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Laterality Handedness When Completing a Tool-Use Task in Asian Small-Clawed Otters (*Aonyx cinerea*)

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Laterality is defined as the occurrence of each cerebral hemisphere having asymmetric control over the different sides of the body, leading to preferences to use one side of the body over the other for various behaviors. Many types of laterality exist, but handedness is the form that is most predominantly assessed. Handedness in animals is of special interest to laterality researchers, as humans were once thought to be the only species that exhibited lateralized hand preferences. The aim of the current study was to determine if Asian small-clawed otters (*Aonyx cinerea*) exhibit significant paw preferences in behaviors associated with completing a specific tool-use task. Video data of the otters completing the task was analyzed for specific paw interactions with the tool-use apparatus, and the percentage of correct completion of the task was documented for each otter. Overall, no significant population level paw preference was present. However, individual differences in paw preference and differing trends in handedness on each focal behavior was present. The results showed that paw preference (or lack thereof) did affect the tool-use task completion for some otters, and for others, the preference did not seem to have an effect. The main implications of this study are that paw preferences in Asian small-clawed otters are present on an individual level when solving a novel tool-use task.

Keywords: Asian small-clawed otters, handedness, laterality, paw preference, tool use

コツメカワウソ（*Aonyx cinerea*）における道具使用課題達成時の左右の前肢の使い分け

ラテラリティとは，それぞれの大脳半球が体の左右を非対称に制御することで，さまざまな行動において，体のどちらか片側を使う偏好性が強まることと定義される．ラテラリティには様々な種類があるが，利き手は最も主要な評価対象である。ヒトは、手の偏好性を示す唯一の種であると考えられていたため，ラテラリティの研究者にとって動物の利き手に関する研究は特に関心度が高い．本研究の目的は，コツメカワウソ（*Aonyx cinerea*）が，特定の道具使用課題を行う際の行動において，使用する前足に有意な偏好性を示すかどうかを明らかにすることである．課題を達成したカワウソのビデオデータをもとに，使用器具と特定の前肢のインタラクションを分析し，課題を正しく完了した割合を個体ごとに記録した．全体で見ると，集団レベルでは使用する前肢の選択に有意な差は見られなかった．しかし，使用する前肢の選択には個体差があり，焦点としたそれぞれの行動において，使用する前肢の選択には異なる傾向が見られた．この結果は，前肢の偏好性（またはその欠如）が道具使用課題の達成に影響するカワウソもいれば，影響しないカワウソもいることを示している．本研究が主に示唆することは，コツメカワウソの前肢の偏好性は，新しい道具使用課題を解決する際に個体レベルで存在するということである．

キーワード：コツメカワウソ，利き手，ラテラリティ，前肢の偏好性，道具使用

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Lateralidad Manual al Completar una Tarea De Uso De Herramienta en la Nutrias Asiáticas de Garras Pequeñas (*Aonyx cinerea*)

Lateralidad es definida como la ocurrencia de que cada hemisferio cerebral tenga control asimétrico sobre los diferentes lados del cuerpo, lo que lleva a preferencias por utilizar un lado del cuerpo sobre el otro para diversos comportamientos. Existen muchos tipos de lateralidad, pero la lateralidad manual es la forma que se evalúa más predominantemente. La lateralidad manual en los animales es de especial interés para los investigadores de lateralidad, ya que alguna vez se pensó que los humanos eran la única especie que exhibía preferencias de manos lateralizadas. El objetivo del presente estudio fue determinar si las nutrias asiáticas de garras pequeñas (*Aonyx cinerea*) exhiben preferencias significativas de las patas en comportamientos asociados con la realización de una tarea específica de uso de herramienta. Se analizaron los datos de vídeo de las nutrias completando la tarea para detectar interacciones específicas de las patas con el aparato de uso de herramienta, y se documentó el porcentaje de finalización correcta de la tarea para cada nutria. En general, no hubo preferencia significativa por las patas a nivel de la población. Sin embargo, estuvieron presentes diferencias individuales en la preferencia de las patas y diferentes tendencias en la lateralidad en cada comportamiento focal. Los resultados mostraron que la preferencia por las patas (o la falta de ella) sí afectó la realización de tareas de uso de herramienta para algunas nutrias, y para otras, la preferencia no pareció tener ningún efecto. Las principales implicaciones de este estudio son que las preferencias de patas en las nutrias asiáticas de garras pequeñas están presentes a nivel individual al resolver una tarea novedosa de uso de herramienta.

Palabras clave: nutrias asiáticas de garras pequeñas, lateralidad manual, lateralidad, preferencia de patas, uso de herramienta.

Laterality is defined as each hemisphere of the cerebral cortex having asymmetrical control over certain functions (Frost, 1980), which can indicate preferences for one side of the body over the other (Kalichman et al., 2014). Laterality studies supporting individualized preferences have been conducted in several species, including wombats (*Lasiorhinus latifrons*; Descovich et al., 2013), chickens (*Gallus gallus domesticus;* Dharmaretnam & Rogers, 2005), orcas (*Orcinus orca*; Chanvallon et al., 2017; Karenina et al., 2013), lizards (*Podarcis muralis*; Martin et al., 2010), cats (*Felis silvestris catus*; Pike & Maitland, 1997), horses (*Equus caballus*; Sinischalchi et al., 2014), and bottlenose dolphins (*Tursiops truncatus*; Thieltges et al., 2011). Many of these studies have investigated several different types of laterality (i.e., visual, auditory, spatial, and forelimb preference) in respect to which hemisphere of the brain processes such information.

The current study focuses on forelimb laterality preferences in Asian small-clawed otters (*Aonyx cinerea*) on a tool-use task (see Frick et al. [2016] for the tool use task). Asymmetrical preferences in forearm usage are observed in vertebrates (for a review, see Ströckens et al., 2013). Handedness, or bias in forelimb use, can be assessed in relation to specialized targeted tasks that involve use of the forearm, such as spatial memory tasks as observed in humans (Mellet et al., 2014), as well as during opportunistic assessments of natural behaviors that involve reaching and/or physical handling of objects or food (e.g., Asian small clawed otters; Manns et al., 2018). Previous studies support that task-dependent and sex-dependent preferences in forearm use are prevalent, but the detection of these lateralized preferences is best observed at the individual level (Ströckens et al., 2013).

Individual forelimb preference has been widely studied in primates and some marsupial species. Sex-related differences in forelimb preference are found in marsupial species, grey short-tailed opossum (*Monodelphis domestica*) and sugar glider (*Petaurus breviceps*), with females preferring the left forelimb and males preferring the right in feeding and supporting the body in a tri-pedal standing position (Giljoy et al., 2013). Squirrel monkeys (*Saimiri sciureus*) also show sex differences in handedness; females had a right-hand preference for a reaching task requiring only one hand, while the males showed a left-hand preference during a bi-manual task (Meguerditchian et al., 2012). Chimpanzees (*Pan troglogytes*) housed in human care show sex-related differences with males showing more of a left-hand preference than females when performing a simulated termite-fishing task to obtain food (Hopkins et al., 2009). A study with wild chimpanzees showed no sex-related differences, but rather an overall population-level left-hand preference when termite-fishing (Lonsdorf et al., 2005). These results suggest that sex-related differences in hand preference, if any, might be unique across species.

Another factor that influences hand preference is the exigency of the task. Lonsdorf et al. (2005) showed that hand preferences in wild chimpanzees are task-specific and depend on the motor and cognitive requirements of the task. These results are consistent with those of Hopkins and Rabinowitz (1997) in the assessment of uni-manual and bi-manual task performance in chimpanzees, which also showed that hand preferences depended on the demands of the task. Whether a task required one hand or two hands has also been found to influence hand preference and strength of lateralization. Additionally, tufted capuchins (*Cebus apella*) exhibit a right-hand bias for retrieving food, but the preference is stronger when the task requires the use of two hands (Spinozzi & Truppa, 1999). A similar trend is reported by Meguerditchian et al. (2012), in which squirrel monkeys showed a right-hand preference in the uni-manual reaching task while showing a left-hand preference in the bi-manual tasks, suggesting that hand preferences can differ between uni-manual and bi-manual tasks. Though these results were dependent on sex as described previously, a task-dependent difference in hand preference is still shown. Hand preference, as well as strength of the preference, may depend on whether the task is completed using a uni-manual or bi-manual strategy, as well as other demands of the task.

Tool-use tasks are thought to be a mechanism for assessing laterality that can provide insight to handedness preferences in a variety of species for whether the right or left forelimb is utilized in the handling of the tool. However, a universal definition of tool-use has presented numerous difficulties to agree upon, and its definition is inconsistent in the literature which can make categorizing tool-use behavior prone to subjectivity (Crain et al., 2013). Frick et al. (2016) utilized the definition offered by Mann & Patterson (2013) that states it is the use of an environmental object to alter the orientation or state of another object while the user handles the tool during and before altering the object. Mann and Patterson (2013) were specifically discussing aquatic species such as dolphins and otters. Sea otters (*Enhydra lutris)* are known to use rocks as tools to obtain food. They have been shown to improve their usage of tools through practice, and sea otters learn how to use tools through observational learning from parents (Tinker et al., 2009). Sea otters tend to use tools when preying on bivalves and snails as opposed to prey with softer bodies (Fujii et al., 2014). Evidence shows that wild Asian small-clawed otters prefer to eat invertebrates such as snails and crabs rather than fish (Abdul-Patah et al., 2014). Given the findings of the latter two studies, it can be proposed that since Asian small-clawed otters prefer prey with a hard exterior surface, they may be more inclined to use tools.

Asian small-clawed otters are excellent candidates for assessing lateralized preferences in handedness due to their curious nature, frequent use of hand-based play, and strong reliance on their hand dexterity to explore and navigate their environment (Bandini et al., 2020; Perdue et al., 2013). Previously, Manns et al. (2018) investigated paw preferences in Asian small-clawed otters through observational behavioral data looking at forelimb use for four focal behaviors: reaching for food, reaching for non-food, reaching into a hole, and carrying an object. They recorded whether or not the right paw, left paw, or both paws were used for the occurrences of these behaviors across two populations of Asian small-clawed otters housed in a zoological setting, which allowed for more consistent opportunities to record and view the animals engaging in the focal behaviors. Results from this work determined that no asymmetrical preference was common across all focal behaviors, but a strong right paw preference was observed across the study population for the “reaching into a hole” behavior. Preferences were detected for right or left paw use for individual otters. No sex differences were observed, as the study population was predominantly male.

While prior laterality results in Asian small-clawed otters were observed for general naturally occurring behaviors, the current study sought to further investigate forelimb preferences on a targeted task. This species shows intelligent behavior and cognitive abilities, such as spatial memory for food locations (Perdue et al., 2013) and ability to use a tool in a forced-choice tool-use task (Frick et al., 2016). Paw preference on such a task may affect the animal’s ability to perform specific or specialized tasks effectively. This study analyzed the forelimb use of six Asian small-clawed otters on a tool-use task (e.g., Frick et al., 2016) in order to determine if individual paw bias existed, and what the relationship was (if any) to their individual performance on solving the task they were given. It was predicted that individual differences in paw preferences would emerge for the subjects that completed this task.

Method

Subjects

The subjects used in this study included six Asian small-clawed otters, two males (coded as O1 and O2) and four females (O3, O4, O5, and O6), all approximately 2 years of age, from the same litter, and weighed approximately 9-12 lbs. Each otter was previously a subject in a tool-use task, and the data from that task was analyzed for handedness in the present study (Frick et al., 2016). At the time of the data collection for this study, all otters had resided since infancy at the SeaFari Theater facility at Six Flags Great Adventure in Jackson, New Jersey, USA.

Experimental Design

The tool-use apparatus (Figure 1) consisted of a flat platform outside of the otters' enclosure. On the platform, two hook-shaped tools were oriented as an upside-down hook when viewed by the otter with one placed on the right side of the platform and one on the left. The tools were connected via a pulley system by a line strung through a curved pipe above the tools. Food was placed in the crook of one of the tools so that if the otter made the choice to pull that tool, the food would be moved to a position within reach of the otter. Food was also placed away from the other tool so that if the otter made the choice to pull that tool, the food would not be moved and the otter would be unable to reach it. The position of the food relative to the tools was altered for each trial, but the food always stayed in the crook of one tool and away from the other tool. Each tool had a blue line around the top so that if the otter pulled the tool to make the blue line reach the end of the platform, then this occurrence counted as a choice. A choice also occurred if the otter pulled the tool to the point that the opposite tool was too far away and out of reach of the otter (Frick et al., 2016; Hanna et al., 2016). Each of the six otters performed 60 trials with the apparatus, and these trials were recorded over the summer of 2014 using an Olympus 1080 dual photo/video camera mounted on a tripod. The trial began once the apparatus was placed at the gate of the otter's enclosure. The trial ended when the otter made a choice or after five minutes of no choice, whichever occurred first. This research was IACUC approved under University of Southern Mississippi IACUC protocol #1405082.

Figure 1

Tool Use Apparatus

Note. Apparatus is from Frick et al. (2016). The base of the apparatus was a plastic cutting board (61 cm x 91 cm) with a PVC pipe pulley system attached to (2) hook-shaped tools. Each of the (2) hook-tools was the same size, shape, weight, and color.

Data Analysis

All 360 videos were observed, and operational definitions related to hand-specific behaviors were established. Each behavior was coded for which paw was used to contact the apparatus first for that specific behavior with an "R" for right paw, "L" for left paw, or "Bi" for an event in which the otter used two paws to perform the behavior. The behavior definitions included "reach," "pull," "push," "tactile," "choice," or "grabs food" (Table 1). The tool that the otter used to make the choice was also coded as either "R" or "L" as viewed from the position of the otter**.**

Table 1

Behavior Definitions

Behavior	**Definition**
Reach	Otter extends its forelimb or forelimbs across platform
Pull	Otter moved the tool toward itself, but not enough to be considered a choice
Choice	Otter pulled the tool all the way down to the blue line/end of the platform, or to the point where the other tool was inaccessible
Push	Otter moved the tool away from itself
Tactile	Otter touched the tool with its paw(s) without moving the tool
Grabs Food	Otter acquires food with its paw

Overall paw preferences for each otter were determined using nonparametric tests due to the small sample size. Wilcoxin-Signed Ranks tests were performed to determine population level differences and individual hand preferences for each otter. Laterality indices for overall paw use per individual were calculated utilizing the formula observed in Manns et al. (2018) (LI $= \frac{Left\ paw\ use - right\ paw\ use}{left\ paw\ use + right\ paw\ use}$). Range for LI scores were -1.0 — +1.0 with positive scores indicating a left paw use bias and negative scores indicating a right paw bias.

Individual differences in paw preferences were observed when looking at each otters' percentage of behaviors done per side, per focal behavior. The otters' paw preferences were also compared to their success in the tool-use task to determine if there were any patterns that may have explained how handedness affected tool use (e.g., if a left-handed otter consistently chose the left tool whether it was the correct choice or not).

Results

A total of 1808 gross motor acts (852 with the left, 956 with the right) associated with the outcome of the tool-use task were analyzed. Due to the comparative infrequency of the bi-manual use, analyses focused on comparisons between left and right paw use predominantly with bi-manual data only discussed descriptively by behavior type. Each otter was observed engaging in all focal behaviors included in this study using either the left, right, or both paws. While no significant population level preferences were detected ($z = -0.44$, $p > .05$), individualized patterns emerged for possible paw preference based on the behavior type and overall individual paw preference.

At the individual level, otters preferentially used their paws (Table 2). Laterality indices were calculated per individual otter, showing that a left paw bias was detected for three otters, and a right paw bias present for the other three otters (Figure 2). These preferences were more pronounced for some otters compared to others. A Wilcoxin-Signed Ranks test was calculated for each individual otter's overall forearm use to determine the strength of individual paw preferences. O1's use of the right paw across all behavioral events was significant ($z = -2.2$, $p = .028$). Both O3's ($z = -1.76$, $p = .08$) and O6's ($z = -1.78$, $p = .075$) use of the left paw were approaching significance. Laterality indices for each of these otters also supported their right and left paw preferences, respectively. While laterality indices showed bias towards the right paw for O2 and O4 and the left paw for O5, this overall preference was not statistically significant.

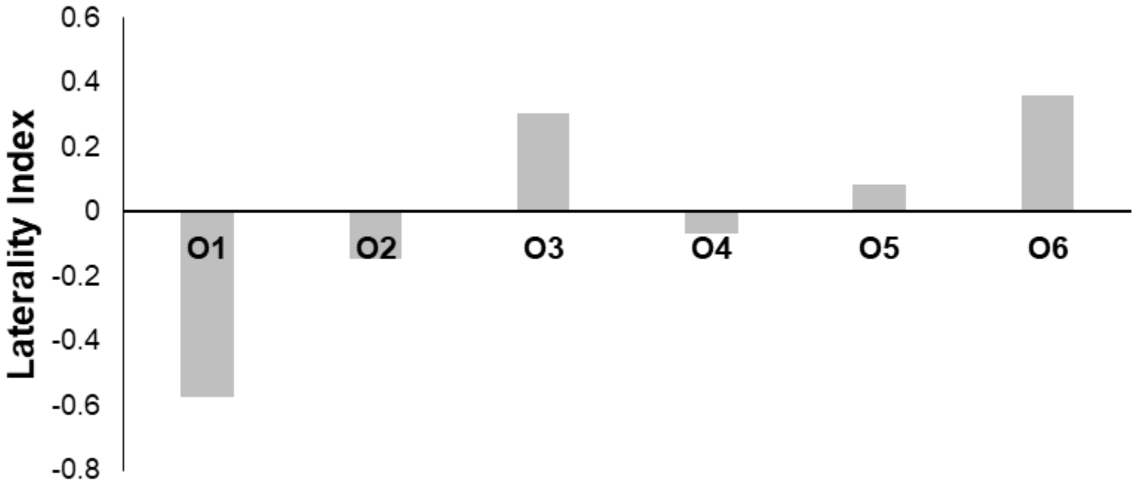
Table 2

Individual Percentage of Paw Use Bias Data Across All Behaviors

	Left	**Right**
O1	21.40	78.60
O2	42.66	57.35
O3	65.16	34.84
O4	46.61	53.39
O5	54.14	45.86
O6	68.09	31.91

Figure 2

Laterality Index of Paw Use Bias Across All Behaviors

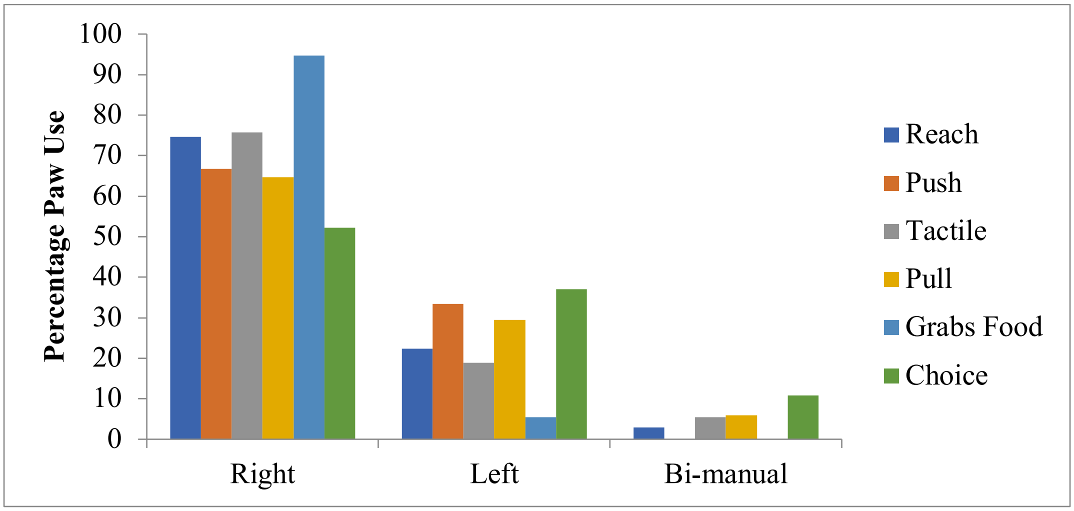


Note. Positive index values indicate a left-side bias, and negative values indicate right-side bias.

In looking at each of the focal behaviors, individual preferences were present for most behaviors. The percentages of O1's right paw usage within each behavior were well above chance level for "reach" (74.67%), "push" (66.67%), "tactile" (75.68%), "pull" (64.71%), and "grabs food" (94.62%) (Figure 3). O1 used his right paw for "choice" only slightly above chance level (52.17%). The percentages of his left paw usage were lower than chance levels for "reach" (22.39%), "push" (33.33%), "tactile" (18.92%), "pull" (29.41%), "grabs food" (5.38%), and "choice" (36.96%). O1's percentages of bi-manual usage were much lower than chance levels for "reach" (2.99%), "push" (0%), "tactile" (5.41%), "pull" (5.88%), "grabs food" (0%), and "choice" (10.87%).

Figure 3

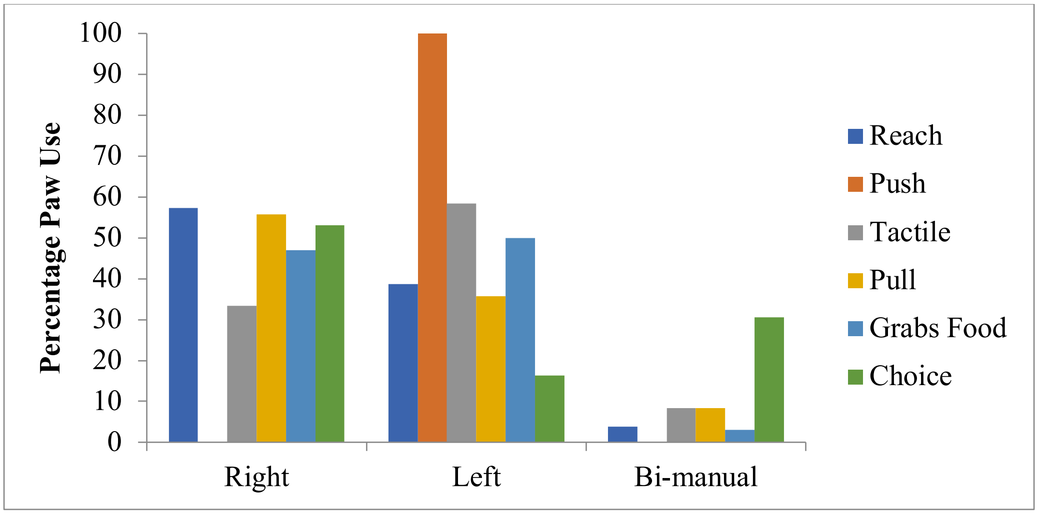
O1's Percentages of Right, Left, and Bimanual Paw Usage for Each Behavior



O2's percentages of right and left paw usage within each behavior were varied (Figure 4). He used his right paw at a percentage below chance levels for "push" and "tactile" (0% and 33.33% respectively). His right paw was used only slightly below chance level for "grabs food" (46.94%), and slightly above chance levels for the "reach," "pull," and "choice" behaviors (57.36%, 55.79%, and 53.06%, respectively). O2 used his left paw for 100% of the "push" behaviors. His left paw usage for "grabs food" occurred at exactly chance level (50%). O2 used his left paw for "tactile" only slightly above chance (58.33%). O2's left paw usage was below chance levels for "reach" (38.76%), "pull" (35.79%), and "choice" (16.33%). O2's percentages of bi-manual usage were below chance levels for "reach" (3.876%), "push" (0%), "tactile" (8.33%), "pull" (8.42%), "grabs food" (3.06%), and "choice" (30.61%).

Figure 4

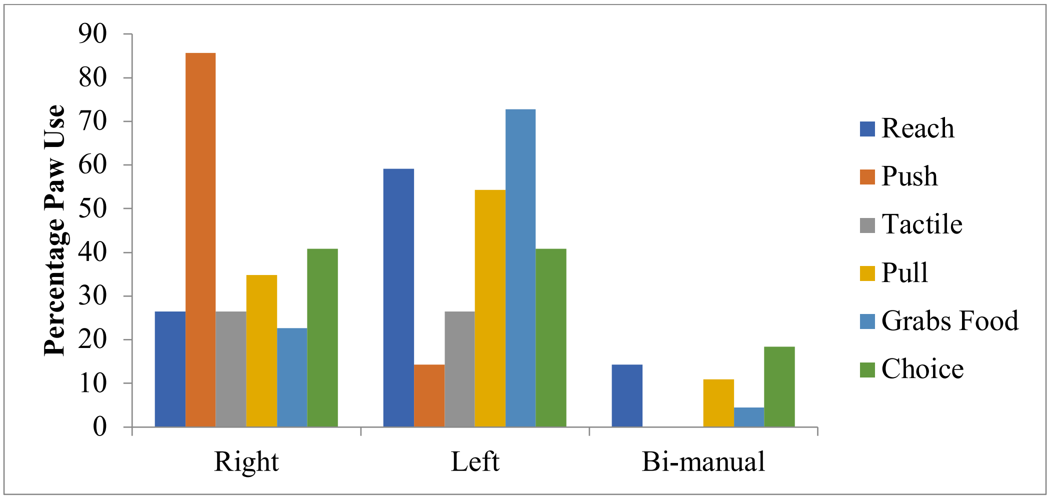
O2's Percentages of Right, Left, and Bimanual Paw Usage for Each Behavior



The percentage of O3's right paw usage was above chance level only for the "push" behavior (85.71%) (Figure 5). O3 used her right paw at a proportion below chance levels for "reach" (26.53%), "tactile" (26.47%), "pull" (34.78%), and "grabs food" (22.73%). O3 used her right paw for "choice" at a level that was slightly below chance (40.82%). O3's left paw percentages were below chance levels for the "push" and "tactile" behaviors (14.29% and 26.47%, respectively). O3 used her left paw for "choice" at a level that was only slightly below chance (40.82%). O3 performed the "grabs food" behavior with the left paw well above chance level (72.72%), while "pull" and "reach" were performed with the left paw slightly above chance level (54.35% and 59.18%, respectively). O3's percentages of bi-manual usage were below chance levels for "reach" (14.29%), "push" (0%), "tactile" (0%), "pull" (10.87%), "grabs food" (4.55%), and "choice" (18.37%).

Figure 5

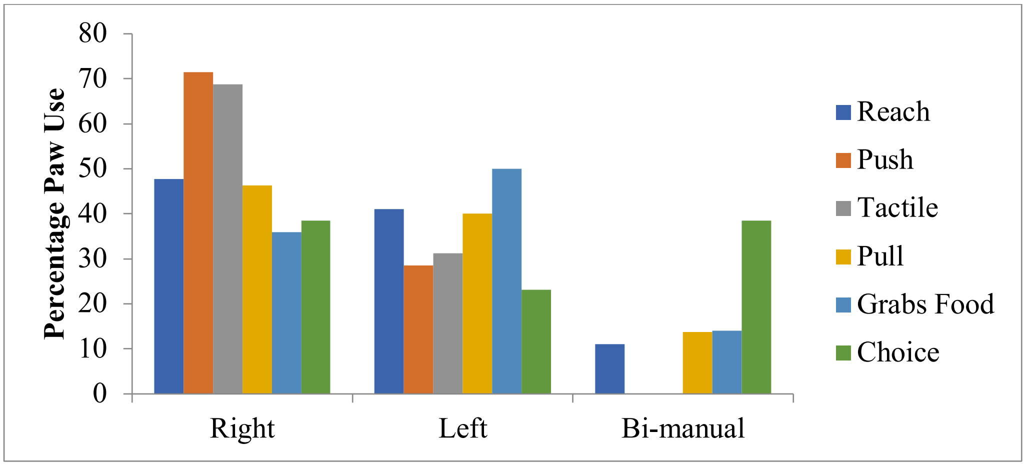
O3's Percentages of Right, Left, and Bimanual Paw Usage for Each Behavior



O4's percentages of right paw usage were above chance levels for "tactile" and "push" (68.75% and 71.43%, respectively) (Figure 6). The proportion of right paw usage for the "grabs food" and "choice" was below chance levels (35.94% and 38.46%). O4 used her right paw for "pull" and "reach" at levels that were only slightly below chance (46.25% and 47.78%, respectively). O4's percentages of left paw usage were below chance levels for "push" (28.57%), "tactile" (31.25%), and "choice" (23.08%). O4 used her left paw for "reach" and "pull" at levels only slightly below chance (41.11% and 40%, respectively). O4's left paw usage for "grabs food" was at exactly chance level (50%). O4's bi-manual percentages were below chance levels for "reach" (11.11%), "push" (0%), "tactile" (0%), "pull" (13.75%), "grabs food" (14.06%), and "choice" (38.46%).

Figure 6

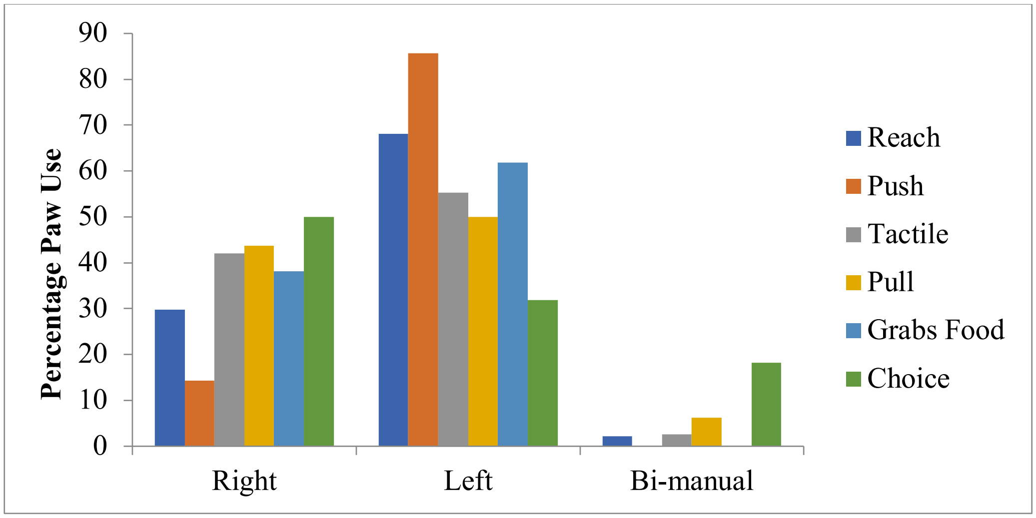
O4's Percentages of Right, Left, and Bimanual Paw Usage for Each Behavior



O5's percentages of right paw usage for each behavior were below chance levels for "reach" (29.79%), "push" (14.29%), and "grabs food" (38.10%) (Figure 7). O5 used her right paw for "tactile" and "pull" at levels only slightly below chance (42.11% and 43.75%, respectively). O5 used her right paw for "choice" at exactly chance level (50%). O5's percentage of left paw usage was above chance levels for the "grabs food", "reach", and "push" behaviors (61.90%, 68.09%, and 85.71%, respectively). O5 used her left paw for "pull" at exactly chance level (50%). O5's left paw usage for the "tactile" behavior was slightly above chance level (55.26%). O5's bi-manual percentages were below chance levels for "reach" (2.13%), "push" (0%), "tactile" (2.63%), "pull" (6.25%), "grabs food" (0%), and "choice" (18.18%).

Figure 7

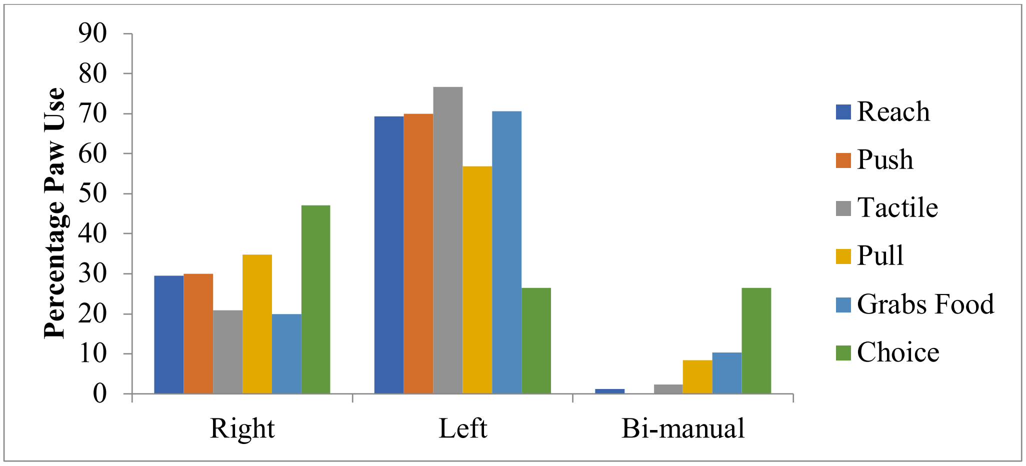
O5's Percentages of Right, Left, and Bimanual Paw Usage for Each Behavior



O6's percentages of right paw usage for each behavior were below chance levels for "reach" (29.55%), "push" (30%), "tactile" (20.93%), "pull" (34.72%), and "grabs food" (18.97%) (Figure 8). O6's right paw usage for "choice" was only slightly below chance level (47.06%). O6's percentages of left paw usage were above chance levels for "reach" (69.32%), "push" (70%), "tactile" (76.74%), and "grabs food" (70.69%). O6 performed the "pull" behavior with her left paw at a level only slightly above chance level (56.94%). O6's left paw usage for the "choice" behavior was below chance level (26.47%). O6's bi-manual actions were below chance levels for "reach" (1.136%), "push" (0%), "tactile" (2.33%), "pull" (8.33%), "grabs food" (10.34%), and "choice" (26.47%).

Figure 8

O6's Percentages of Right, Left, and Bimanual Paw Usage for Each Behavior



Tool Use Performance

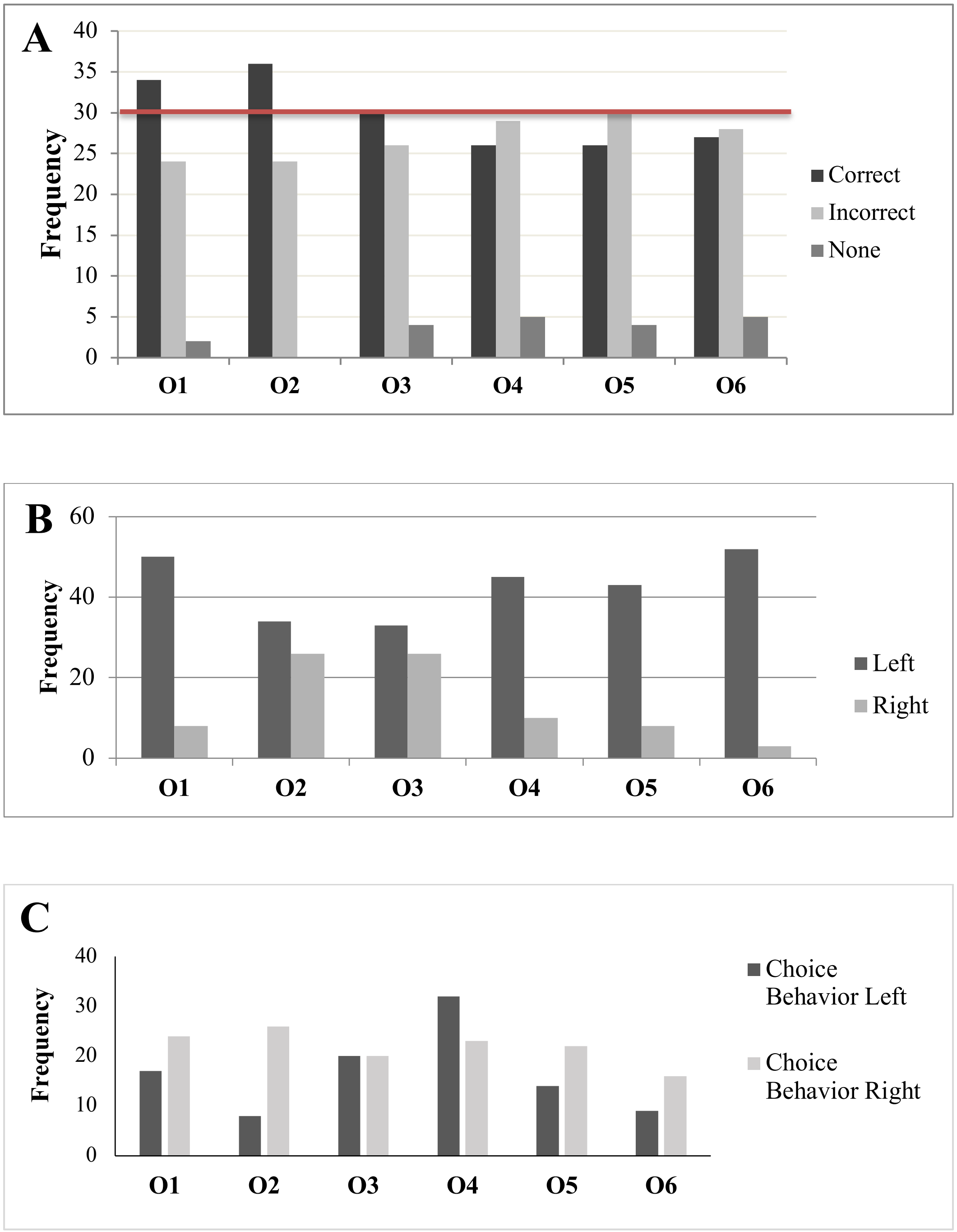
Based on the previous study by Frick et al. (2016), O1 and O2 completed the tool-use task correctly above chance levels (>50%), whereas O4, O5, and O6 performed the task correctly below chance levels (<50%). O3 completed the task correctly at exactly chance levels (=50%). Instances of no choice outcomes were infrequent.

To compare paw preference with the actual lateralized choices made during the tool-use task, Frick et al. (2016) reported that there was a significant difference in the overall number of times the otters chose the left tool ($M = 43$, $SD = 7.72$) compared to the right tool ($M = 13.33$, $SD = 9.71$); $t(5) = -4.22$, $p = .008$). Frick et al. (2016) also found that when looking at individual differences, four of the subjects chose the left tool significantly more than chance (O1: $p < .001$; O4: $p < .001$; O5: $p < .001$; and O6: $p < .001$), whereas the other two subjects did not show a significant side preference (O2: $p = .123$; O3: $p = .218$).

When looking at the laterality data, individual otter paw preference did not seem to impact the side choice (i.e., if choosing the left or right tool) that otters made in completing the tool use task (Figure 9). The only otter's pattern of interest was O3, who both used the left and right paw equally during "choice" behavior specifically, and also exhibited an equal chance of solving the tool-use task correctly or incorrectly. Side bias with regards to choice observed in some otters did not correspond to any detected overall paw preference, nor was there any significant relationship detected between paw use for the "choice" behavior and which tool the otters selected in completing the task.

Figure 9

Comparison of Correct and Incorrect Selections to Paw Preference on "Choice" Behavior



Note. **A**: Figure exhibiting the frequency of each otter's correct vs incorrect responses taken from Frick et al. (2016). **B**: Figure exhibiting the choice of the left or right too taken from Frick et al. (2016). **C**: Frequency of otter using the left vs right paw in the "choice" behavior specifically.

Discussion

Overall Laterality Trends

Overall, these otters had no significant population-level paw preference. Rather, individual differences in which an otter exhibited a paw preference were present. One of the otters exhibited a significant paw preference for the right paw, with two otters showing preferences for the left paw trending towards significance. The remaining three otters had detected nonsignificant paw preferences. These results demonstrate individual paw bias detected on a specific task (i.e., a tool-use task) in Asian small-clawed otters. This is the second study to assess and detect individual preference bias for paw use where no population-level differences were observed, but individual differences in forelimb preference were detected (Manns et al., 2018). Similarly, several other studies involving species from order *Carnivora* (the same order that otter species belong to) concluded forelimb preference detected at the individual level (e.g., Ströckens et al., 2013). For example, a comparable trend on a larger scale was observed in a paw preference study involving cats, in which the cats reached toward a moving spot of light. Of 44 cats, approximately half of the sample had a paw preference, and the majority of those preferences were for the left paw (Fabre-Thorpe et al., 1993). Individual differences existed between cats with a paw preference (some preferred the right and some preferred the left), as was observed in the current study.

Differences in paw preference detected at the individual level have also been observed in northern tree shrews (*Tupaia belangeri*) in a forced food-grasping task, in which the animals were required to use their paws, rather than their mouths, to grasp the food (Maille et al., 2013). Several other paw preference studies involving non-primate mammals result in population-level preference, sometimes differing between sex (e.g., *Rattus norvegicus*; Guven et al., 2003; *Canis familiaris*; Wells, 2003, 2009). Paw preference may also depend on the task, as several studies suggest that left forelimb use may be correlated to expected or routine behaviors, whereas right forelimb use may be correlated to novelty or unexpected stimuli (e.g., Lippolis et al., 2009; MacNeilage et al., 2009; Vallortigara et al., 2000). The relationship between specific contexts for a task and laterality preferences warrants further investigation.

Individual Differences

O1 was shown to have a significant preference for the use of his right paw across all behavioral events coded. However, he was one of the otters that consistently chose the tool located on the left side of the apparatus when completing the tool-use task. O1's tool-use task performance was above chance levels, which suggests that his forelimb preference did not affect his success in the task. In vertebrates, the left hemisphere of the brain is responsible for routine behaviors such as feeding and foraging, and it is believed that many animals show a preference for the right side of the body when performing these actions because of this hemispheric specialization, such as obtaining food on the right side while under direction of the right eye (MacNeilage et al., 2009). O1's "grabs food" behavior could be considered connected to feeding and foraging, and was performed 94.62% of the time with the right paw. The specialization of his left brain hemisphere for feeding behaviors may have influenced his preference for using his right paw with the guidance of his right eye. The other otters who had individual paw preferences trending towards significance (i.e., O3 and O6) on the same behavior, "grabs food," had stronger preference for left paw use. This suggests that if this specialization is present in Asian small-clawed otters, it may not be guiding behavior for this experimental design (i.e., the presentation of a novel tool-use task) that would not be encountered in their natural environment. Comparison across a specialized task in a controlled setting that simulated natural foraging conditions could be conducted as a future direction to investigate this relationship.

While overall sex differences were not investigated due to the small sample size, it may be possible that sex differences influenced the paw preferences present on this task for these otters. O3 and O6 were both females with an overall left paw preference trending towards significance. Similar results were found by Giljoy et al. (2013) in a study of two marsupial species, in which females preferred the left forelimb while males preferred the right in four different tasks: reaching for a food item, catching a live insect, supporting the body in a tri-pedal position, and manipulating food. Contrarily, Hopkins et al. (2009) found different sex-related differences in chimpanzees, in which males preferred the left hand and females preferred the right for a simulated termite-fishing task. These results show that sex-related differences in handedness or forelimb preference can occur in different directions for different species (i.e., male and female preferences can switch depending on the species). Sex differences may also be dependent on the task or the context surrounding the focal behavior and warrant further investigation.

A sex-related difference in paw preference could be the explanation for the trends seen in the results of the current study, because within the significantly lateralized individuals, the females preferred the left paw and the male preferred the right. However, this explanation would only be sufficient within the group of otters that did show a strong paw preference, and does not account for those otters that did not show a significant preference. Due to the overall small sample size with only one otter (male) showing a significant paw preference and two females showing preferences trending towards significance, it was not possible to compare sex related trends in preference with our current study population. Nonetheless, Perdue et al. (2011) found that Asian small-clawed otters did not exhibit sex-related differences in performance of a spatial memory task. Perhaps the presence of sex-related differences in this species is task-dependent. The sex-related difference in paw preference leading to the two females having a left-paw preference in the current study may have affected O3 and O6's success in the tool-use task. O3's tool-use task performance was at exactly chance level and O6's tool-use task performance was below chance level. These results suggest that the left-paw preference may have had a detrimental effect on O3 and O6's task performance.

O2 did not have a significant paw preference, but his tool-use task performance was above chance level (Frick et al., 2016). Horster & Ettlinger (1985) found that rhesus monkeys (*Macaca mulatta*) without a hand preference learned faster on a tactile discrimination task than monkeys that did have a preference. This explanation could be the reason behind the trend seen in O2's results. He may have performed well on the task because of his lack of overall paw preference, and a paw preference might have actually hindered his performance in the task. Although, in many studies comparing paw preference to success in certain tasks, the results suggest that having a preference correlates to better success on the task. Van Alphen et al. (2005) showed that dogs departing with the right paw in a search task typically had greater success in the task than those departing with the left. Perhaps the effect of paw preference on task performance is dependent on the task and the individual animal. More research should be conducted in this area to gain a better understanding of how a paw preference may help or hinder performance on a task.

Conclusions

The results of the current study show that Asian small-clawed otters do not show a significant population-level paw preference on a specialized tool-use task, but they show differences in paw preference on an individual level. Because of the differences in paw preference for the individual otters, the effect of paw preference on tool use also varied for each otter. Paw preference and preference strength did not seem to affect success in the tool-use task for these otters. This is the second study to specifically investigate laterality preferences in Asian small-clawed otters, and future paw preference studies should be conducted using different apparatuses and different tasks to establish a broader range of evidence for this subject and this species. More data from a variety of environments will provide a better foundation for researchers to understand paw preference and how it may relate to tool use. Hopkins and Cantalupo (2005) state that differences in hand preference between individuals of a species can occur due to different environmental settings. Both the current study and previous study investigating paw preference in Asian small-clawed otters utilized data collected in a semi-controlled setting (e.g., a zoological facility; Manns et al., 2018). Therefore, future studies should attempt to investigate paw preference in wild Asian small-clawed otters, as well, for possible comparisons. Additionally, future studies may want to look at how genetics contributes to paw preference and tool use, since some genes have been shown to be associated with tool use and are expressed when an animal learns a new task (Matsunaga et al., 2015). Asian small-clawed otters, due to their high sensitivity of the paws and wide range of digital movement, are an excellent candidate for studying cognitive abilities and their relationship to laterality in forelimb preference (Perdue et al., 2013). Tool-use studies, therefore, can help provide information on the full manual abilities of this otter. Future research on Asian small-clawed otters in these areas can help the facilities that house these animals to establish better opportunities for mental and physical stimulation for these animals, as well as give new insight to the animals' cognitive abilities.

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