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Patterns and laterality of hand use in free-ranging aye-ayes (*Daubentonia madagascariensis*) and a comparison with captive studies

Stanislav Lhota · Tomáš Jůnek · Luděk Bartoš

Abstract We observed hand use in free-ranging aye-ayes (*Daubentonia madagascariensis*) on an island in the Mananara River, eastern Madagascar. The results were compared with those of two conflicting studies on hand laterality in captive aye-ayes. We argue that patterns of hand preference in wild aye-ayes are comparable to those of captive animals and that discrepancies between studies are—at least partly—caused by different ways of collecting and processing data. Aye-ayes fit Level 2 of the categories of hand laterality described by McGrew and Marchant (Yearb Phys Anthropol 40:201–232, 1997), with some individuals showing significant hand preference, but with the proportion of right- to left-preferent animals being very close to 1:1. We observed hand preference to be consistent for two of the most frequent behaviors, tapping and probing with fingers. Reaching and holding objects in hands is rare in aye-ayes, and the patterns of hand use in aye-ayes are therefore not directly comparable with those of other prosimians in which laterality has been studied. We detected no effect of sex on hand preference and were unable to determine whether there is an effect of age. The posture adopted by the animals did not influence hand preference.

Keywords *Daubentonia madagascariensis* · Foraging · Hand · Laterality · Madagascar · Primates · Prosimians

Introduction

While some researchers have proposed that the predominance of right-handedness is unique to humans (Warren 1980; McGrew and Marchant 1997), others believe that laterality in hand use is a very ancient trait that we share with non-human primates (MacNeilage et al. 1987; Ward 1995). Hand (or paw or foot) laterality has been reported in a diverse range of animals, such as toads, parrots, chickens, cats, dogs, rats, mice, lemurs, bushbabies, monkeys, and apes (for review see Hook 2004). McGrew and Marchant (1997) proposed several categories of hand laterality in primates. In this paper, we will consider their basic category, *hand preference*, which describes a significant bias in hand use in any direction (right or left) in a given animal and in a given task that needs not be stable between individuals and tasks.

Prosimians appear to show a bias for using the left hand for visually guided reaching (Sanford et al. 1984; Larson et al. 1989), which has sometimes been found to be stronger in males (Ward et al. 1990; Milliken et al. 2005). The strength of laterality but also the proportion of animals that show the right-hand bias may increase with age (Ward et al. 1990). A predominantly right-hand preference is sometimes found in females (Milliken et al. 1991; Dodson et al. 1992) and possibly in old animals (Forsythe and Ward 1988).

S. Lhota (✉)
Department of Zoology, Faculty of Science,
University of South Bohemia, Branišovská 31,
370 05 České Budějovice, Czech Republic
e-mail: stanlhota@yahoo.com

S. Lhota
Ústí nad Labem Zoo, Drážďanská 23,
400 07 Ústí nad Labem, Czech Republic

T. Jůnek
Department of Zoology, Faculty of Science,
Charles University, Viniènà 7, Prague, Czech Republic

L. Bartoš
Ethology Group, Institute of Animal Science,
Praha-Uhříněves, Czech Republic

The aye-aye (*Daubentonia madagascariensis*) from Madagascar is remarkable among prosimians for its advanced specialization of the hand. This animal forages on mechanically defended food resources, such as nut kernels or wood-boring insects, which it can access using its rodent-like incisors (Sterling 1994). The thin third finger rapidly taps on the surface, enabling the animal to inspect the internal structure by perceiving resonations (Erickson 1994). After opening a cavity, the aye-aye probes inside with one of its two specialized fingers (third or fourth) to extract the contents (Lhota et al. 2008). Although it has never been studied in the wild, it is likely that the specialized manner in which the aye-aye acquires food requires a long period of learning foraging skills (Krakauer 2004). Referring to the aye-aye's unique patterns of hand use, Feistner et al. (1994) raised the question of whether the patterns of the aye-aye hand preference also follow the patterns described for some other prosimians.

Being nocturnal, rare and cryptic, aye-ayes are not easily observed in the wild. We have taken opportunity to study details of hand use in well-habituated free-ranging aye-ayes in eastern Madagascar. In contrast to previous studies on prosimians, we did not concentrate only on selected specific examples of hand use behavior. Instead, we recorded all types of non-positional hand use that occurred during our observations (although the hand use in the context of social behavior occurred too infrequently to be captured by our sampling method). Here, we present descriptive data on the observed patterns of hand use with the aim of determining whether these patterns can be directly comparable with those investigated in previous laterality studies in prosimians. We subsequently test whether there is lateral preference in these hand use behaviors in individual aye-ayes.

We also addressed the question of whether there is any effect of body position on the strength of hand use laterality. The evolutionary scenario presented by MacNeilage et al. (1987) associates the prosimian left hand bias to the posture-related hand preference pattern they hypothesized for anthropoids. Other authors have proposed specific effects of body posture on the strength of hand laterality. It has been argued that when an animal adopts an unstable position (such as a bipedal stance in a lesser bushbaby, *Galago senegalensis*, or a specific sitting position in ruffed lemurs, *Varecia variegata*), the need for a coordinated input from the neural motoric systems also activates systems responsible for laterality, thereby strengthening the laterality (Forsythe et al. 1988; Larson et al. 1989; Dodson et al. 1992). Contrariwise to this hypothesis, it has also been suggested that the need to maintain a comfortable position on branches might constrain the expression of hand preference. In gentle lemurs (*Hapalemur griseus* and *H. alaotrensis*), hand preference is stronger during feeding

on a platform than when foraging on bamboo shoots. In bamboo feeding, the lateralization was found to be stronger after a shoot was already detached from the stalk and the animal was free to re-position itself (Stafford et al. 1993). Aye-ayes employ a variety of more or less demanding body positions when using their hands, but the effect of the postural demands on the strength of hand preference has not been yet tested.

In this article, we also compare our field data with those collected earlier on captive aye-ayes. In several anthropoid primates, findings on hand preference appear to differ between the field and captive setting (Marchant and McGrew 1996; Mittra et al. 1997; Panger 1998; McGrew and Marchant 2001). This need not be the case in prosimians. Shaw et al. (2004) in their study of ring-tailed lemurs (*Lemur catta*) suggest that if there is any effect of captivity on hand preference, it may be caused by artificial food presentation. This was also shown in sifakas (Milliken et al. 2005), but in their study on gentle lemurs, Stafford et al. (1993) found a correspondence between hand preference in reaching for chopped fruits and species-specific bamboo feeding. Aye-ayes provide us with an opportunity to compare three settings: wild, captive–naturalistic and captive–test. Feistner et al. (1994) reported on natural-like free feeding in captive aye-ayes in the Jersey Wildlife Preservation Trust (JWPC; now called the Durrell Wildlife Preservation Trust, DWPC) and Duke University Primate Center (DUPC), and Milliken (1995) reported data on hand preferences in controlled test conditions in DUPC. The results of these two captive studies lead the authors to different conclusions. During free feeding, some animals did not show any significant hand preference while others were lateralized in both directions. In contrast, all four animals in the controlled test setting showed significant right hand bias in several preference and performance measures of digit use. We discussed these conflicting results in the light of our new data collected on free-feeding free-ranging aye-ayes.

Materials and methods

Study area and subjects

We observed free-ranging aye-ayes on a small (14 ha) island in the Mananara River (16°10′S, 49°44′E), close to Verezanantsoro National Park, eastern Madagascar. Most of the island is covered with mixed plantation, dominated by fruit trees, coconut palms, and secondary forest trees (Adriamasimanana 1994). The aye-ayes were introduced onto the island in the 1980s. During our fieldwork, there were four aye-ayes that were well habituated to the presence of observers: Lucy, a mature adult female; Rarach, her subadult son; Gomez, a young adult male; Koulic, a mature

adult male. All individuals could be recognized reliably from their distinct body features. The age of Rarach was estimated to be 2 years at the beginning of our study, based on consultation with experienced aye-aye keepers from DWPT and DUPC. In addition to these four animals, two new adults appeared on the island, apparently following their release by villagers. They were not habituated, but we were able to observe one of them (Darja, a young adult female) for one and a half night.

Procedure

Aye-ayes were followed by two observers (SL and TJ) between April 2003 and October 2003. Data on hand preference were collected during 83 nights. One observer usually followed the animals during their whole active period (beginning when the animals emerged from the nest until they retired to the nest), while the other observer only followed them during the first half of this active period (ending at midnight). If possible, a single individual would be followed for a given night by each observer, but in the event that the observer lost track of the focal animal, another animal would be tracked. We used light-emitting diode (LED) headlamps and binoculars (8 × 30 and 8 × 40) to observe behavior.

Behavioral sampling techniques were based on those described by Altmann (1974). There were some limitations to the data collection due to the demanding nature of nocturnal observations. Visibility was not always good enough to reliably identify which hand was used and, as a result, some bouts of hand use were missed. Although we attempted to use the continuous focal animal sampling method, we had to collect data using the ad libitum sampling method instead. In ad libitum sampling, we observed the animal continuously during the sampling period, but we recorded instances of hand use only when the animal was visible enough to allow recording details of its hand use. We also collected data using the focal instantaneous sampling in 1-min intervals. Ad libitum and focal instantaneous data were collected simultaneously during sampling periods of 30 min separated by 30-min breaks during which time the observer remained with the animal.

Four recorded categories of hand use were defined:

1. *Hold*, in which the animal holds an object in its hands, using any form of grip with more than a single finger. This includes holding any detached object and may also include holding an attached object if it represents manipulation rather than securing postural support.

2. *Tap*, in which the animal rhythmically taps on the substrate with its finger in a stereotypic, species-specific way.

3. *Probe*, in which the animal uses a single finger to insert it into any crevice and/or to insert a food item into its mouth. This includes behavior described as digit-feeding by Feistner et al. (1994).

4. *Groom*, in which the animal scratches or combs its fur (we recorded whether hands, feet, or mouth were used).

In addition to recording the category of hand use and the hand (right, left, or both), for each data entry we also described the object that was being processed and the behavioral context in as many details as practicable. We were, however, not always able to differentiate whether the aye-aye used the third or fourth finger for probing and grooming and we therefore pooled data for both fingers.

Data on body posture were also simultaneously collected with those for hand use during the focal instantaneous sampling sessions. We classified a number of postures, but most were rare and for the present analysis, we had to lump them into two broad categories: easy and demanding postures. These categories were based on our assessment of the difficulty involved in the animal securing a stable position on the substrate. *Easy postures* included sitting, lying, standing, or quadrupedal moving along a substrate inclined less than an estimated 55°. *Demanding postures* included all suspended positions, descending head-down, and clinging or moving on a substrate with an estimated inclination of 55° or more. Estimated substrate inclination was recorded to the nearest multiple of 5°; the threshold of 55° was selected post hoc as the value where the total frequency of the substrate-use instantaneous sampling points dropped most rapidly.

Data processing and analysis

We assigned sequences of consecutive data entries to bouts of hand use that we considered independent under our assumption that non-independence would result predominantly from specific requirements of the positioning on the substrate and the specific body posture adopted by the animal. Two sequences of data points were considered as two bouts if they were separated by either (1) the animal moving to another place while not engaged in tapping or probing or (2) the animal changing its body posture or mode of locomotion (while still engaged in hand use). Data entries were still considered to belong to a single bout if they were separated by an interval of inactivity or by a different behavioral act (e.g., gnawing, vigilance, or different hand use) without changing body posture or place. These criteria are more conservative than those used by most authors (McGrew and Marchant 1997). However, a sequence of continuous feeding, exploration, or grooming

could lead to several independent bouts of hand use in the event that the animal changed its place or posture.

Most of bouts of hand use were recorded as several interdependent data entries, with the beginning of the bout often noted ad libitum, and one or several additional focal instantaneous data points recorded in the case that the bout continued in the following minutes. To generate a set of independent data, we post hoc characterized the hand use for each bout in two ways. The 'first-noted hand' measure was intended to enable us to use the binomial test, as has been also used in other studies. For each bout, only the first recorded hand was considered. This was an ad libitum record (when visibility was good to note the proper beginning of sequence) or the first instantaneous entry. The disadvantage of using the 'first-noted hand' may be that it may not be representative of a whole sequence of hand use, which may last several minutes (Hopkins 1999). We therefore invented a second measure, the 'bout score'. This score is based on the focal instantaneous data points collected on a given bout and represents the difference in number of instantaneous entries for the right and left hand. A positive score represents right hand preference for a given bout.

To test for lateral biases in the 'first-noted hand' measure, we followed a procedure that has been applied in a number of previous studies on prosimians where data for each animal are analyzed using binomial tests. z-scores were computed according to the formula $z = [x - (n \cdot p)]/$ [square root $(n \cdot p \cdot q)$], where $n =$ total number of responses, $x =$ number of right hand responses, and p and q are the proportions of right and left responses, respectively, under the null hypothesis, i.e., $p = q = 0.5$ (MacNeilage et al. 1987; Ward 1995). The z-scores outside the two-tailed confidence interval of 0.05 (i.e., $-1.95 < z < 1.95$) were considered to be significant. In addition to z-scores, we also present the handedness indices (HI) computed from right (R) and left (L) hand responses according to the following formula: HI = (#R − #L)/(#R + #L) (Hopkins 1999). The HIs are descriptive measures of the magnitude of the bias.

All of the following tests were performed using JMP 3.2.2.0 (SAS Institute, Cary, NC) software, and the results were considered to be significant at $\alpha = 0.05$ level. The non-parametric Wilcoxon signed rank test was used to detect laterality in bout scores (null hypothesis; median bout score = 0). A log-linear model was applied to test for the effect of posture on hand preferences in four wild animals in Mananara, excluding the less-observed female Darja. Probing bouts rather than tapping bouts were analyzed because we had more data entries for the former; some bouts had to be omitted due to the posture not being identified. The 'first-noted hand' was used as a dependent nominal variable and individual and posture as independent variables; the interaction of the latter was also considered.

Finally, an analogous two-way analysis of variance (ANOVA) with an interaction with the 'bout score' as a continuous dependent variable was conducted.

For the combined sample of the wild animals (the study reported here) and captive animals (data extracted from the literature), we applied parametric tests for comparing HIs that did not deviate from a normal distribution. The t test was applied to compare HIs for probing and tapping in wild animals with those computed from the published data on captive aye-ayes (Feistner et al. 1994). To test for the strength of lateralization with no regard to its direction, we also analyzed absolute values of HIs. In this case, because the Levene test detected significant differences in variance between wild and captive animals, we did not use the t test but, rather, the Welch ANOVA, which allows variances to be unequal. We used the Pearson correlation coefficient to test for correlation between HIs for probing and tapping across all individuals.

After finding no significant difference in HIs, the data for wild and captive aye-ayes were pooled, and HIs for probing and tapping were analyzed as continuous dependent variables in two-way ANOVA with interaction, with age and sex as the independent variables.

Results

Hand use patterns and laterality among wild aye-ayes

We obtained a total of 1451 instantaneous sampling point entries of identified use of right, left, or both hands in wild animals in Mananara (Lucy: 492; Koulic: 230; Gomez: 262; Rarach: 417; Darja: 50). The majority of these records did not include a whole-hand grasp but rather ones in which the specialized fingers were used for tapping (215 points), probing (1075 points), grooming (113 points), and inserting into the mouth, probably cleaning teeth (13 points). Aye-ayes never used both hands simultaneously for the specialized finger tasks, and only in ten sampling points did the other hand assist by holding the object. Sequential bimanual use of fingers (i.e., alternations of both hands during a single bout of tapping, probing, or grooming) appeared to be common; this was, however, not systematically quantified.

Tapping with the third finger occurred in the context of exploration and feeding, but these two behaviors were often indistinguishable. Aye-ayes tapped most often on wood and bark, but also on coconuts, fruits, flowers, palm leaves, or aye-aye urine marks left on branches. None of the individuals showed significant z-scores for hand preference for tapping (Table 1).

Probing (including feeding with a finger) was the prevalent form of hand use. It was highly variable and could

Table 1 Frequencies of hand use, z-scores, and handedness indices describing hand preference in tapping, probing (or digit-feeding), and grooming on free-ranging aye-ayes in Mananara (present study)

Animal	Measure	Left	Right	z-score	Handedness index
Gomez (am)	Probe	26	38	1.50	0.19
	Tap	16	25	1.41	0.22
	Groom	9	7	−0.50	−0.13
Koulic (am)	Probe	28	12	−2.53*	−0.40
	Tap	6	10	1.00	0.25
	Groom	3	5	0.71	0.25
Lucy (af)	Probe	53	80	2.34*	0.20
	Tap	38	32	−0.72	−0.09
	Groom	10	14	0.82	0.17
Rarach (im)	Probe	39	46	0.76	0.08
	Tap	18	25	1.07	0.16
	Groom	10	12	0.43	0.09
Darja (af)	Probe	9	6	−0.77	−0.20
	Tap	10	6	−1.00	−0.25
	Groom	2	1	−0.27	−0.33

Asterisks indicate significance of binomial tests of hand preference (*$P < 0.05$)

am Adult male, *im* immature male, *if* immature female, *af* adult female

take the form of soft probing into minute crevices as well as relatively harsh scratching inside deep holes with either the third or fourth finger. Objects of probing included wood, bark, twigs, bamboo, coconuts, kernels, fruits, flowers, galls on bark, touchwood, palm sheaths, and palm leaves. As with tapping, the context included feeding and exploration, but these two were often indistinguishable. Based on z-scores (Table 1), there was a significant hand preference for probing in two individuals. Lucy preferably used her right hand, while Koulic preferred to use his left.

Grooming was performed with hands (113 sampling points), feet (26 points), or mouth (seven points). The aye-ayes repeatedly scratched their fur in a simple, stereotypic sequence while using their hind feet, but grooming with the hands was more variable. Besides simple scratching sequences, there were also careful and attentive bouts of less stereotyped combing of the fur. In most cases, we were able to confirm that only one finger was used, either the fourth or the third one. We did not notice any differences in hand use in allogrooming compared to grooming of own fur. As the former was very rare (four sampling points of Lucy grooming her infant), we combined both for the laterality analysis. None of the individuals showed significant z-scores for hand preference, but the sample sizes are small compared to the other measures (Table 1).

Holding objects in hands was infrequent, accounting for only 46 of 1451 hand-use sampling points, and occurred during foraging (33 points) and grooming (13 points). In foraging, this behavior accompanied gnawing (fruits, twigs, or a piece bark being peeled), inspecting of or probing detached objects (fruits, twigs, and galls on bark), and inserting a piece of coconut flesh or a big larva into the mouth. Holding whilst foraging was bimanual in 21 sampling points; the left hand only was used in eight points and the right hand only was used in four points. Due to the small sample size, the differences were not tested statistically. During grooming, the animals sometimes held their tail in their hands (being often suspended head-down by hind legs). The tail was held with both hands when grooming it with the mouth (five points); the unimanual hold was adopted only when the animal used the opposite hand for grooming (eight points). Holding was occasionally noted also outside the foraging and grooming context, such as when gnawing off twigs or leaves to build the nest or when restraining an infant.

Table 2 presents the results of Wilcoxon signed rank tests of hand preference based on the bout scores of the same animals. These tests appear to be less sensitive than the binomial tests based on the 'first-noted' hand use. The only significant result was the left hand bias shown by Koulic. However, the directions shown by the bout scores were—with no exception—the same as those shown by HIs based on 'first-noted' hand use for tapping and probing. This result suggests that the 'first-noted' hand measure is a good representative measure of the whole hand use sequence.

To test for the effect of posture on hand preference for probing, we used data for the four extensively observed animals (excluding the female Darja). The log-linear model shows that there was no effect of individual, posture, and their interaction on the 'first-noted hand' ($\chi^2_7 = 6.59$, $P = 0.47$). An analogous ANOVA with the 'bout score' as a dependent variable revealed a significant whole-model effect ($F_{7,257} = 3.60$, $P = 0.001$). Of the independent variables, however, only the effect of individual identity was significant ($F_3 = 4.21$, $P = 0.006$), with the left-handed Koulic being most divergent from the other individuals. Body posture had no significant effect on the 'bout score' either alone or in interaction with individual identity.

Laterality in the combined sample of wild and captive aye-ayes

Table 3 shows results of binomial tests for the 'first-noted hand' measure for the captive animals reported by Feistner et al. (1994), with handedness indices (HI) added. We have combined data from Tables 1 and 3 for further analyses. The modal pattern within this extended sample shows no significant hand preference and a low HI of 0.2 or less. But five of the 16 animals did show significant hand preference

Table 2 Descriptive statistics on hand use bout scores of free-ranging animals in Mananara and results of the Wilcoxon signed rank test of the hypothesis that the median bout score = 0

Animal	Measure	n	Mean bout score	Standard error	Median bout score	P
Gomez	Probe	64	0.28	0.26	1	0.202
	Tap	40	0.23	0.17	1	0.184
	Groom	16	−0.06	0.28	−1	1.000
Koulic	Probe	40	−1.83	0.62	−1	0.003**
	Tap	16	0.06	0.36	1	0.651
	Groom	8	0.38	0.38	0.5	0.531
Lucy	Probe	133	0.24	0.18	1	0.098
	Tap	70	−1.17	1.15	−1	0.295
	Groom	24	−0.13	0.34	1	0.977
Rarach	Probe	85	0.34	0.33	1	0.225
	Tap	42	0.21	1.16	1	0.221
	Groom	22	0.14	0.29	0	0.826
Darja	Probe	9	1.33	0.90	1	0.215
	Tap	6	−0.33	0.42	−1	0.688
	Groom	2	0.50	1.50	0.5	1.000

for taping and 7 did so for probing. There are significant results in both directions across the range of sample sizes and some animals have very high values of HIs.

Patterns of individual hand preferences were very similar for wild and captive aye-ayes. There are no significant differences between wild and captive animals in HIs for probing ($t_{14} = −0.06$, $P = 0.95$) and tapping ($t_{14} = −0.52$, $P = 0.61$). When comparing absolute values of HIs, the variance was lower in wild animals in both measures (probing: $F_{1,14} = 4.31$, $P = 0.06$; tapping: $F_{1,14} = 6.59$, $P = 0.02$), so we used the Welch ANOVA. There were again no significant differences between wild and captive aye-ayes (probing: $F_{1,13.999} = 2.10$, $P = 0.17$; tapping: $F_{1,12.908} = 1.23$, $P = 0.29$).

The direction of hand preference (left or right) differs between individuals in the combined sample. If only significant results are considered, in terms of probing four animals show a right hand preference and three show a left hand preference. For the tapping action, two animals show a right hand bias and three show a left hand bias. If all data are considered, the counts of right (positive) to left (negative) handedness indices are seven to nine, respectively, for probing, and eight to eight for tapping. However, the hand preference does show stability between tasks; there is a marginally significant correlation between HIs for taping and probing across all individuals ($r = 0.49$, $P = 0.05$). In three animals with significant hand preference for both tapping and probing, these are always in the same direction (right for Patrice, left for Mina and Samantha).

When HIs are analyzed as a function of age category, sex, and the interaction of those two variables, the whole-model test shows non-significant results for HIs for probing ($F_{3,12} = 1.56$, $P = 0.25$). The results are significant for

Table 3 Frequencies of hand use, z-scores, and handedness indices describing hand preference in tapping and probing (or digit-feeding) from the previous studies on captive animals (Feistner et al. 1994)

Animals	Measure	Left	Right	z-score	Handedness index
Alain (am, JWPT)	Probe	60	47	−1.26	−0.12
	Tap	12	9	−0.65	−0.14
Patrice (am, JWPT)	Probe	12	37	3.57***	0.51
	Tap	4	24	3.78***	0.71
Nosferatu (am, DUPC)	Probe	6	3	−1.00	−0.33
	Tap	3	4	0.38	0.14
Poe (am, DUPC)	Probe	8	3	−1.51	−0.46
	Tap	15	28	1.58*	0.30
Juliet (af, JWPT)	Probe	25	21	−0.59	−0.09
	Tap	33	29	−0.51	−0.07
Mina (af, JWPT)	Probe	97	65	−2.51**	−0.20
	Tap	58	17	−4.73***	−0.55
Samantha (af, DUPC)	Probe	18	1	−3.90***	−0.90
	Tap	31	7	−3.89***	−0.63
Zaza (if, JWPT)	Probe	21	53	3.72***	0.43
	Tap	116	145	1.80	0.11
Fred (if, JWPT)	Probe	57	73	1.40	0.12
	Tap	124	112	−0.78	−0.05
Sambany (if, JWPT)	Probe	88	77	−0.06	−0.07
	Tap	141	73	−4.65***	−0.32
Annabellee (if, DUPC)	Probe	3	15	2.83**	0.67
	Tap	12	14	0.39	0.08

Captive aye-ayes in the Jersey Wildlife Preservation Trust (JWPC; now called the Durrell Wildlife Preservation Trust, DWPC) and Duke University Primate Center (DUPC)

Asterisks indicate significance of binomial tests of hand preference (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)

HIs for tapping ($F_{3,12} = 4.67$, $P = 0.02$), with females more left-preferent than males ($F_1 = 5.72$, $P = 0.03$); the other effects are non-significant. When only the strength of lateralization is considered (i.e., the absolute values of HIs are used), the whole-model test shows non-significant results for both probing ($F_{3,12} = 1.49$, $P = 0.27$) and tapping ($F_{3,12} = 0.66$, $P = 0.59$).

Discussion

In aye-ayes studied here, some appeared to be ambipreferent in their hand use, while others showed hand preference. There was, however, no indication of the population-wide left hand bias, regardless of sex. This pattern corresponds to the Level 2 of the McGrew and Marchant's (1997) framework.

No consistent population bias in hand use, as reported earlier by Feistner et al. (1994) for captive aye-ayes, was cited by McGrew and Marchant (1997) and Rigamonti et al. (2005), thereby contradicting the general pattern of hand preferences in other prosimians reported in various studies that found the left hand preference being the most common pattern (Sanford et al. 1984; Larson et al. 1989; Forsythe and Ward 1988; Forsythe et al. 1988; Ward et al. 1990; Milliken et al. 2005). There are at least three other reports on species-specific free foraging in prosimians that show a lack of left-hand population bias (Stafford et al. 1993; Shaw et al. 2004; Rigamonti et al. 2005). However, the data on aye-ayes must not be considered in the same context as that of other prosimians because the behaviors under consideration differ. Left hand preference in prosimians has been most commonly detected in visually guided reaching and holding, yet aye-ayes rarely reach for or hold objects, and this is even more apparent in wild animals. Wild aye-ayes mostly forage on attached objects (often directly on the wooden substrate) that need not be—or even cannot be—held. Even when the objects are not attached, the aye-ayes often use their mouth rather than their hands to pick up the object before transferring it to the hand (Feistner et al. 1994), as has been reported for several other lemurs (Ward et al. 1993; Milliken et al. 2005; Rigamonti et al. 2005). The specialized aye-aye hand with elongated fingers appears not to be well suited for grasping and holding objects, and holding food items or nesting materials often results in the accidental dropping the objects (Lhota and Jůnek, unpublished data). On the other hand, behaviors comparable to aye-aye's tapping, probing, and cleaning teeth with a finger appear to have no equivalents in other prosimians. This is even the case of grooming with fingers, as to our knowledge, no other prosimian species has been described to regularly use fingers, instead of toothcomb or the toilet claw on the hind foot, for grooming

fur. Therefore, compared to other prosimians where laterality was studied, the lack of left hand bias in aye-ayes may reflect qualitatively different patterns of hand use rather than different patterns of lateralization of neural substrates.

The relevance of studying laterality in captive animals with the aim of gaining an understanding of natural evolution has been questioned (Marchant and McGrew 1996; McGrew and Marchant 1997; Panger 1998; Rigamonti et al. 2005). However, the patterns of lateralized hand use we observed in the wild aye-ayes of this study resemble what has been reported earlier for the free feeding in captivity (Feistner et al. 1994), with some animals being ambipreferent and others biased evenly to either direction. The similarity pertains despite the fact that the wild aye-ayes use their hands differently than captive ones, which are presented mostly with detached and easy-to-process food and are subjected to more stereotypy.

Our results and those of Feistner et al. (1994) do, however, differ from the findings of Milliken (1995) on four of the same animals in DUPC. When presented with two test apparatuses, these aye-ayes expressed right hand preference and performance biases in several measures of probing. Milliken (1995) concluded that the right hand bias in digit use is species-specific for aye-ayes. The sample of four animals is too small—even when all of them are right handed, this does not significantly deviate from 1:1 ratio on the population level using any test (if α is set at 0.05). This small population still does not fully account for the observed differences because Samantha, right-biased in probing when tested by Milliken, was significantly and strongly (HI = −0.90) left-biased in the other study, probably during the same year (Feistner et al. 1994). Milliken (1995) mentions that Samantha lost the claw on her right third finger (for a reason not related to testing) and became left hand preferent in finger use thereafter. However, the other study took place before she lost her claw (Milliken, personal communication), so this injury cannot explain the discrepancy.

A possible explanation of Milliken's (1995) different findings is that his z-scores capture different aspects of lateralization because they are sensitive to asymmetries in probing persistence. Milliken shows that the right hand preferences in shallow cavities of the vertical cavity apparatus (VCA) were due to higher persistence of the right finger; the animals tended to use it in longer sequences of repeated probing acts. Milliken counted each entering a cavity as one event, while we have used only the first-noted entering in each such sequence. Feistner and colleagues recorded digit-to-mouth feeding on fruits that is typically represented by continuous bouts, with "enterings" being less distinct than inserting the finger into a cavity. It is likely that a sequence of such "enterings" was regularly counted as a single event. Only interruptions or changes of hands

Table 4 Comparison of various measures on lateralized finger use in four DUPC aye-ayes. *z*-scores, and and handedness indices were computed as in our Table 1

Name	Probe VCA[a]	Tap[b]	Digit-feed[b]	Probe VCA rearranged[c]	Probe VCA rearranged[d]	Probe HCA[a]
Nosferatu						
n	419	7	9	50	84	160
z-score	3.08**	0.38	1.00	0.85	0.87	−1.11
Handedness index	0.15	0.14	0.33	0.12	0.10	−0.09
Poe						
n	629	43	11	121	153	160
z-score	13.44***	1.98*	−1.51	3.18**	3.31***	2.21*
Handedness index	0.54	0.30	−0.46	0.29	0.27	0.18
Samantha						
n	419	38	19	98	152	0
z-score	2.30*	−3.90***	−3.89***	1.01	1.14	–
Handedness index	0.11	−0.63	−0.90	0.10	0.09	–
Annabellee						
n	260	26	18	49	82	135
z-score	2.73**	2.83**	0.39	−0.71	0.00	−0.26
Handedness index	0.17	0.08	0.67	−0.10	0.00	−0.02

Asterisks indicate significance of hand preference (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)

VCA Vertical cavity apparatus, *HCA* horizontal cavity apparatus

[a] Table 3 from Milliken (1995)

[b] Table 2 from Feistner et al. (1994)

[c] Data from Table 4 from Milliken (1995) rearranged to resemble the design of our study where only the first-noted hand was recorded. Only data from Milliken's (1995) columns Initiated Sequences Left and Initiated Sequences Right were used; data from all four cavities were pooled

[d] Data from Table 4 from Milliken (1995) rearranged to resemble design of the study of (Feistner et al. 1994) where continuous digit-feeding and any change of hands were recorded. We summed Milliken's (1995) data from columns Initiates Sequences Left and Changes R → L to represent frequencies of left hand use, and data from columns Initiates Sequences Right and Changes L → R to represent frequencies of right hand use; data from all four cavities were pooled

were recorded as new events (this actually biases the data toward ambipreference: the direction of shifts is dependent on the preceding act—it can only be the opposite hand). When we rearrange the data from the Table 4 of Milliken (1995) to simulate the other two sampling designs, the differences between the three studies become less distinct, as shown in our Table 4. In both alternative arrangements, the HIs are relatively low, and the only significantly right-preferent animal is Poe. This is the animal for whom the original results are significant for both apparatuses and for all cavity depths in the VCA apparatus. This also corresponds with his right-hand preference in tapping reported independently by Feistner et al. (1994). Leaving Poe aside, all other significant right-hand biases in probing frequency, persistence, and productivity in Milliken's (1995) paper were detected in the easiest tasks—in the two shallower holes of the VCA. Milliken states that as the complexity of the cavity increased, the aye-ayes soon switched to a variable probing strategy with alternating ways of probing into the cavity, including using the other hand.

There are two other brief reports on hand preference in aye-ayes. Ancrenaz et al. (1994) observed three free-ranging aye-ayes in degraded secondary forest and agro-ecosystems 12 km west of Mananara-Nord, close to our field site. When probing for nectar in flowers of *Ravenala madagascariesis*, a female preferred her right hand, while two males preferred their left hand. These results are consistent with the finding of the lack of the population-wide hand bias. Iwano (1991) reports on hand use in a wild-caught female aye-aye kept in the Tsimbazaza zoo in Madagascar. When feeding with her left hand, she used the third digit more frequently, but she used the fourth digit more frequently when feeding with her right hand. The author, however, explains this as a likely artifact of the sampling method. Focal instantaneous sampling has been employed with sampling points only 30 s apart; such data cannot be considered as independent and the sample size is likely to be inflated.

The absence of the demonstrable effect of age category in the combined data requires further discussion. It is very likely that learning during the juvenile period is an important factor in the development of the aye-aye's unique foraging strategy (Krakauer 2004). Also, the ratio of right hand- to left hand-preferent aye-ayes closely approaching

1:1 indicates that the hand preference is not inborn in this species and instead develops with practice as a motoric habit, in an evenly weighted direction. If this is true, then the strength of laterality should increase with age—at least among younger animals. This trend has been shown for some other prosimians (Ward et al. 1990; Milliken et al. 1991). Feistner et al. (1994) indeed suggested that this was also the case for the aye-ayes they studied, with only the youngest of these captive animals, Fred (10 months old), showing ambipreference in all measures and the other three juveniles and subadults (Zaza, Sambany, and Annabellee) showing hand preference in at least one measure. The 3-year-old captive adult male Poe, who was close in age to the 2-year-old wild subadult male Rarach, was right-handed in several measures in the studies of Feistner et al. (1994) and Milliken (1995). In contrast, the wild animals from Mananara were ranked in their handedness just as they were ranked in age, with subadult Rarach (2 years) being the most ambipreferent and only two aged animals (Lucy and Koulic) showing significant hand preferences. We strongly suspect that hand preference does indeed increase with age in aye-ayes but that the process is relatively fast in captive animals. More routine in captivity may lead to the faster development of motoric habits, including hand preference.

The 1:1 ratio of left- to right-preferent aye-ayes does not support the postural origin hypothesis by MacNeilage et al. (1987), which predicts a population-wide left hand preference bias for manipulative tasks. Postural support is a very relevant issue for aye-ayes that tend to forage in a variety of demanding postures, including suspension, climbing head-down, or clinging to trunks of large diameters (Curtis and Feistner 1994; Lhota and Jůnek, unpublished data). If the right hand specializes for securing postural support, as suggested by MacNeilage and colleagues, left hand preference in the digit-use should develop so that the function of the right hand is not compromised. But this is not the case. We found no effect of the easiness of the position on the strength of hand preferences. It is possible that a minute effect would emerge if more data were available enabling the position to be classified in a detailed way, but we may still conclude that the postural demands are probably not the major factor that would invoke (Forsythe et al. 1988; Larson et al. 1989; Dodson et al. 1992) or limit (Stafford et al. 1993) the expression of hand preference in aye-ayes. In JWPT animals, the effect of posture was controlled by presenting food in identical dishes on a platform (Feistner et al. 1994) and still the animals did not substantially differ from the wild ones in terms of their hand preference patterns.

We can, however, speculate about other untested factors that may limit the degree of hand preferences in aye-ayes, and it is possible that more than one factor plays a role. The aye-ayes often move during foraging, especially when feeding on branches; they then need to use both forelimbs for locomotion and thus would tend to switch the hand used for tapping or probing at each step. When the aye-ayes investigate the internal structure of objects by tapping, the use of both hands would provide information from a wider area. When probing into a complex cavity, the use of both hands may enable the aye-aye to inspect it most thoroughly. When grooming fur, there is a symmetric pattern of one side of the body being better accessible with one hand and the other side with the opposite hand. Finally, there is a risk of getting one hand injured, which would have serious consequences for the animal if there were a strong efficiency bias for that hand.

If hand preferences develop slowly during maturation, as suggested by data on wild aye-ayes, it would help the animals to counteract some of the above-mentioned disadvantages. The juveniles and subadults would practice using both hands during the period when most of their motoric skills are being formed. If then hand preference develops as a motoric habit at a more advanced age, the animal would still be able to use both hands efficiently. A longitudinal study on development of foraging of individual aye-ayes, preferably in the field setting, would help to address this hypothesis.

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