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Laterality Preferences Completing a Tool-Use Task in Asian Small-Clawed Otters (*Aonyx cinereus*)

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The University of Southern Mississippi

Laterality Preferences Completing a Tool-Use Task in Asian Small-Clawed Otters (*Aonyx cinereus*)

by

Stephanie James

A Thesis
Submitted to the Honors College of
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in Partial Fulfillment
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Abstract

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 exhibit significant paw preferences in behaviors associated with completing a 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 paw preference was present. However, individual differences in paw preference as well as differences in task performance were 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.

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

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Chapter 1 – Introduction

Laterality, the concept of the different hemispheres of the brain having asymmetric control over the body, has been widely studied in humans as well as several animal species (Frost, 1980). One specific type of laterality that is the subject of much research is hand preference. Most members of the human population are right-handed, but researchers have been investigating whether or not non-human animals also show a hand preference and how this preference might be exhibited. These hand preferences can occur at the population level (e.g., chimpanzees, *Pan troglodytes*; Lonsdorf, Hopkins, & de Waal, 2005), or they can be sex-dependent (e.g., grey short-tailed opossum, *Monodelphis domestica* and sugar glider, *Petaurus breviceps*; Giljoy, Karenina, & Malaschichev, 2013). Hand preference can also depend on the motor requirements of the task, such as whether the task requires use of one or two hands (e.g., squirrel monkeys, *Saimiri* sp.; Meguerditchian, Donnot, Molesti, Francioly, & Vauclair, 2012).

One method of assessing handedness in animals is observing tool-use behaviors. Handedness can affect tool use in that the animal is thought to use the dominant hand to perform an action in most instances of the task (Hopkins & Rabinowitz, 1997). The focus of the current study was to determine if Asian small-clawed otters showed a paw preference when using tools. The majority of the literature regarding handedness has involved primates such as chimpanzees (Lonsdorf et al., 2005). To date, no research has been conducted examining paw preference in otters. Studies looking at tool use in otters dealt primarily with wild sea otters (*Enhydra lutris*; Fujii, Ralls, & Tinker, 2014), with limited examinations of tool-use in a captive setting or in any other otter species (Frick, Friedman, Peranteau, Beachman, & Kuczaj, 2016; Hannah, Frick & Kuczaj, 2016). Therefore, the present study provides new information about handedness and tool use in Asian small-clawed otters.

This study aimed to answer two specific questions: (1) do Asian small-clawed otters have a paw preference? (2) How might this paw preference affect tool use? To answer these questions, video data from a prior tool-use study involving Asian small-clawed otters were analyzed (Frick et al., 2016). Subjects included six captive otters at Six Flags Great Adventure, New Jersey. These videos were recorded in summer of 2014 from a tool-use study conducted by the Marine Mammal Behavior and Cognition Lab at the University of Southern Mississippi. This data set consists of 60 trials for each of the six otters with a tool-use apparatus. These videos were coded for specific paw-related behaviors performed by the otters when interacting with the apparatus. Once each paw behavior was identified as a right, left, or bi-manual paw, the results were then compiled to determine if each otter had a paw preference. These preferences were analyzed and conclusions were drawn regarding how the paw preferences were distributed in this sample of otters and how these preferences affected their performance on the tool-use task. These results provide a basis for future studies regarding tool use and paw preference in otters, as well as how these two concepts may relate to one another.

Chapter II – Literature Review

Laterality

Laterality is defined as each hemisphere of the cerebral cortex having asymmetrical control over certain functions (Frost, 1980), indicating preferences for one side of the body over the other (Kalichman, Batsevich, & Kobylansky, 2014). Examples of laterality include hand/foot preference, eye dominance, and ear dominance (Fitch & Braccini, 2013). One method for assessing laterality that has garnered attention in the literature in human and non-human animals is handedness, which can be analyzed in relation to cognitive performance such as language and spatial memory tests in order to determine if a connection exists between

lateralization and task performance in an individual (Mellet et al., 2014). For example, D'Anselmo, Giuliani, Marzoli, Tommasi, and Brancucci (2015) measured laterality in pianists during a sight-reading exercise. This study related hand performance to visual stimuli, and the results showed that stimuli (i.e., musical notation) presented on a certain side was more accurately played with the ipsilateral hand (i.e., hand on the same side as stimulus). These results showed that lateralization could sometimes be a component to an individual's success in completing a task.

Origin of Laterality

Though laterality can be applied and related to many aspects of the body, the origin of laterality and handedness is highly debated. Handedness is believed to have evolved in humans due to the developing need to use and make tools (Frost, 1980). However, Cochet and Byrne (2013) argue that tool use was not the origin of human handedness, proposing instead that communicative gestures initiated the need for hand preference in humans. Fitch and Braccini (2013) support the latter argument by suggesting that right-handedness in humans arose because the left hemisphere of the brain is responsible for social functions, showing that a certain hemisphere of the brain controls the opposite hemifield on an animal. Scientists previously believed that handedness and the lateralized brain were unique to humans only, and no similar traits were found in other organisms. However, hand preferences in primates have been studied extensively and have been found to be influenced by learning and experience, but primate hand biases are not believed to be homologous to those of humans (Warren, 1980). This raises the question: do non-human animal species exhibit laterality preferences homologous to those observed in humans?

Cerebral Connection with Laterality in Animals

Laterality studies have also been conducted on a wide variety of non-primate animals including wombats (*Lasiorninus latifrons*; Descovich, Reints Bok, Lisle, & Phillips, 2013), chicks (*Gallus gallus domesticus*; Dharmaretnam & Rogers, 2005), orcas (*Orcinus orca*; Karenina, Giljov, Ivkovich, Burdin, & Malashichev, 2013), lizards (*Podarcis muralis*; Martin, Lopez, Bonati, & Csermely, 2010), cats (*Felis silvestris catus*; Pike & Maitland, 1997), horses (*Equus caballus*; Sinischalchi, Padalino, Lusito, & Quaranta, 2014), and bottlenose dolphins (*Tursiops truncatus*; Thieltges, Lemasson, Kuczaj, Boye, & Blois-Heulin, 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. For example, Martin et al. (2010) concluded that the right hemisphere of the brain is responsible for anti-predatory and aggressive behaviors after observing 140 wild lizards showing a significant preference to watch a predator with the left eye (i.e., visual laterality). Auditory laterality has been studied in wombats (Descovich et al., 2013) by observing head turn direction in response to bilaterally presented sounds. The researchers concluded that the right hemisphere of the brain processes novel concepts because the head turns were mostly to the left in response to the presentation of novel sound stimuli. Spatial laterality has also been studied. For example, results from an observation of 30 mother-infant pairs of orcas show that infant orcas prefer to swim on the mother's right side in a non-threatening situation, and then they switch to the mother's left side in a threatening situation. These findings suggest that the right hemisphere of the brain is responsible for social interactions in orcas because the infant swimming on the mother's right side sees the mother with its left eye (Karenina et al., 2013). These conclusions of brain hemisphere function are contradictory to those of Fitch and Braccini (2013) that social

functions in humans are due to the left hemisphere of the brain. These examples are only a few of many studies on this subject and conflicting results are present. Further dissemination of the current literature is needed to determine specialization of brain hemisphere across species.

Influences on Hand Preference in Animals

Though brain hemisphere control is important to note with laterality in order to understand which hemisphere of the brain is related to certain functions, the current study focuses on laterality in respect to tool use and hand preference. Hand preference has been widely studied in primates, as well as some marsupial species. Hand preference has also been shown to depend on certain factors such as sex. Sex-related differences in forelimb preference are found in marsupials, 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 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). From these results, it can be suggested that sex-related differences in hand preference, if any, might be unique across species.

Captive chimpanzees have also been known to 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, Russell, Schaeffer, Gardner, & Schapiro 2009). However, a study with wild chimpanzees showed no sex-related differences but an overall population-level left hand preference when termite-fishing (Lonsdorf et al., 2005). This difference in hand preference between wild and captive chimpanzees could be due to the fact that simulated termite-fishing does not exactly represent termite-fishing in the wild, or perhaps this difference could reflect the distinct learning experiences between captive and wild animals (Hopkins et al., 2009).

Therefore, these findings suggest that differences in hand preference can exist between wild and captive animals possibly due to different social and environmental settings.

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 captive 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 exhibit a right hand bias for retrieving food, but the preference is stronger when the task requires use of two hands (*Cebus apella*; Spinozzi & Truppa, 1999), showing that strength of lateralization can depend on whether one or two hands is used. A similar trend is also observed in the study conducted 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. These results show that hand preference, as well as strength of the preference, can depend on whether the task is completed using a uni-manual or bi-manual strategy, as well as other demands of the task.

Hand preference in chimpanzees may also arise from learning and social interactions, as originally suggested by Warren (1980). These results are supported by those of Hopkins et al. (2009), which showed that hand preferences in captive chimpanzees often were the same as those of the mother. Lonsdorf et al. (2005) also supported these results by suggesting that hand

preferences may be heritable either by learning or genetic factors in wild chimpanzees. These conclusions are all drawn from studies on primates, specifically chimpanzees, so this heritability of hand preference may be different or nonexistent in other species.

Tool Use

Studies assessing tool use are thought to provide insight to handedness preferences in primate and non-primate species. Tool use has been defined as the use of an environmental object to alter the orientation or state of another object, while the user handles the tool during and before using it (Mann & Patterson, 2013). Some animals, such as macaques, have specialized genes for tool use that are expressed when new cognitive tasks are learned (*Macaca fuscata*; Matsunaga et al., 2015). Many tool-use studies have been conducted on primates, such as Hopkins and Rabinowitz (1997) in which captive chimpanzees dipped a stick into a container to retrieve food. However, only a few researchers have investigated tool use in aquatic animals, most likely due to aquatic animals' tool use being difficult to observe. Despite this, literature shows that aquatic animals use tools for a variety of purposes. For example, bottlenose dolphins have been shown to use sponges to protect their rostrums while foraging in the sand on the seafloor, and sea otters sometimes wrap kelp around their bodies to help them float (Mann & Patterson, 2013).

Sea otters have been shown to improve their usage of tools through practice, and they learn how to use tools through observational learning from parents (Tinker, Mangel, & Estes, 2009). Sea otters tend to use tools mostly when preying on bivalves and snails, rather than on 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, Nur-Syuhada, Md-Nor, Sasaki, & Md-Zain, 2014). Given the findings of the latter two studies, it can be

proposed that since Asian small-clawed otters prefer prey that has a hard exterior surface, they may be more inclined to use tools than species that eat soft bodied organisms.

Though most of the studies on hand preference and tool use have been performed examining primates, the current study focuses on Asian small-clawed otters. This species shows intelligent behavior and cognitive abilities, such as spatial memory for food locations (Perdue, Snyder, & Maple, 2013) and ability to use a tool in a forced-choice tool-use task (Frick et al., 2016). However, a paw preference might affect the animals' abilities to perform this task effectively. I hypothesized that the otters would show a paw preference when using the tools, and that this preference would affect their success in choosing the correct tool. From the results of this study, I aimed to provide a better understanding of how paw preference affects tool use in otters, as well as suggest topics for future research.

Chapter III – Methods

Subjects

The sample of six otters that was observed in this study consisted of four females (Cali, Pearl, Roxi, and Sushi) and two males (Baxter and Jackson). These otters are housed at Six Flags Great Adventure in New Jersey. These otters are siblings and were two years old at the time of the data collection.

Experimental Design

The tool-use apparatus 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 and placed so that one is on the right side of the platform and one is 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 so that the blue line reached 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). Figure 1 shows the tool-use apparatus, and the cookies represent an example of how the food was placed for the otter. 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.



Figure 1. Tool-use apparatus

Data Analysis

All 360 videos were observed and operational definitions related to hand-specific behaviors were established. Each behavior was coded as 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”. The definitions for each behavior are listed in Table 1. The tool that the otter used to make the choice was also coded as “R” or “L” as viewed from the position of the otter.

Table 1. Behavior definitions

Behavior	Definition
Reach	Otter extended 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 to blue line/end of the platform, or to the point where the other tool is inaccessible
Push	Otter moved the tool away from itself
Tactile	Otter touched the tool without moving it
Grabs Food	Otter’s acquisition of food

Once the all the videos were coded for these behaviors, the results were compiled and analyzed to determine if each otter has a paw preference. Overall paw preferences for all the otters were determined using ANOVA tests. A Bonferroni post-hoc analysis was performed to determine if any significant difference in paw preference between each otter were shown. A Wilcoxin-Signed Ranks test was performed to determine individual hand preferences for each otter. The frequency the use of each paw (R, L, or Bi) for each behavior was also calculated for each otter (e.g., Baxter used his right paw for 74.63% of the “reach” behaviors). Trends in these preferences were observed, such as paw preferences in relation to sex of the otter or if paw preferences were shown only during specific behaviors. The otters’ paw preferences were also compared to their success in the tool-use task in order to determine if there were any patterns that may have explained how handedness affected tool use (e.g., a left-handed otter consistently choosing the left tool whether it is the correct choice or not).

Chapter IV – Results

Paw Preference

Due to the small sample size, alpha level of 0.15 was set as criteria for significance. Friedman one-way ANOVA revealed that across all otters, significant differences in preference for using either the right or left paw were present across all behavioral events ($F(4,25) = 3.160$, $p < 0.15$). A Bonferroni post-hoc analysis showed that significant differences in paw preference were exhibited between Baxter and Pearl ($p < 0.15$) and Baxter and Sushi ($p < 0.15$). No other significant differences between otters were detected.

A Wilcoxin-Signed Ranks test was calculated for each individual otter to determine individual paw preferences. Baxter's use of the right paw across all behavioral events was significant ($z = -2.201$, $p < 0.15$). Baxter used his right paw 74.11% of the time, his left paw 21.85% of the time, and both paws 4.04% of the time. A significant preference for the use of the left paw was exhibited by Cali ($z = -1.758$, $p < 0.15$) and Sushi ($z = -1.782$, $p < 0.15$). Cali used her right paw 31.21% of the time, her left paw 58.38% of the time, and both paws 10.40% of the time; similarly, Sushi used her right paw 29.51% of the time, her left paw 62.95% of the time, and both paws 7.54%. Jackson, Pearl, and Roxi showed no significant preference for use of the right versus left paw. Jackson used his right paw 52.59% of the time, his left paw 39.12% of the time, and both paws 8.29% of the time. Pearl used her right paw 45.27% of the time, her left paw 39.53% of the time, and both paws 15.20% of the time. Roxi used her right paw 40% of the time, her left paw 53.66% of the time, and both paws 6.34% of the time. These values are illustrated in Figure 2.

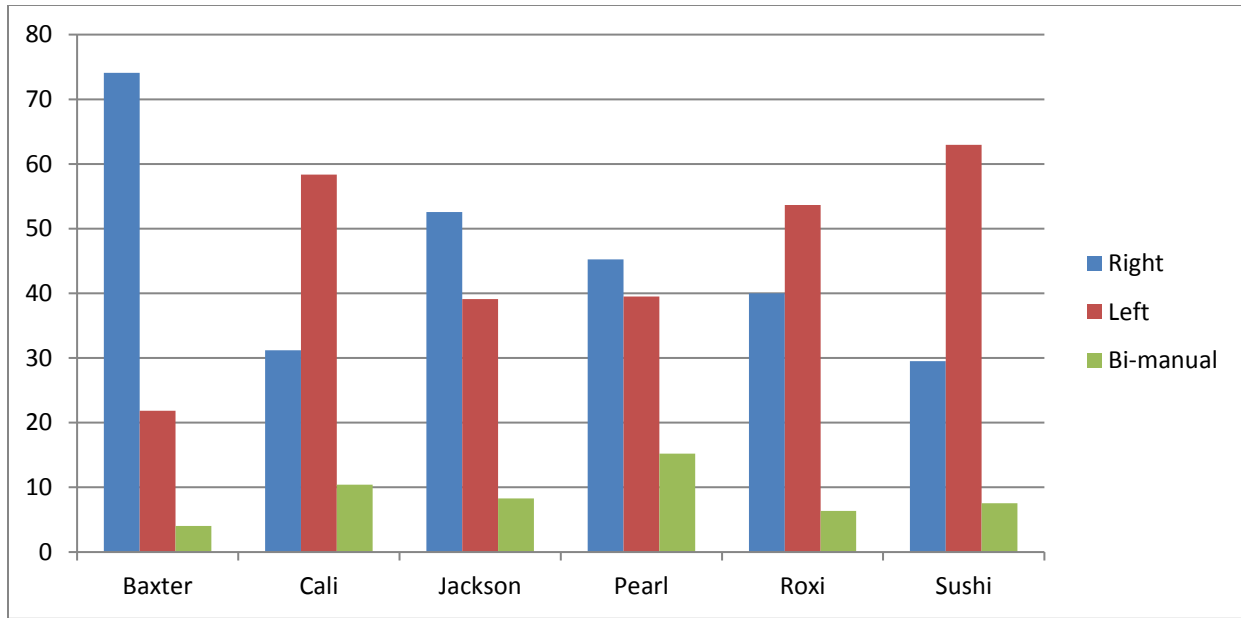


Figure 2. Percentages of right, left, and bi-manual usage among the otters.

Behavioral Differences

The percentages of Baxter’s right paw usage within each behavior were well above chance for “reach” (74.67%), “push” (66.67%), “tactile” (75.68%), “pull” (64.71%), and “grabs food” (94.62%). Baxter used his right paw for “choice” at a frequency that was only slightly above chance level (52.17%). The percentages of his left paw usage were lower than chance for “reach” (22.39%), “push” (33.33%), “tactile” (18.92%), “pull” (29.41%), “grabs food” (5.376%), and “choice” (36.96%). Baxter’s percentages of bi-manual usage were lower than chance for “reach” (2.985%), “push” (0%), “tactile” (5.405%), “pull” (5.882%), “grabs food” (0%), and “choice” (10.87%). These values are illustrated in Figure 3.

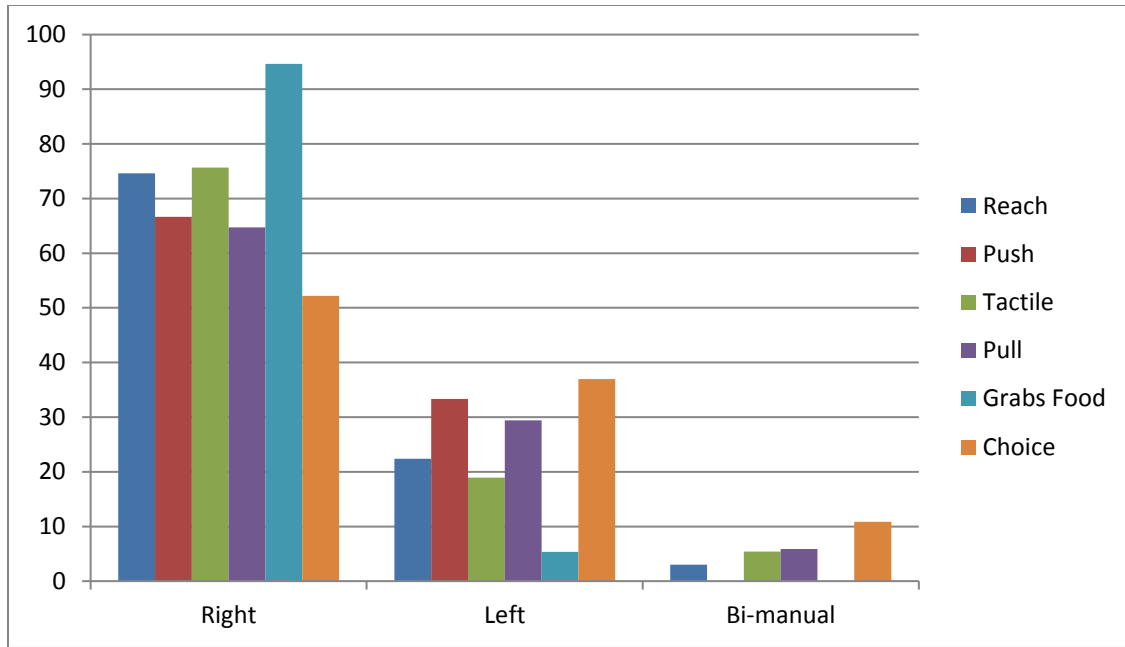


Figure 3. Baxter's percentages of right, left, and bi-manual paw usage in each behavior type.

The percentage of Cali's right paw usage was above chance only for the "push" behavior (85.71%). Cali 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%). Cali used her right paw for "choice" at a level that was slightly below chance (40.82%). Cali's left paw percentages were below chance levels for the "push" and "tactile" behaviors (14.29% and 26.47%, respectively). Cali used her left paw for "choice" at a level that was only slightly below chance (40.82%). Cali 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). Cali's percentages of bi-manual usage were below chance for "reach" (14.29%), "push" (0%), "tactile" (0%), "pull" (10.87%), "grabs food" (4.545%), and "choice" (18.37%). These values are illustrated in Figure 4.

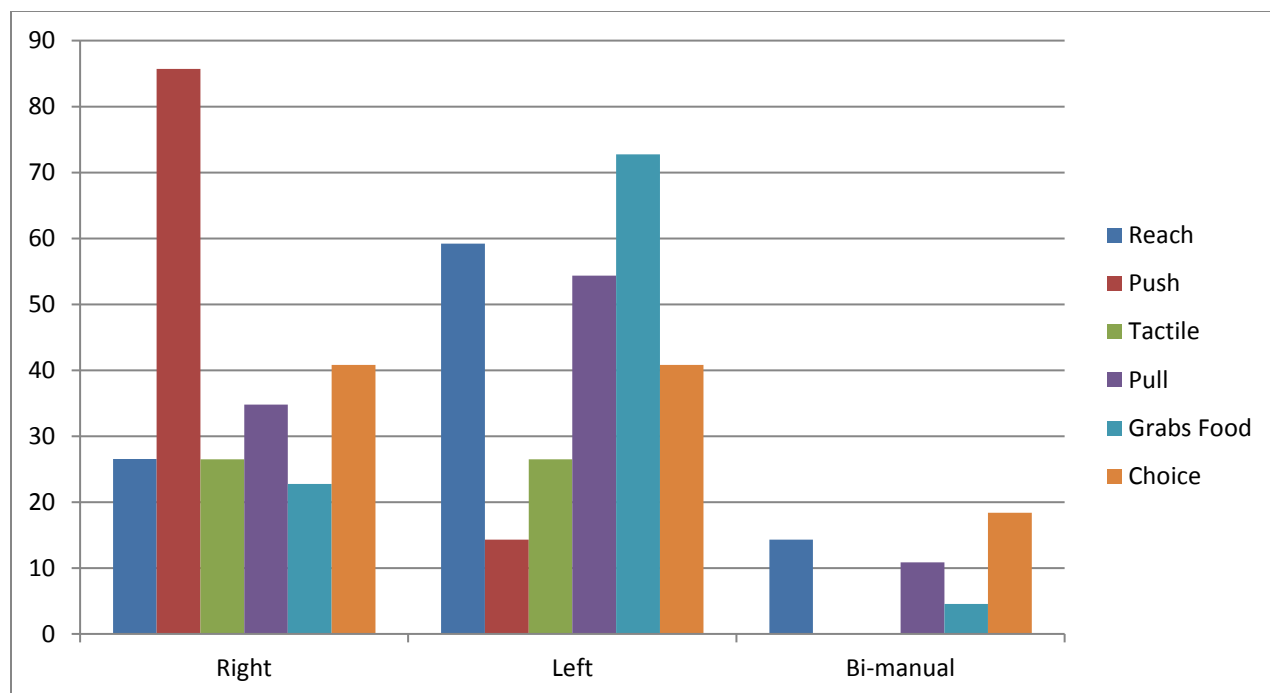


Figure 4. Cali's percentages of right, left, and bi-manual paw usage in each behavior type.

Jackson's percentages of right and left paw usage within each behavior were varied. 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 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). Jackson used his left paw for 100% of the "push" behaviors. His left paw usage for "grabs food" occurred at exactly chance level (50%). Jackson used his left paw for "tactile" only slightly above chance (58.33%). Jackson's left paw usage was below chance for "reach" (38.76%), "pull" (35.79%), and "choice" (16.33%). Jackson's percentages of bi-manual usage were below chance for "reach" (3.876%), "push" (0%), "tactile" (8.333%), "pull" (8.421%), "grabs food" (3.061%), and "choice" (30.61%). These values are illustrated in Figure 5.

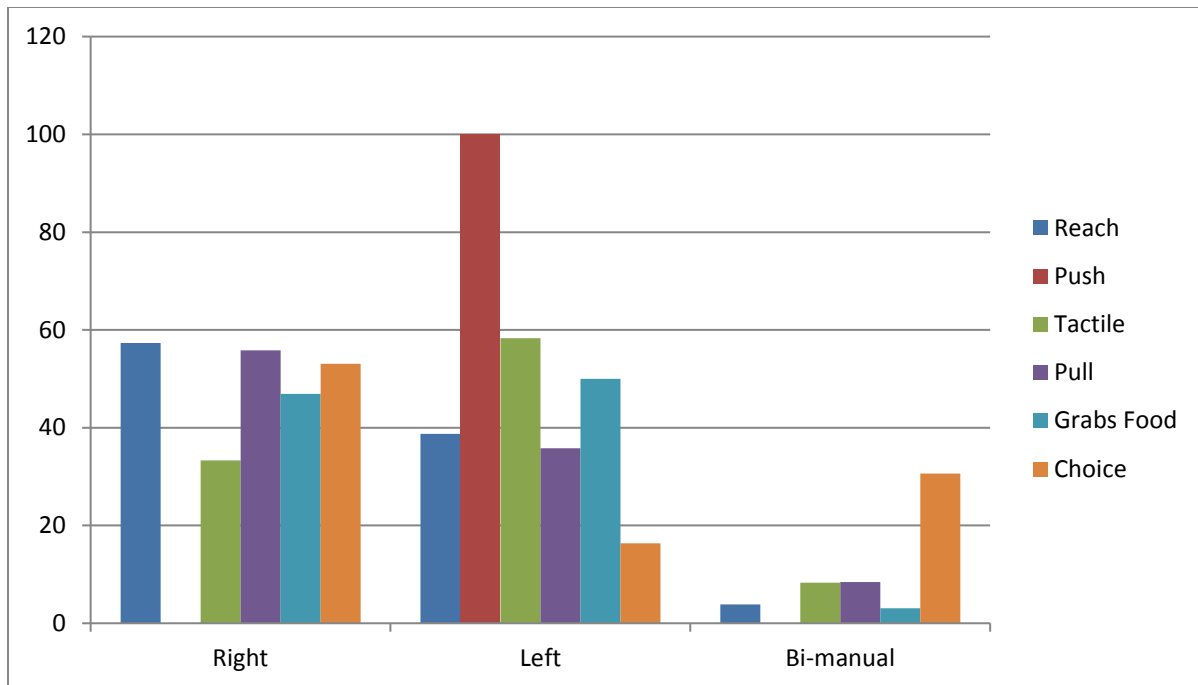


Figure 5. Jackson’s percentages of right, left, and bi-manual paw usage in each behavior type.

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

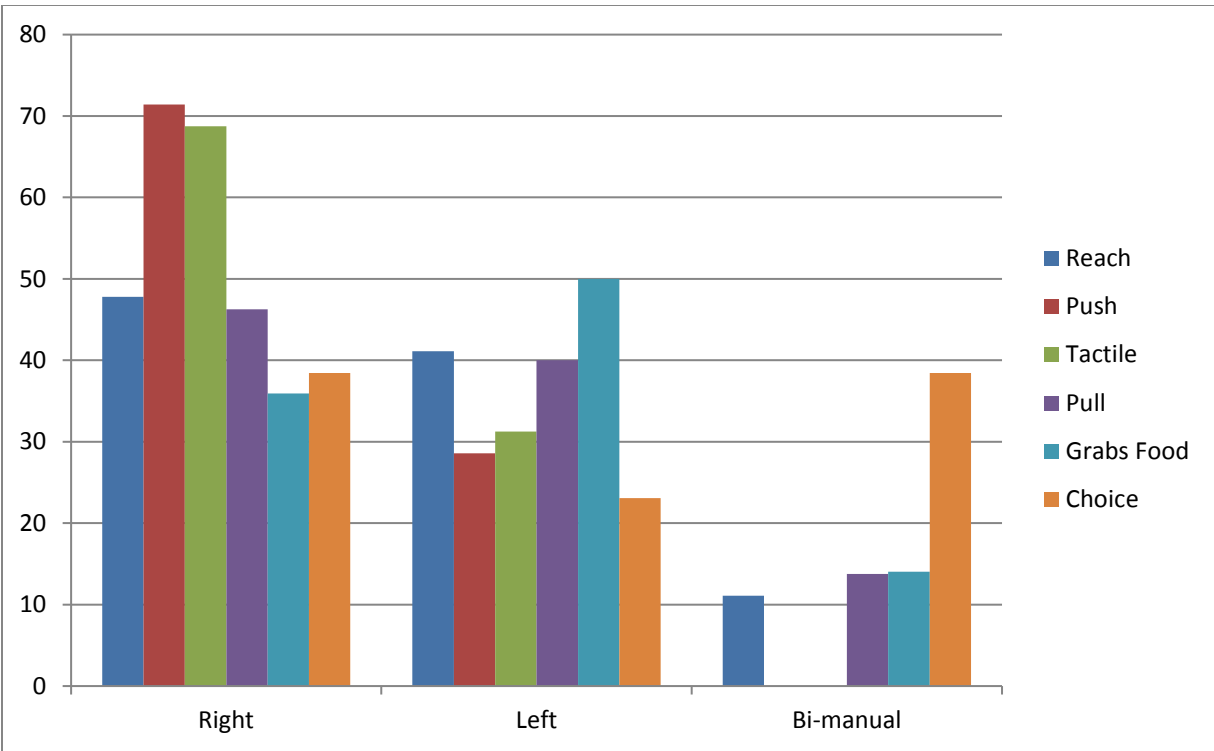


Figure 6. Pearl’s percentages of right, left, and bi-manual paw usage in each behavior type.

Roxi’s percentages of right paw usage for each behavior were below chance for “reach” (29.79%), “push” (14.29%), and “grabs food” (38.10%). Roxi used her right paw for “tactile” and “pull” at levels only slightly below chance (42.11% and 43.75%, respectively). Roxi used her right paw for “choice” at exactly chance level (50%). Roxi’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). Roxi used her left paw for “pull” at exactly chance level (50%). Roxi’s left paw usage for the “tactile” behavior was slightly above chance (55.26%). Roxi’s bi-manual percentages were below chance for “reach” (2.128%), “push” (0%), “tactile” (2.632%), “pull” (6.250%), “grabs food” (0%), and “choice” (18.18%). These values are illustrated in Figure 7. Roxi also occasionally manipulated the tools using her mouth, and this behavior occurred in 71.67% of the trials.

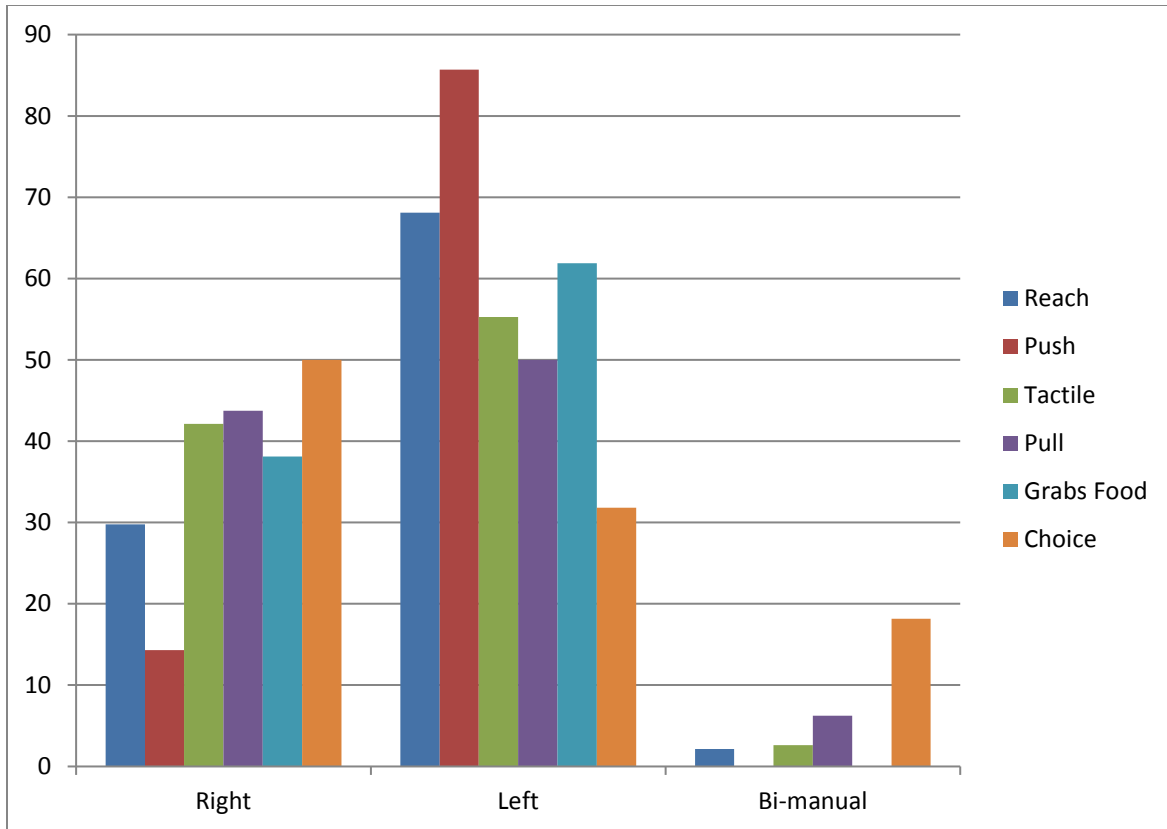


Figure 7. Roxi's percentages of right, left, and bi-manual paw usage in each behavior type.

Sushi's percentages of right paw usage for each behavior were below chance for "reach" (29.55%), "push" (30%), "tactile" (20.93%), "pull" (34.72%), and "grabs food" (18.97%). Sushi's right paw usage for "choice" was only slightly below chance (47.06%). Sushi's percentages of left paw usage were above chance for "reach" (69.32%), "push" (70%), "tactile" (76.74%), and "grabs food" (70.69%). Sushi performed the "pull" behavior with her left paw at a level only slightly above chance (56.94%). Sushi's left paw usage for the "choice" behavior was below chance (26.47%). Sushi's bi-manual actions were below chance for "reach" (1.136%), "push" (0%), "tactile" (2.326%), "pull" (8.333%), "grabs food" (10.34%), and "choice" (26.47%). These values are illustrated in Figure 8.

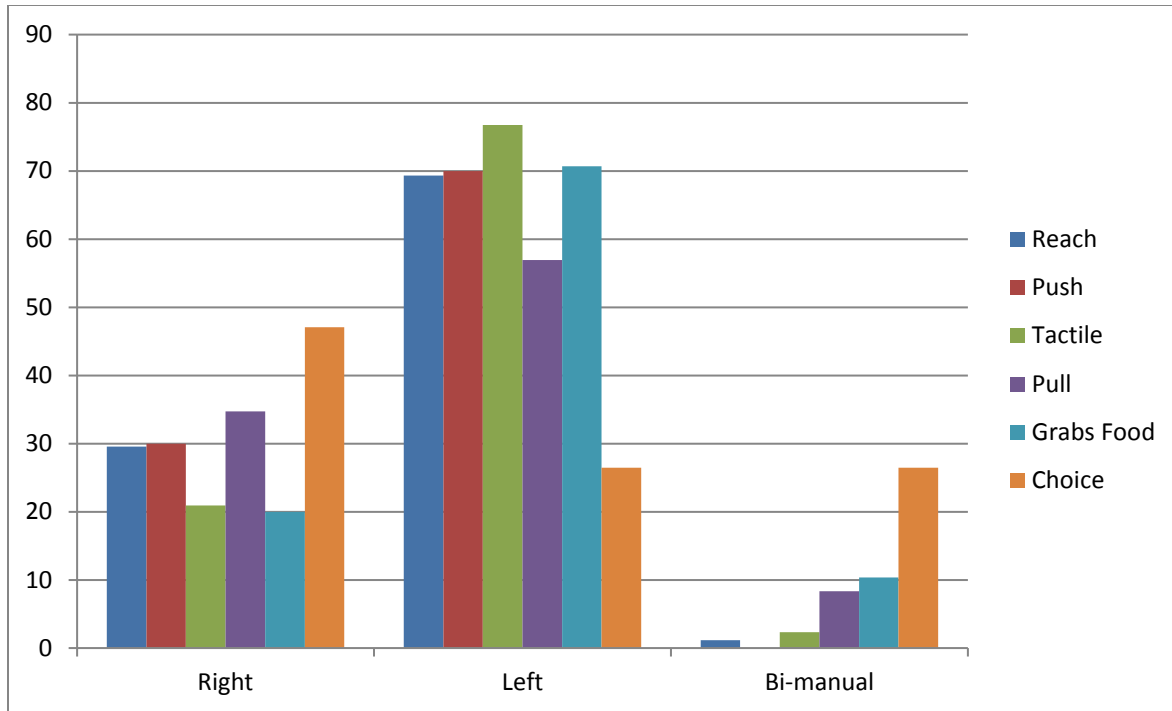


Figure 8. Sushi's percentages of right, left, and bi-manual paw usage in each behavior type.

Tool-Use Performance

Based on the previous study by Frick et al. (in prep), Baxter and Jackson completed the tool-use task correctly above chance levels (>50%), whereas Pearl, Roxi, and Sushi performed the task correctly below chance levels (<50%). Cali 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 ($M = 43$, $SD = 7.720$) compared to the right tool ($M = 13.333$, $SD = 9.709$); $t(5) = -4.219$, $p = 0.008$). Frick et al. (2016) also found that when looking at individual differences, four of the subjects chose the left tool significantly more than chance (Baxter: $p = 0.000$; Pearl: $p = 0.000$; Roxi: $p = 0.000$; and Sushi: $p = 0.000$), whereas the other two subjects did not show a significant side preference (Jackson: $p = 0.123$; Cali: $p = 0.218$).

Chapter V – Discussion

Population-Level Preference

Overall, these otters had no significant population-level paw preference. Rather, individual differences in which otter exhibited a paw preference were present. Three of the otters exhibited a significant paw preference, with two of those preferences being the left paw and one preference being the right paw. A similar 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, Fagot, Lorenz, Levesque, & Vauclair, 1993). These results are similar to those of the current study, in that approximately half of the sample had a paw preference, and most of those lateralized individuals preferred the left paw. Additionally, individual differences existed between cats with a paw preference (some preferred the right and some preferred the left) like in the current study with otters. Individual differences in paw preference, rather than a population-level preference, have also been observed in the tree shrew in a forced food-grasping task, in which the animals were required to use their paws to grasp the food rather than their mouths (*Tupaia belangeri*; Maille et al., 2013). However, many other paw preference studies involving non-primate mammals result in population-level preference, sometimes differing between sex (*Rattus norvegicus*; Guven, Elalmis, Binokay, & Tan, 2003; *Canis familiaris*; Wells, 2003, 2009), but individual differences in paw preferences still occur in some samples of certain species.

Individual Differences

Baxter was shown to have a significant preference for the use of his right paw for all behavioral events coded. However, he was one of the otters that consistently chose the tool

located on the left side of the apparatus. Baxter's tool-use task performance was above chance levels, which suggests that his paw 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, Rogers, & Vallortigara, 2009). This could be an explanation for Baxter's right paw preference, as he performed 94.62% of his "grabs food" behaviors 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. However, this explanation would not be sufficient for Cali and Sushi's paw preference because they exhibited significant preference for the left paw. Cali performed only 22.73% of the "grabs food" behaviors with her right paw, and Sushi performed only 19.97% of the same behavior with her right paw. These percentages suggest that the specialization of the left hemisphere did not seem to influence Cali and Sushi to use the right paw for the "grabs food" behavior, and this specialization, if present, does not sufficiently explain their paw preferences.

Cali and Sushi's left paw preference could be an example of a sex-related difference in paw preference. Similar results were found by Giljoy et al. (2013) in a study with marsupials, 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 tripod 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). 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 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 paw preference, and does not account for those otters that did not show a significant preference. With the otters that did not show a paw preference, no significant paw preference data was available with which to compare trends in preferences, such as sex-related differences. However, Perdue, Snyder, Zhihe, Marr, and Maple (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 Cali and Sushi's success in the tool-use task. Cali's tool-use task performance was at exactly chance level and Sushi's tool-use task performance was below chance level. These results suggest that the left-paw preference may have had a detrimental effect on Cali and Sushi's task performance.

Jackson did not have a significant paw preference, but his tool-use task performance was above chance level (Frick et al., 2016). Horster & Ettliger (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 Jackson'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. However, 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. A study by Van Alphen, Bosse, Frank, Jonker, and Koeman (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 in order to gain a better understanding of how a paw preference may help or hinder performance on a task.

Roxi was one of the otters that lacked a significant paw preference. However, she used her mouth to manipulate the tools in approximately 75% of the trials. The frequent mouthing behaviors exhibited in the tool-use task may be the reason that she did not exhibit a significant paw preference. As well as mouthing, Roxi tended to be quick to make a choice, in that she did not spend much time with tool-use apparatus before completing the task. Roxi's tool-use task performance was below chance level, possibly due to her rushing through the task (Frick et al., 2016). In the current study, the otter that was presented with the tool-use apparatus was visually isolated from the other otters, but he or she could still hear them. Asian small-clawed otters are highly vocal animals, and research suggests that an otter may use vocalizations to communicate its current activity, and otters can also discriminate between individuals based on vocalization alone (Lemasson, Mikus, Blois-Heulin, & Lodé, 2014, 2013). The importance of vocalization to this species may explain Roxi's rushing to make a choice; perhaps Roxi deduced that once she completed the task, she was reunited with the other otters and found that using her mouth was the fastest method of choosing. For Roxi, lack of motivation to attempt to complete the task correctly may have caused her results for paw preference relating to success in the tool-use task to be inconclusive.

Pearl did not exhibit a significant paw preference, and her tool-use task performance was below chance level. Jackson, Nicolson, and Lots (1998) show that cape sugarbirds, *Promerops cafer*, and lesser double-collared sunbirds, *Cinnyris chalybeus*, show a side bias but no lateralization in a sugar preference study, in that the birds consistently chose the feeder on one particular side because of stereotyped foraging behavior rather than because of a lateralization preference. Similarly, Pearl chose the left tool consistently, exhibiting a possible side bias with no paw preference, so side bias may exist independently of laterality. Additionally, Pearl showed the highest percentage of bi-manual behaviors of all the otters, but these occurred at a frequency below chance levels. Westergaard and Suomi (1996) found that hand preference in capuchins was stronger in adults than in younger animals in a food retrieval task. Though all the otters in the current study are the same age, perhaps Pearl has not yet developed a paw preference due to individual differences in development. Research has also shown that bi-manual coordination is an important method for gorillas in manipulating food items (*Gorilla gorilla beringei*; Byrne & Byrne, 2001). Similarly, Pearl may have found that bi-manual actions are an effective way to manipulate the tools as well as uni-manual actions, so she used both methods. Since she did not show a significant paw preference, it is difficult to conclude whether her bi-manual actions affected her success in the tool-use task. However, this bi-manual strategy could have affected her numbers in the statistical analyses, possibly explaining why she did not show a paw preference.

Limitations and Future Research

Several limitations to this study were present. The otters in this study were captive, so paw preference in this species may be different in the wild. This particular tool-use task is also not one that these animals would encounter in their natural habitat, as this apparatus was

specifically designed to test the animals' cognitive abilities. Due to the captive environment, the otters may also have been influenced by other noises and activities taking place, which could have affected the results of the current study. Additionally, this was a small sample of otters, so they may not be an effective representation of the species. Another limitation could be that these otters are siblings. Hopkins, Adams, and Weiss (2013) suggests that handedness in chimpanzees may be genetic, so paw preference results may be different in a study where more genetic diversity is present among the otters.

Due to the lack of literature in this area, future studies should be conducted. Laterality is a widely studied subject in the animal kingdom, with studies ranging from auditory laterality (Descovich et al., 2013), spatial laterality (Karenina et al., 2013), visual laterality (Martin et al., 2010), and handedness/forelimb preference (Rogers, 2009; Sinischalchi et al., 2014). The latter is only a sub-category of laterality, and handedness/forelimb preference can be studied in many different applications with many different animals. Though laterality studies on Asian small-clawed otters are lacking in all areas, future paw preference studies should be conducted using different apparatuses and different tasks in order to establish broader range of evidence for this subject. This way, 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. Therefore, future studies should look at paw preference in wild Asian small-clawed otters. Additionally, future studies may want to look at how genetics contribute 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 are an excellent candidate for studying cognitive abilities, for they exhibit highly intelligent behaviors such as laying clams out in the sun forcing them to crack open and assisting fisherman in herding fish into nets (Perdue et al., 2013). This species also shows high sensitivity of the paws and has a wide range of digital movement, therefore tool-use studies can help provide information on the full manual abilities of this otter (Snyder & Maple, 2013). 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.

Conclusions

In conclusion, the results of the current study show that Asian small-clawed otters do not show a significant population-level paw preference, but they show differences in paw preference on an individual level. These differences in paw preference may be sex-related or they may be connected to asymmetric cerebral hemispheric specialization. Some otters did not show a significant paw preference, possibly due to mouth usage from lack of motivation to participate in the tool-use task or from bi-manual actions. Because of the differences in paw preference for the individual otters, the effect of paw preference on tool use also varied for each otter. In some, a paw preference (or lack thereof) did not seem to affect success in tool use while it did seem to affect the tool use success in others. In the case of Pearl and Roxi, the results relating paw preference and tool use were inconclusive.

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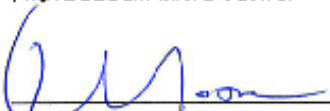
INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE
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INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER:	14050802
PROJECT TITLE:	Flexibility and Use of Novel Tool in Asian Small-Clawed Otters (<i>Aonyx cinerea</i>)
PROPOSED PROJECT DATES:	5/2014-9/2016
PROJECT TYPE:	New
PRINCIPAL INVESTIGATOR(S):	Stan Kuczaj
DEPARTMENT:	Experimental Psychology
FUNDING AGENCY/SPONSOR:	
IACUC COMMITTEE ACTION:	Full Committee Approval
PROTOCOL EXPIRATION DATE:	September 30, 2016



Frank Moore, Ph.D.
IACUC Chair

Date 5/12/2014

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