeys because capuchins and *R. bieti* carry with different postures. Capuchin monkeys carry with bipedal or tripedal postures, and sometimes hold items against their chests. For example, the white-throated capuchin monkeys preferred a right hand for tripedal carrying (Fagot & Vauclair, 1991) and the tufted capuchins lacked hand preference for carrying (mixed with 166 bipedal and 382 tripedal responses) (Westergaard, Haynie, Lundquist, & Suomi, 1999). Wild bearded capuchins (*Cebus libidinosus*) carried heavy hammer stones bipedally (Liu et al., 2009). Carrying in capuchins was difficult to classify in the low- vs high-level/frequency tasks (Panger, 1998), and so was carrying in *R. bieti*.

Extractive foraging involved bimanual coordination (McGrew & Marchant, 1997a) and bimanual hand role differentiation (Uomini, 2009). The “subordinate” hand in McGrew and Marchant’s (1997a) term, which holds the fruit, is performing “support an object” as a given example of a low-frequency task of the bimanual complementary role differentiation model. The bimanual complementary role differentiation model could have proposed an empirical and independent measurement of the degree of “finer spatial and temporal resolution” in the high-frequency task of the bimanual complementary role differentiation model. As suggested by McGrew and Marchant (1997a), an independent measurement of the gradation of the task complexity in Fagot and Vauclair’s (1991) model would also help to calibrate the degree of task complexity for extractive foraging.

For object manipulation, our results agreed with Fagot and Vauclair’s (1991) prediction of an asymmetric pattern of hand use in high-level tasks. Subjects showed asymmetric patterns of hand use in object manipulation: subjects were significantly more likely to use the right hand than to use the left vs right equally (as was revealed by the one-sample *t* test), and than for reaching and carrying (as was revealed by the logistic regression). Object manipulation is a given example of high-level tasks involving novel and fine-tuned motor acts in Fagot and Vauclair’s (1991) model. Examples of object manipulation in this study, such as twisting a screw nut and moving a metal plate between meshes with the index finger, could not be found in nature and instances happened in young adults only. Thus object manipulation was novel and needed precise manipulation, but cannot be a routine act since it happened at rare instances. If the spatial-temporal resolution of the object manipulation could be measured as “finer” as in a high-frequency task, the bimanual complementary role differentiation model further pointed out that right-handers use the right hand more often in high-frequency tasks. In

addition, for the object manipulation to be asymmetric in our sample, the hand preference was significantly more towards the right hand, which coincided with the bimanual complementary role differentiation model's prediction. As was reported in wild capuchin monkeys (Panger, 1998), the objects obtained in our study were pounded or rubbed against a substance to make noise, and cagemates would approach the subject with the noise-making object without making the alarm vocalisation for noisy objects not controlled by subjects (such as the noise of motor vehicles that were invisible to the monkeys). Whether the subjects intended to evoke play by manipulating the object as "toys" (McGrew & Marchant, 1997b) remains an open question.

Sex differences at carrying and reaching

However, sexual dimorphism, hormones, differential hemispheric development, and differential hemispheric arousal in the sexes are related to sex effects on hand preference (Ward, Milliken, Dodson, Stafford, & Wallace, 1990; Ward et al., 1993). In our study we found a sex effect on hand preference for reaching and carrying but not extractive foraging and object manipulation. The absence of a significant sex effect on extractive foraging or object manipulation could merely be due to the much smaller number of bouts collected on both tasks. For the sex effect on reaching, our results were different from those from *R. roxellana*. Zhao et al. (2008b) found no sex effect on the direction and strength of *R. roxellana*'s hand preference in unimanual reaching. Ma et al. (1988) found male *R. roxellana* ($n = 8$) used their right hand more often than females ($n = 4$) in picking up food thrown far away from the subjects. The causes of the difference in the two studies on *R. roxellana* were discussed in Zhao et al. (2008b). If both Zhao et al.'s (2008b) conclusion (no sex effect on hand preference in *R. roxellana*) and ours (males preferred the left hand for reaching and carrying significantly more often than females in *R. bieti*) were correct, then the differential sex effect on hand preference between *R. roxellana* and *R. bieti* might correlate to the sexual dimorphism between the two species. If sexual dimorphism results in the sex difference in hand preference (Ward et al., 1990, 1993), and if *R. bieti* is sexually more dimorphic than *R. roxellana* (Jablonski & Pan, 1995), then it is reasonable to find a stronger sex effect on hand preference in *R. bieti* than in *R. roxellana*, which agrees with the results from Zhao et al.'s (2008b) study and our study.

This study adds the species *R. bieti* to a body of literature testing hand preference among non-human primates, and enables future meta-analysis because the study qualifies the seven criteria for meta-analysis (McGrew &

Marchant, 1997a) and provides precise descriptions of the tasks and individual data for future analysis (Papademetriou et al., 2005).

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