Title: Slow lorises (*Nycticebus* spp.) display evidence of handedness in the wild and in captivity

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Abstract:

It has been suggested that strepsirrhines (lemurs, lorises, and galagos) retain the more primitive left hand preference, whilst monkeys and apes more regularly display a right hand preference at the individual-level. We looked to address questions of laterality in the slow loris (*Nycticebus* spp.) using spontaneous observations of seven wild individuals, unimanual tests in six captive individuals, and photos of 44 individuals in a bilateral posture assessing handedness at the individual- and group-level. During the unimanual reach task, we found at the individual-level, only four slow lorises showed a hand use bias (R: 3, L:1), Handedness index (HI) ranged from -0.57-1.00. In the wild unimanual grasp task we found at the individual-level two individual showed a right-hand bias, the HI ranged from -0.19-0.70. The bilateral venom pose showed a trend toward a right hand dominant grip in those photographed in captivity, but an ambiguous difference in wild individuals. There are many environmental constraints in captivity that wild animals do not face, thus data collected in wild settings are more representative of their natural state. The presence of right-handedness in these species suggest that there is a need to re-evaluate the evolution of handedness in primates.

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Introduction

Humans show a bias for right-handedness across all populations, regardless of culture and geographic location (Faurie & Raymond, 2004; Faurie, Schiefenhvel, le Bomin, Billiard, & Raymond, 2005; McGrew & Marchant, 1994; Raymond & Pontier, 2004). No other species shows this level of consistency in hand preference (Cashmore, Uomini, & Chapelain, 2008; Cochet & Byrne, 2013). The roots of motor asymmetries can be traced back to early vertebrates (Vallortigara, Rogers, & Bisazza, 1999). To uncover the root of this asymmetry, researchers investigated handedness and laterality in invertebrates and vertebrates including non-human primates (MacNeilage, Rogers, & Vallortigara, 2009; Neufuss et al., 2015; Regaiolli, Spiezio, & Hopkins, 2016a; Regaiolli, Spiezio, & Vallortigara 2016b; Wiper, 2017). Hopkins (2013) suggested that the lack of universal handedness in primates compared to humans was related to a qualitative difference in the way behavioural and brain asymmetries are expressed. Others noted that there is a more prominent disconnection between the species-wide handedness seen in humans versus non-human hand preference (Cashmore et al., 2008; Marchant & McGrew, 2013). Despite these debates, nearly 70% of non-human vertebrates that have been tested display hand preference (Ströckens, Güntürkün, & Ocklenburg, 2013).

Some researchers report the presence of an individual-level bias, but not a group-level bias in hand preference among various non-human primates (McGrew & Marchant, 1997; Papademetriou, Sheu, & Michel, 2005), as evidenced by studies of lemurs (Schnoell, Huebner, Kappeler, & Fichtel, 2014), Old World monkeys (Chapelain et al., 2012; Regaiolli, Spezio, & Hopkins, 2016b), and New World monkeys (Cameron & Rogers, 1999; Hook-

Costigan & Rogers, 1996; Hook & Rogers, 2008). Extensive research on chimpanzees, gorillas, baboons, and capuchins not only found an individual- and group-level bias, but they reported a preferential use of the right hand, similar to humans (Hopkins, 2006; Meguerditchian, Calcutt, Lonsdorf, Ross, & Hopkins, 2010; Vauclair, Meguerditchian, & Hopkins, 2005). At the individual-level, far more primate species display hand preferences in both unimanual and bimanual tasks, suggesting that individual-level handedness is not uniquely human (McGrew & Marchant 1997; Papademetriou et al., 2005; Hopkins, 2007).

MacNeilage, Studdert-Kennedy, & Lindblom (1987) suggested that strepsirrhines (e.g., lemurs, lorises, pottos and galagos) are characterized by a left hand preference, whilst in all other primates the right hand is used preferentially. Despite this assertion, most formal studies examining handedness in strepsirrhines have reported various results. At the group-level, Papademetriou et al. (2005) found that strepsirrhines, New World monkeys, and Old World monkeys often showed a left-hand bias, whereas most apes show a right-hand bias (e.g. Lonsdorf & Hopkins, 2005). Studies on strepsirrhines have covered lemur species (e.g. Nelson, O'Karma, Ruperti, & Novak, 2009; Regaiolli et al., 2016a; Schnoell et al., 2014), galagos (e.g. Dodson, Stafford, Forsythe, Seltzer, & Ward, 1992; Sanford, Guin, & Ward, 1984) and pottos (Karberger, 1980), using both spontaneous and experimental conditions in both unimanual and bimanual tasks though primarily were tested in captive settings (e.g. Fagot & Vauclair, 1991)

Reports of a right hand preference and a left hand preference at the individual- and group-level further contribute to the confusion and debate as to the primitive state of laterality in primates and ultimately humans. Rogers (2009) noted that hand preferences at the individual-level are linked to general aspects of behaviour. The task used to measure hand preference and laterality can have a strong effect on individual- and group-level preferences. Complex bimanual tasks are consistently associated with a stronger asymmetric response in primates at the individual- and group-level contrary to unimanual tasks (Cantalupo, Vauclair, & Meunier, 2013; Hopkins et al., 2011; Meguerditchian, Vauclair, & Hopkins, 2013). Thus it is vital to diversify the types of tasks examined in relation to laterality and to examine both the individual- and the group-level.

Slow lorises were once classified as solitary primates, but following more in-depth studies across species, we now know that they exhibit levels of social interaction comparable to many diurnal primates (Wiens & Zitzmann, 2003; Nekaris, 2014). Slow lorises display unique morphological and physiological features related to a hind-limb dominated non-leaping locomotion. They are characterised by a vice-like grip, as they hold on to branches for long durations throughout the day as they sleep, and when they cling to trunks for exudate feeding at night. In addition to this strong grip, they use precision while quickly grabbing insects, and reeling in flowers on fine branches to drink nectar, without damaging the flower (Nekaris, 2014). Physiologically, slow lorises are the only venomous primates. When preparing to bite, slow loris species regularly clasp their arms in a bilateral position called the venom pose (Nekaris, Moore, Rode, & Fry, 2013). This unique posture is similar to hand-clasping in humans and the hand clasp grooming of chimpanzees. In the venom pose, slow lorises use one hand to grasp the wrist of the other arm above their head in threatening situations; this position enables them to mix the oils secreted from a brachial gland with their saliva (Nekaris, Moore, Rode, & Fry, 2013). The venom pose is seen in most species of slow loris, during instances of handling both in captivity and in the wild, providing a unique opportunity to incorporate another behaviour to examine lateralization.

Most studies on strepsirrhine manual laterality focused on the influence of posture on hand preference and simple hand reach preferences, where ‘primitive’ primates used their right hand for holding on to branches, and their left hand for reaching and grasping items. (Sanford & Ward, 1986; Forsythe, Milliken, Stafford, & Ward, 1988; Forsythe & Ward, 1988; Sanford & Ward, 1986). Many studies on laterality in primates have been conducted in captivity, although it has been suggested that the surrounding environment can influence the development of a hand preference.

Researchers noted that strepsirrhines represent a valuable model for hemispheric lateralization because of their simple neural system and basal phylogenetic placement (Ward, 1991). Our goal in this study was to investigate hand preference in spontaneous unimanual tasks, including bilateral hand-clasp position in slow lorises, to determine if there is an individual or group- level lateralization. For the unimanual task, handedness was assessed by observing simple reaching for presented food items in captivity and spontaneous grabbing in the wild. For the bilateral position, we observed which hand subjects used to clasp their wrist during physical examinations.

Methods

Bilateral hand clasp position (Venom pose):

We analyzed photos taken during physical examinations in both wild and captive populations of slow lorises. These photos were taken between 2006 and 2014, and included three species of slow lorises (Javan slow loris *Nycticebus javanicus,* greater slow loris *N. coucang,* and Sumatran slow loris *N. hilleri*) as they employed the venom pose in which arms are crossed above the animal's head as a defensive position (Figure 1). Forty-two individuals made up the analysis of the slow loris bilateral clasp, which were photographed either at wild field sites or rescue centres (Table 1). The species was determined based on the geographic location and pelage coloration. We included only one photo of each of 42 observed individuals in the analysis, because any subsequent photos were from the same session and lacked independence. We defined left hand preference as the left hand clasping the right wrist and the digits are forward facing, and right hand preference was the right hand grasping the left wrist and the digits are forward facing (Figure 1). The experienced handling team followed a protocol approved by the Animal Ethics Subcommittee at Oxford Brookes University and did not restrict arm movement in a way that would influence which hand clasp their wrist during the venom pose.

Unimanual reach in captive slow lorises

We observed six individually-housed adult Sumatran slow lorises (M: 3| F: 3) at Cikananga Wildlife Center (CWC) in Sukabumi, West Java, Indonesia, as they reached for presented food items, which we classified as a unimanual reach tasks. We recorded which hand was used each time a study subject reached for a presented food item. Individuals were sitting symmetrically in front of three dishes presented to them outside of their cage. They had equal access to each dish and were presented with either a thin slice of fruit or a small mealworm in one of the dishes. All participants employed a single handed reach, which was the only way they could successfully access the dishes through the mesh of their enclosures.

Here each single handed reach was defined as a unimanual reach task event, where we coded right, as the animal's right hand reaching for the dish and left represented the animal's left hand reaching for the dish.

Unimanual grasping in wild slow lorises

From June 2015 - December 2017 we recorded the feeding techniques used in a population of wild Javan slow lorises as a part of ongoing research at the Little Fireface Project field station (LFP), Cipaganti, West Java, Indonesia (S7°6'6" 7°7' and E107°46' 107°46'5"). We collected direct observational data using five-minute instantaneous sample points and all occurrences of grasping behaviours (Altman, 1974). The main study area encompasses a 60 ha area of patches of cultivated lands, bamboo, shrubs, and trees used as lines of demarcation (Nekaris et al., 2017). Nightly observations took place between 18:00 and 05:00, which constitute the slow lorises' active hours. Here we defined instances where seven adult Javan slow lorises (M: 3| F: 4) used their right or left hand to bring a food item towards their mouth, as a unimanual grasp task (Figure 2).

Data analysis

To analyse the bilateral hand clasp we used descriptive statistic due to the lack of repeated occurrence per individual. Results are reported as the mean count of either right- or left-handed clasping across all photos. To determine the preference at each site we used a one-sample binomial test. To determine individual preference in the two unimanual tasks, we calculated the Handedness index (HI), or manual preference index for each slow loris across all recorded hand grasping and reaching occurrences (Schmitt, Melchisedech, Hammerschmidt, & Fischer, 2008). An HI of -1 represents a totally left-handed individual and an HI of +1 represents a totally right-handed individual. A one-sample binomial test for each slow loris in the unimanual reach and grasp task determined the significant bias in the use of the right or left hand (Brand, Marchant, Boose, White, Rood, & Meinelt, 2017). To analyse the unimanual task and spontaneous unimanual grasping at the group-level, we performed a one-Sample T-test on the distribution of the Absolute Handedness index (ABS-HI) with significance set to $p \leq 0.05$.

Results

Bilateral hand clasp position (venom pose):

We found no significant difference between the two bilateral venom poses across all sites and species (binomial test, N=42, p=0.090). A total of 64% of lorises favoured the right position; 36% favoured the left position. The photos taken at the CWC centre (binomial test, N=16, p=0.804), IAR centre (binomial test, N=15, p=0.118), and SPC centre (binomial test, N=5, p=0.750) showed no significant difference. The mean right hand use was 56%, 73%, and 67%, respectively. The mean hand use for the photos taken of wild slow lorises was 50% right and 50% left, statistically there was no difference (binomial test, N=6, p=1.000).

Unimanual reach in captive slow lorises

At the group-level, we found a significant difference in the distribution of the HI (One-sample Test, N=6, t=4.92, p=0.004). When considered as one sample, the slow lorises used their right hand 57% of the observations and their left hand 43% of the observations. The mean absolute HI for this task was 0.45 ± 0.16 (Figure 3). At the individual-level only four slow lorises showed a hand use bias (R: 3, L:1), HI ranged from -0.57-1, two individuals (FO & MD) displayed a negative HI value, the other four had positive HI values (Table 2).

Unimanual grasping in wild slow lorises

At the group-level, we found a significant difference in the distribution of HI (One-sample Test, N=7, t=3.29, p=0.016). When considered as one sample, slow lorises used their right hand 64% of the observations and their left hand 37% of the observations. The mean absolute Handedness Index (HI) for this task was 0.56±0.34 (Figure 4). At the individual-level two individual showed a right-hand bias (AL & FE), the HI ranged from -0.19-0.70, two individuals (MA & SH) displayed negative values, TE had a value of zero, and the others displayed positive values (Table 2).

Discussion

Despite the small sample size, the results of this study suggest that there is variation between hand preference in wild and captive individuals during unimanual reaching and grasping tasks, but not during bilateral positions. In the bilateral position, there was no difference in the preferred clasping hand during venom poses. In the unimanual task in captive slow lorises, there was a difference at the group-level. At the individual-level one individual showed a left hand preference. The unimanual grasping in the wild slow lorises also displayed significant right-hand preferences as a group. In addition to a lack of continuity regarding strepsirrhine laterality, each tested task has a varying effect on the manifestation of hemispheric biases (Fagot & Vauclair, 1991). The results in this study offer a counterpoint to the idea that strepsirrhines have retained a left hand bias, as an assumed ancestral state for primates including humans (Papademetriou et al., 2005).

MacNeilage et al. (1987) observed that the hands of strepsirrhines showed some specialization such as grasping for supports with the right hand (left hemisphere) and striking prey with the left hand (right hemisphere), revealing that task demands elicited the obligate use of a particular hemisphere. It has been suggested that the left hemisphere develops before the right hemisphere (Fagard, 2013; MacNeilage, Rogers, & Vallortigara, 2009) and based on studies of a wide range of vertebrates without forelimbs/hands it is known that the brain became lateralized well before handedness. Studies show that there may be subtle functional differences between the left and right hand (Sainburg, 2014; Schabowsky, Hidler, & Lum, 2007). These authors provide a structure for understanding the motor control process that lead to handedness. In this dynamic dominance model, the left hemisphere in right-handed animals is most proficient at processes that predict the effects of body and environmental dynamics, whereas left-handed animals relying on the right hemisphere are most proficient at object manipulation. Futhermore, zoo-housed gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*) display varied hand use bias when engaging with animate and inanimate objects suggesting that object characteristics effect how the right and left hemisphere process manual actions (Foster, Quaresmini, Leavens, Spiezip & Vallortigara, 2012; Forrester, Quaresmini, Leavens & Vallortigara, 2011).

The right or left hand dominance in the slow loris venom pose at the included rescue centres and in the wild varied from one slow loris to the next, showing no group-level preference. Despite our insignificant findings, we did observe right-hand dominated clasping in 64% of the slow lorises compared to 36% of the slow loris using a left hand dominated clasp. We suggest that this variation may be linked to the strong I-V grasp known to slow loris species (Gebo, 1987). The I-V grasp relies heavily on the thumb, which Morino, Uchikoshi, Bercovitch, Hopkins, & Matsuzawa (2017) suggested may motivate a shift in hemispheric involvement. Grips using the thumb in other primates including humans are typically associated with right hand use (Christel, 1994; Hopkins, Cantalupo, Wesley, Hostetter, & Pilcher, 2002; Hopkins & Russell 2004; Meguerditchian et al., 2015). In human studies of arm folding and hand clasping, there was no evidence of consistent lateral preferences that could be associated with handedness (Reiss & Reiss, 1998), noting that bilateral preference has a weak connection to hemispheric lateralization. There is another plausible factor, which may influence the left or right hand dominated grasp during the slow loris venom pose. This posture serves the function of delivering brachial oil to the mouth, to enable a venomous bite (Nekaris et al., 2013). Using either the right or left hand to grasp the other wrist could be linked to the amount of brachial oil present on the right or left brachial gland. To further discuss this theory, we would need to incorporate data on brachial oil production at each instance of observing the venom pose.

Hand clasping in non-human primates is very rarely reported in publications, outside of a posture used by chimpanzees. McGrew and Tutin (1978) described this pattern of behaviour as the grooming hand-clasp in the chimpanzees of K-group in the Mahale Mountains of western Tanzania. This behaviour was absent in other chimpanzee populations, nearby and in other countries (McGrew, Marchant, Nakamura, & Nishida, 2001). The presence or absence of hand-clasp grooming in chimpanzee groups is related to cultural differences between various populations (McGrew, Marchant, Nakamura, & Nishida, 2001). In humans hand-clasping shows a lateral preference but there appears to be an east to west variation. Indeed, left hand clasping (the thumb of the left hand resting on top of the thumb of the right hand) is more dominant in populations near the Greenwich Meridian, and decreases east of the Meridian, with the lowest level of left hand clasping in India and Australasia (McManus & Mascie-Taylor, 1979; Reiss, 1999). This cultural influence suggests that although hand-clasping shows lateral preference similar to manual tasks it has a weaker connection to brain hemispheric lateralization (Critchley, 1972; Reiss, 1999; Reiss M., Reiss G., & Freye, 1998). In this study we included three slow loris species in varying conditions. The lack of an identifiable preference supports what is seen in humans, that unlike other manual tasks this bilateral position displays less of a universal hand preference.

Our results in the unimanual task in captive lorises suggest a group-level bias. At the individual-level one of six individuals had a negative HI, representing a left hand bias, the other three that displayed a significant preference were right handed. These results refer back to Sanford and Ward's (1986) suggestion that posture has a significant influence in manual lateralization. As captive slow loris species generally maintain a sitting posture and did so throughout testing, our findings are congruent with findings in strepsirrhines (Sanford et al., 1984; Ward, Milliken, & Stafford, 1993), monkeys (Fagot & Vanclair, 1991; King & Landau, 1993; Roney & King, 1993), and apes (Hopkins, 1996). Similar to the bilateral posture, the simple unimanual hand reach recorded in the captive slow lorises is a poor indicator of hemispheric specialization, as seen in other quadrupeds (Vauclair et al., 2005). Merguerditchian and colleagues (2015) concluded that any hand preferences seen in this task are likely due to situational and postural conditions. Our observations support this assertion as individual slow lorises did not consistently rotate their bodies to use a specific hand, but instead often used the hand closest to the presented food dish, which varied based on where the individual was at the start of the testing session.

In the Javan slow loris we found a group-level right-hand bias in the unimanual grasping in wild individuals. This right-hand preference acts as a counter point to studies that report a higher right-hand bias for nongrasping actions (Cochet & Vauclair, 2010; Esseily, Nadel, & Fagard, 2010; Hopkins et al., 2005). If as suggested by Molesti et al. (2016) that precise and complex manipulative activities may be selective pressures for the evolution of handedness in the primate lineage, it is increasingly important for researchers exploring questions of laterality to consider strepsirrhines, who like most haplorhines, engage in precise and manipulative activities. In particular, Javan slow lorises observed in the wild used a precision grip to grasp and reel in thin braches to access the flowers located on the end, or to grab insects quickly (Moore, 2012). Given that precision and the visual demand of a motor action are hallmark traits of task complexity (Fagot & Vauclair, 1991; Meunier & Vauclair, 2007), the spontaneous unimanual grasping observed in free-ranging slow lorises could explain the lateralization seen at the individual- and group-level.

We found a right-hand bias, whereas prior studies of lemurs and galagos show a left-handed bias (Leliveld, Scheumann, & Zimmermann, 2008; Lhota, Jůnek, & Bartoš, 2009; Milliken, Forsythe, & Ward, 1989; Rigamonti, Spiezio, Poli, & Fazio, 2005; Schnoell et al., 2014; Ward, Milliken, Dodson, Stafford, & Wallace, 1990). Hopkins et al. (2006) noted the impact of sample size especially in comparative studies, thus the reported findings may change when we analyse a larger dataset. Furthermore, it has been reported that right-handedness is more common among terrestrial compared to arboreal non-human primate species, given that they do not need their hands to support their posture (Hopkins et al., 2011; MacNeilage et al., 1987; Meguerditchian et al., 2013). Following this justification, the slow loris may deviate from other arboreal animals, due to their strong reliance on their hindlimbs to maintain their posture. They regularly use both hands to grasp insects as they stretch between discontinuous substrates using only their core and hindlimbs to support their position (Poindexter & Nekaris, 2017).

In this study we included both a bilateral posture and unimanual tasks, but to create a truly comprehensive picture of *Nycticebus* laterality, we should complete further research including a more complex bimanual task. Bimanual tasks require a higher level of fine motor skill and manipulation, thus they are believed to have a higher likelihood to induce hand preferences at the group-level (Colell, Segarra, & Sabater-Pi, 1995). In conclusion, results of this study revealed a group-level right hand preference in the Javan slow loris during observed unimanual grasping in the wild, but not in the bilateral venom pose or the unimanual reach observed in captivity. These findings suggest that lateralization can be elicited in unimanual tasks depending on the level of complexity needed to complete the task. Lastly, our findings support the need to further consider strepsirrhines in the wild and during more complex tasks as these results follow those in another strepsirrhine, the ring-tailed lemur (*Lemur catta*) (Ragaiolli, Spiezio, & Vallortigara, 2016a). The presence of right-handedness in this species and in these conditions highlights the importance of re-evaluating the evolution of hand preference in strepsirrhines.

References

Bisazza, A., Cantalupo, C., Capocchiano, M., & Vallortigara, G. (2000). Population lateralisation and social behaviour: a study with 16 species of fish. Laterality: Asymmetries of Body, Brain and Cognition, 5(3), 269-284.

Brand, C.M., Marchant, L.F., Boose, K.J., White, F.J., Rood, T.M. & Meinelt, A., 2017. Laterality of Grooming and Tool Use in a Group of Captive Bonobos (*Pan paniscus*). Folia Primatologica, *88*(2), 210-222.

Cameron, R., & Rogers, L. J. (1999). Hand preference of the common marmoset (*Callithrix jacchus*): Problem solving and responses in a novel setting. Journal of Comparative Psychology, *113*(2), 149.

Cashmore, L., Uomini, N., & Chapelain, A. (2008). The evolution of handedness in humans and great apes: a review and current issues. Journal of Anthropological Sciences, 86, 7-35.

Chapelain, A., Laurence, A., Vimond, M., Maille, A., Meunier, H., Fagard, J., Vauclair, J. & Blois-Heulin, C. (2012). Hand preference and its flexibility according to the position of the object: a study in cercopithecines examining spontaneous behaviour and an experimental task (the Bishop QHP task). Animal Cognition, 15(5), pp.937-953.

Cochet, H., & Vauclair, J. (2010). Pointing gestures produced by toddlers from 15 to 30 months: Different functions, hand shapes and laterality patterns. Infant Behavior and Development, 33(4), 431-441.

Cochet, H., & Byrne, R. W. (2013). Evolutionary origins of human handedness: evaluating contrasting hypotheses. Animal Cognition, 16(4), 531-542.

Colell, M., Segarra, M. D., & Sabater-Pi, J. (1995). Manual laterality in chimpanzees (*Pan troglodytes*) in complex tasks. Journal of Comparative Psychology, 109(3), 298.

Dodson, D. L., Stafford, D., Forsythe, C., Seltzer, C. P., & Ward, J. P. (1992). Laterality in quadrupedal and bipedal prosimians: Reach and whole-body turn in the mouse lemur (*Microcebus murinus*) and the galago (*Galago moholi*). American Journal of Primatology, 26(3), 191-202.

Esseily, R., Nadel, J. and Fagard, J. (2010). Object retrieval through observational learning in 8-to 18-month-old infants. Infant Behavior and Development, *33*(4), 695-699.

Fagot, J., & Vauclair, J. (1991). Manual laterality in nonhuman primates: a distinction between handedness and manual specialization. Psychological Bulletin, 109(1), 76.

Faurie, C., Schiefenhvel, W., leBomin, S., Billiard, S., & Raymond, M. (2005). Variation in the frequency of left-handedness in traditional societies. Current Anthropology, 46(1), 142-147.

Forsythe, C., Milliken, G. W., Stafford, D. K., & Ward, J. P. (1988). Posturally related variations in the hand preferences of the ruffed lemur (*Varecia variegata variegata*). Journal of Comparative Psychology, 102(3), 248.

Forsythe, C., & Ward, J. P. (1988). Black lemur (*Lemur macaco*) hand preference in food reaching. Primates, 29(3), 369-374.

Forrester, G. S., Leavens, D. A., Quaresmini, C., & Vallortigara, G. (2011). Target animacy influences gorilla handedness. Animal Cognition, *14*(6), 903-907.

Forrester, G. S., Quaresmini, C., Leavens, D. A., Spiezio, C., & Vallortigara, G. (2012). Target animacy influences chimpanzee handedness. Animal Cognition, *15*(6), 1121-1127.

Gebo, D. L. (1987). Locomotor diversity in prosimian primates. American Journal of Primatology, 13(3), 271-281.

Hook, M. A., & Rogers, L. J. (2008). Visuospatial reaching preferences of common marmosets (*Callithrix jacchus*): An assessment of individual biases across a variety of tasks. Journal of Comparative Psychology, *122*(1), 41.

Hook-Costigan, M. A., & Rogers, L. J. (1996). Hand preferences in New World primates. International Journal of Comparative Psychology, *9*(4).

Hopkins, W. D. (1996). Chimpanzee handedness revisited: 55 years since Finch (1941). Psychonomic Bulletin & Review, 3(4), 449-457.

Hopkins, W. D. (2006). Comparative and familial analysis of handedness in great apes. Psychological Bulletin, 132(4), 538.

Hopkins, W. D. (Ed.). (2007). The evolution of hemispheric specialization in primates (Vol. 5). Elsevier.

Hopkins, W.D. (2013). Neuroanatomical asymmetries and handedness in chimpanzees (*Pan troglodytes*): a case for continuity in the evolution of hemispheric specialization. Annals of the New York Academy of Sciences, *1288*(1),17-35.

Hopkins, W. D., Cantalupo, C., Wesley, M. J., Hostetter, A. B., & Pilcher, D. L. (2002). Grip morphology and hand use in chimpanzees: Evidence of a left hemisphere specialization in motor skill. Journal of Experimental Psychology, 131 (3), 412–423

Hopkins, W.D., Phillips, K.A., Bania, A., Calcutt, S.E., Gardner, M., Russell, J., Schaeffer, J., Lonsdorf, E.V., Ross, S.R. & Schapiro, S.J. (2011). Hand preferences for coordinated bimanual actions in 777 great apes: implications for the evolution of handedness in hominins. Journal of Human Evolution, 60(5), 605-611.

Hopkins, W. D., & Russell, J. L. (2004). Further evidence of a right hand advantage in motor skill by chimpanzees (*Pan troglodytes*). Neuropsychologia, 42(7), 990-996.

Hopkins, W. D., Russell, J., Freeman, H., Buehler, N., Reynolds, E., & Schapiro, S. J. (2005). The distribution and development of handedness for manual gestures in captive chimpanzees (*Pan troglodytes*). Psychological Science, 16(6), 487-493.

King, J. E., & Landau, V. I. (1993). Reaching in Squirrel Monkeys. Primate Laterality: Current Behavioral Evidence of Primate Asymmetries, 107.

Kraberger, A. (1980). Wahlstrategien des Verhaltens von Percodicticus potto am Beispiel des Handeinsatzes. Doctoral Thesis, FU Berlin.

Leliveld, L., Scheumann, M., & Zimmermann, E. (2008). Manual lateralization in early primates: A comparison of two mouse lemur species. American Journal of Physical Anthropology, 137(2), 156-163.

Lhota, S., Jůnek, T., & Bartoš, L. (2009). Patterns and laterality of hand use in free-ranging aye-ayes (*Daubentonia madagascariensis*) and a comparison with captive studies. Journal of Ethology, 27(3), 419-428.

MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Evolutionary origins of your right and left brain. Scientific American, 301, 60-67.

MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. Behavioral and Brain Sciences, 10(2), 247-263.

MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Evolutionary origins of your right and left brain. Scientific American, 301, 60-67.

Marchant, L. F., & McGrew, W. C. (2013). Handedness is more than laterality: lessons from chimpanzees. Annals of the New York Academy of Sciences, 1288(1), 1-8.

McGrew, W. C., & Marchant, L. F. (1994). Primate ethology: A perspective on human and nonhuman handedness. In P. K. Bock (Ed.), Psychological Anthropology, 171-184.

McGrew, W. C., & Marchant, L. F. (1997). On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. American Journal of Physical Anthropology, 104(S25), 201-232.

McGrew, W. C., Marchant, L. F., Nakamura, M., & Nishida, T. (2001). Local customs in wild chimpanzees: The grooming hand-clasp in the Mahale Mountains, Tanzania. In American Journal of Physical Anthropology, 107.

McGrew, W. C., & Tutin, C. E. (1978). Evidence for a social custom in wild chimpanzees?. Man, 234-251.

McManus, I. C., & Mascie-Taylor, C. G. N. (1979). Hand-clasping and arm-folding: A review and a genetic model. Annals of Human Biology, 6(6), 527-558.

Meguerditchian, A., Calcutt, S. E., Lonsdorf, E. V., Ross, S. R., & Hopkins, W. D. (2010). Brief communication: captive gorillas are right-handed for bimanual feeding. American Journal of Physical Anthropology, 141(4), 638-645.

Meguerditchian, A., Phillips, K.A., Chapelain, A., Mahovetz, L.M., Milne, S., Stoinski, T., Bania, A., Lonsdorf, E., Schaeffer, J., Russell, J. & Hopkins, W.D. (2015). Handedness for unimanual grasping in 564 great apes: the effect on grip morphology and a comparison with hand use for a bimanual coordinated task. Frontiers in Psychology, 6.

Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2010). Captive chimpanzees use their right hand to communicate with each other: implications for the origin of the cerebral substrate for language. Cortex, 46(1), 40-48.

Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2013). On the origins of human handedness and language: a comparative review of hand preferences for bimanual coordinated actions and gestural communication in nonhuman primates. Developmental Psychobiology, 55(6), 637-650.

Milliken, G. W., Forsythe, C., & Ward, J. P. (1989). Multiple measures of hand-use lateralization in the ring-tailed lemur (*Lemur catta*). Journal of Comparative Psychology, 103(3), 262.

Morino, L., Uchikoshi, M., Bercovitch, F., Hopkins, W. D., & Matsuzawa, T. (2017). Tube task hand preference in captive hylobatids. Primates, 1-10.

Nekaris, K. A. I., Moore, R. S., Rode, E. J., & Fry, B. G. (2013). Mad, bad and dangerous to know: the biochemistry, ecology and evolution of slow loris venom. Journal of Venomous Animals and Toxins including Tropical Diseases, 19(1), 21.

Nekaris, K. A. I., Poindexter, S., Reinhardt, K. D., Sigaud, M., Cabana, F., Wirdateti, W., & Nijman, V. (2017). Coexistence between Javan slow lorises (*Nycticebus javanicus*) and humans in a dynamic agroforestry landscape in West Java, Indonesia. International Journal of Primatology, *38*(2), 303-320.

Nelson, E. L., O'Karma, J. M., Ruperti, F. S., & Novak, M. A. (2009). Laterality in semi-free-ranging black and white ruffed lemurs (*Varecia variegata variegata*): head-tilt correlates with hand use during feeding. American Journal of Primatology, 71(12), 1032-1040.

Neufuss, J., Humle, T., Deschner, T., Robbins, M.M., Sirianni, G., Boesch, C. & Kivell, T.L. (2015). Diversity of hand grips and laterality in wild African apes. Folia Primatologica, 86(4), pp.329-329.

Papademetriou E., Sheu C.-F. & Michel G.F. (2005). A meta-analysis of primate hand preferences, particularly for reaching. Journal of Comparative Psychology, 119, 33-48.

Poindexter, S.A. and Nekaris, K.A.I. (2017). Vertical clingers and gougers: Rapid acquisition of adult limb proportions facilitates feeding behaviours in young Javan slow lorises (Nycticebus javanicus). Mammalian Biology-Zeitschrift für Säugetierkunde, *87*, 40-49.

Raymond, M. and Pontier, D. (2004). Is there geographical variation in human handedness?. Laterality: Asymmetries of Body, Brain and Cognition, 9(1), 35-51.

Regaiolli, B., Spiezio, C., & Hopkins, W. D. (2016a). Hand preference on unimanual and bimanual tasks in strepsirrhines: The case of the ring-tailed lemur (*Lemur catta*). American Journal of Primatology, 78(8), 851-860.

Regaiolli, B., Spiezio, C. and Vallortigara, G. (2016b). Manual lateralization in macaques: handedness, target laterality and task complexity. Laterality: Asymmetries of Body, Brain and Cognition, 21(2), 100-117.

Reiss, M. (1999). The genetics of hand-clasping a review and a familial study. Annals of Human Biology, 26(1), 39-48.

Reiss, M., & Reiss, G. (1998). Certain aspects of laterality research. Archiv fur Kriminologie, 201(3-4), 103-111.

Reiss, M., Reiss, G., & Freye, H. A. (1998). Some aspects of self-reported hand preference. Perceptual and Motor Skills, 86(3), 953-954.

Rigamonti, M. M., Spiezio, C., Poli, M. D., & Fazio, F. (2005). Laterality of manual function in foraging and positional behavior in wild indri (*Indri indri*). American Journal of Primatology, 65(1), 27-38.

Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. Philosophical Transactions of the Royal Society B: Biological Sciences, *364*(1519), 943-954.

Roney, L. S., & King, J. E. (1993). Postural effects on manual reaching laterality in squirrel monkeys (*Saimiri sciureus*) and cotton-top tamarins (*Saguinus oedipus*). Journal of Comparative Psychology, 107(4), 380.

Sainburg, R. L. (2014). Convergent models of handedness and brain lateralization. Frontiers in Psychology, **5**:1092.

Sanford, C., Guin, K., & Ward, J. P. (1984). Posture and laterality in the bushbaby (*Galago senegalensis).* Brain, Behavior and Evolution, 25(4), 217-224.

Sanford, C. G., & Ward, J. P. (1986). Mirror image discrimination and hand preference in the bushbaby (*Galago senegalensis*). The Psychological Record, 36(4), 439-449.

Schabowsky, C. N., Hidler, J. M., & Lum, P. S. (2007). Greater reliance on impedance control in the nondominant arm compared with the dominant arm when adapting to a novel dynamic environment. Experimental Brain Research, 182(4), 567-577.

Schmitt, V., Melchisedech, S., Hammerschmidt, K., & Fischer, J. (2008). Hand preferences in Barbary macaques (*Macaca sylvanus*). Laterality, *13*(2), 143-157.

Schnoell, A. V., Huebner, F., Kappeler, P. M., & Fichtel, C. (2014). Manual lateralization in wild red fronted lemurs (*Eulemur rufifrons*) during spontaneous actions and in an experimental task. American Journal of Physical Anthropology, 153(1), 61-67.

Ströckens, F., Güntürkün, O., & Ocklenburg, S. (2013). Limb preferences in non-human vertebrates. Laterality: Asymmetries of Body, Brain and Cognition, 18(5), 536-575.

Vauclair, J., Meguerditchian, A., & Hopkins, W. D. (2005). Hand preferences for unimanual and coordinated bimanual tasks in baboons (*Papio anubis*). Cognitive Brain Research, 25(1), 210-216.

Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. Behavioral and brain sciences, *28*(4), 575-588.

Vallortigara, G., Rogers, L. J., & Bisazza, A. (1999). Possible evolutionary origins of cognitive brain lateralization. Brain Research Reviews, *30*(2), 164-175.

Ward, J. P., Milliken, G. W., Dodson, D. L., Stafford, D. K., & Wallace, M. (1990). Handedness as a function of sex and age in a large population of Lemur. Journal of Comparative Psychology, 104(2), 167.

Ward, J. P., Milliken, G. W., & Stafford, D. K. (1993). Patterns of lateralized behavior in prosimians. Primate Laterality: Current behavioral evidence of primate asymmetries, 43-74.

Watson, S. L., & Hanbury, D. B. (2007). Prosimian primates as models of laterality. Special Topics in Primatology, 5, 228-250.

Wiens, F., & Zitzmann, A. (2003). Social structure of the solitary slow loris *Nycticebus coucang* (Lorisidae). Journal of Zoology, *261*(1), 35-46.

Wiper, M. L. (2017). Evolutionary and mechanistic drivers of laterality: A review and new synthesis. Laterality: Asymmetries of Body, Brain and Cognition, 1-31.

Figure 1. *Nycticebus* venom pose.

Figure 2. Wild Javan slow loris (*Nycticebus javanicus*) in the process of grasping a flower in terminal branches of a tree in Cipaganti, West Java, Indonesia.

Figure 3. The bilateral venom pose in two Javan slow lorises (*Nycticebus javanicus*), right-handed grasp (left) and the left-handed grasp (right).

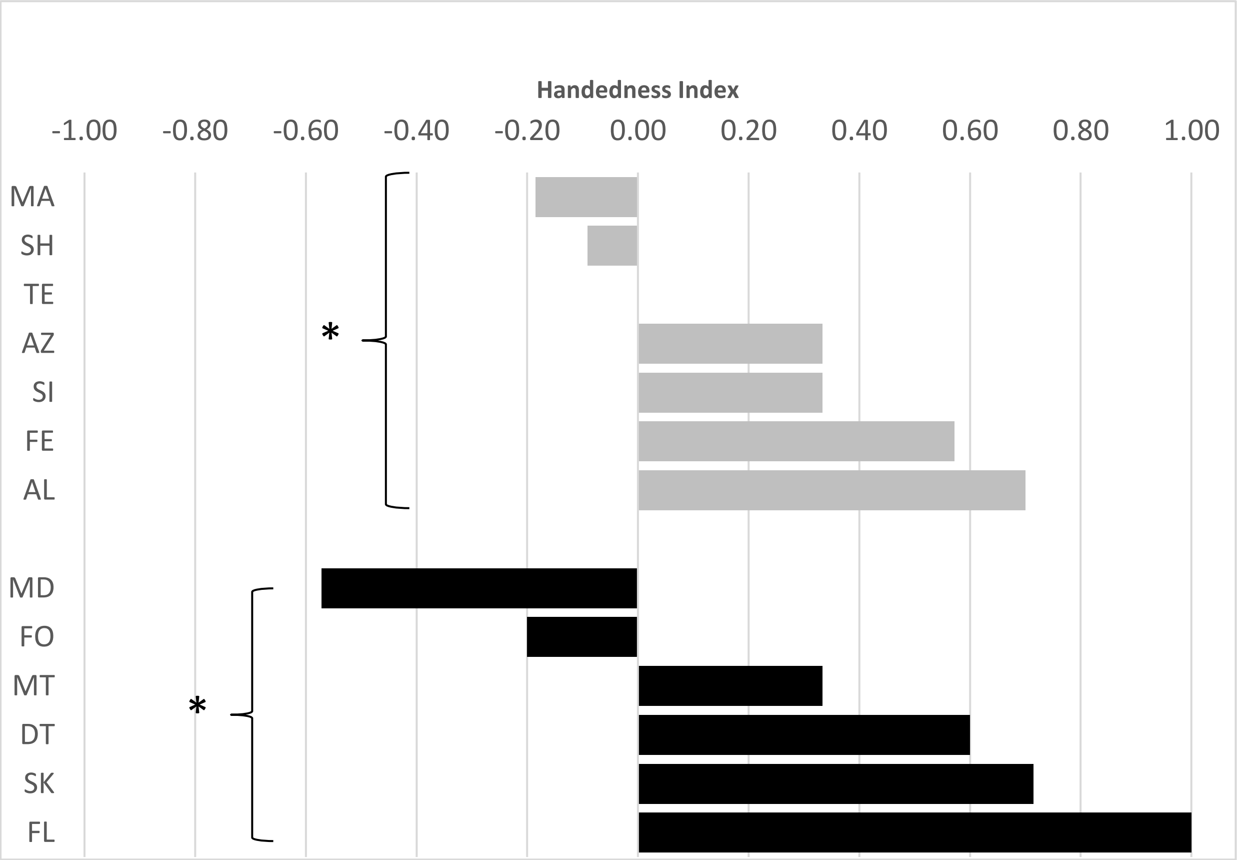

Figure 4. HI value for wild grasping (grey) and captive reach (black) observations in slow lorises. Positive values represent a right hand preference and a negative value represents a left hand preference. The (*) denotes a significant difference between the right and left hand use in the group.

Table 1. Details about the sample size and location of the photographed slow lorises.

***NYCTICEBUS* SPECIES**	**N**	**LOCATION IN INDONESIA**
SUMATRAN	20	Cikananga Conservation Breeding Centre (CCBC), Sukabumi, Java
JAVAN	6	Little Fireface Project Field site (LFP), Garut, Java
JAVAN	9	International Animal Rescue (IAR), Bogor, Java
GREAT	7	Schmutzer Primate Center (SPC), Jakarta, Java

Table 2. Handedness of Unimanual reach and grasping in two species of slow loris (*Nycticebus javanicus* and *N. coucang*).

	SEX	N	RH	LH	HI	ASB-HI	P-VALUE	HAND PREFERENCE
AL	M	20	17	3	0.70	0.70	0.003	R
AZ	M	6	4	2	0.33	0.33	0.688	A
FE	M	28	22	6	0.57	0.57	0.005	R
MA	F	27	11	16	-0.19	0.18	0.556	A
SH	F	11	5	6	-0.09	0.09	1	A
SI	F	6	4	2	0.33	0.33	0.688	A
TE	F	16	8	8	0.00	0.00	1	A
DT	F	15	12	3	0.60	0.60	0.035	R
FO	F	15	6	9	-0.20	0.20	0.607	A
FL	F	15	15	0	1.00	1.00	-	R
MD	F	28	6	22	-0.57	0.57	0.005	L
SK	M	21	18	3	0.71	0.71	-	R
MT	M	18	12	6	0.33	0.33	0.238	A

A, ambivalent hand preference index; HI, handedness index; ABS-HI, LH, left hand reach or grasp; RH, right hand reach or grasp; L, left hand dominance during task; R, right hand dominance during task