PROBLEM SOLVING AND TOOL USE IN THREE SPECIES OF OTTER

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A Thesis Submitted to the Faculty of the University of
Tennessee at Chattanooga in Partial Fulfillment
of the Requirements of the Degree of
Master of Science: Psychology

The University of Tennessee at Chattanooga
Chattanooga, Tennessee

December 2015

ABSTRACT

Sea otters are well known tool users, yet the cognitive capacities of other otter species have been sparsely studied. Precedent exists for non-tool using species closely related to native tool users to display comparable abilities under experimental conditions. The social intelligence hypothesis predicts complex cognitive capacities in socially complex species. Using the Aesop's Fable paradigm – wherein subjects drop stones into a cylinder half-filled with water to acquire floating out-of-reach food items – I assessed North American river otters', Asian small-clawed otters, and giant river otters abilities to solve a novel tool-mediated problem. Sticks and water were presented with the stones, providing opportunities for tool use. No otters successfully completed the task. Interaction with the apparatus decreased significantly across sessions, possibly contributing to the otters not solving the task. A better understanding of the similarities and differences in the cognitive abilities of these species can inform future conservation efforts.

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ACKNOWLEDGEMENTS

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ASCO, Asian small-clawed otter

GRO, Giant river otter

NARO, North American River Otter

CHAPTER I

INTRODUCTION

Problem solving can be as straightforward as a hungry dog moving to an area where food is available and as complex as an experienced chess player planning many moves ahead to win a game. Both require that the problem solving agent engage in goal oriented behavior, but the relative level of cognitive ability required for success is drastically different in each. The near-boundless breadth of behavior encompassed by the term problem solving has generated diverse and dissonant definitions, each emphasizing the facets of problem solving most germane to the author's purposes. As the current study utilizes a complex problem solving task to assess subjects' cognitive capacities, Sternberg's (2004) apposite definition of complex problem solving as the process by which an animal can "overcome barriers between a given state and a desired goal state by means of behavioral and/or cognitive, multistep activities" (p. 147), is used throughout this paper.

One of the earliest examples of problem solving being studied in animal subjects is the research conducted by E. L. Thorndike (1898). In his landmark study, Thorndike placed cats in puzzle boxes that could be opened from the inside by means of a latch. Over continued trials the subjects learned to escape the box in less and less time, displaying relatively gradual learning curves. Thorndike interpreted these results as demonstrating that cats possessed a well-developed capacity for instrumental learning but there was not any evidence of anything resembling insight which would have produced much steeper, if not vertical, learning curves.

In stark contrast to Thorndike, Wolfgang Köhler (1924) believed that there was evidence for non-trial and error learning, which he called insight learning, in nonhumans. In a series of experiments, chimpanzees solved different problems including successfully stacking boxes to obtain food items suspended out of their reach and employing sticks as tools to extend their reach outside of their enclosure to obtain food items.

Köhler (1924) was one of the first to take advantage of the unparalleled number of behavioral and morphological characteristics shared between chimpanzees and humans. These commonalities continue to make chimpanzees one of the most popular subject animals to use for cognitive testing (Kohler, 1924). The wealth of research that has been conducted on chimpanzees has revealed that they are adept at using a variety of different tool types, defined by Shumaker, Walkup, and Beck (2011) as "an external manipulable object used to alter the form or position of another object or organism when the user holds and directly manipulates the tool and when the animal is responsible for the orientation of the tool" (p. 5). Other great apes have also shown themselves to be skillful tool users. However, our more distant primate cousins typically have not been shown to use tools at as high a rate as great apes nor with the same level of sophistication (Bentley-Condit & Smith, 2010). For example, when eight chimpanzees and eight capuchin monkeys (*Cebus paella*) were tested on their abilities to use and understand the functional properties of probe tools, seven of the chimpanzees selected the correct tool based on its length while only one capuchin was successful (Sabbatini et al., 2012). Cross species research such as this is an invaluable tool for studying how, when, and under what conditions the cognitive abilities underlying tool use evolved (MacLean et al., 2012).

In an expansive study of self-control in problem-solving tasks in 36 species MacLean et al. (2014) point out the unfortunate paucity of such systematic studies, given their utility in

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determining the characteristics of species and their environments that have resulted in the problem solving abilities possessed by extant species. Of the 29 mammalian species represented only six were nonprimates, raising the question of whether results regarding primate problem solving are generalizable to nonprimate mammals. Carnivorans (members of the order Carnivora) are one of the largest groups of mammals that have been sparsely researched (Drea & Carter, 2009). Considering the ecological importance of many carnivorans as keystone species (VanBlaricom & Estes, 1988) and problems facing many of its members concerning harmful contact with humans and environmental changes (Boitani & Powell, 2012), it is unfortunate that research concerning their abilities to problem solve and adapt to new circumstances has been so sparse (Drea & Carter, 2009).

Holekamp, Sakai, and Lundrigan (2007b) point out that the *Carnivora* order offers many species sharing environmental and social commonalities with primates facilitating cross-taxa comparisons. Carnivorans and primates are estimated to have differentiated between 90 and 100 million years ago (Springer, Murphy, Eizirik, & O'Brien, 2003), making carnivorans far enough removed to allow testing of whether hypotheses generated from the abundant primate research are generalizable to more distantly related species. One carnivoran has received abundant attention from cognitive scientists: the domestic dog. They have shown themselves to be particularly adept at solving problems in social contexts (Topál, Miklósi, & Csányi, 1997). There is also anecdotal evidence of some dogs even displaying limited tool use (Shumaker et al., 2011). Researchers have also conducted comparative studies of dogs and wolves, which have revealed that wolves oftentimes outperform domestic dogs on problem solving tasks (Frank & Frank, 1985). One study found that when six week old wolves and dogs were tested on the detour task which required them to adaptively navigate around obstacles the wolves were more likely to

solve the problem and solve it faster (Frank & Frank, 1982). Using a similar detour task, dingoes (*Canis dingo*) have also been shown to possess well developed problem solving skills exceeding those of domestic dogs (Smith & Litchfield, 2010). It is, however, difficult to consider studies comparing canines to be true cross-phyla comparisons since their ability to interbreed means they are not truly biologically distinct. As such, the differences in their problem solving abilities may be more due to environmental factors than evolved genetic differences (Frank & Frank, 1982).

As such, it is interesting to compare and contrast the problem solving abilities of evolutionarily farther removed species that through convergent evolution share many physical and behavioral characteristics such as the distantly related wolf and spotted hyena (*Crocuta crocuta*), in order to try to determine the causes of the similarities and differences. For example, when presented with puzzle boxes as tests of problem solving ability both eastern timber wolves (*Canis lycaon*) (Frank & Frank, 1985) and spotted hyenas (Benson-Amram & Holekamp, 2012) have readily solved the problem. The similar performance of these distantly related carnivorans is not as surprising as it might seem since the social intelligence hypothesis predicts a positive correlation between the degree of sociality in a species and the cognitive abilities of its members (Dunbar, 2002).

The highly social spotted hyena has proven well-suited for testing the social intelligence hypothesis of animal intelligence (Holekamp, Sakai, & Lundrigan, 2007a), which posits that the demands of living in large cooperative social groups have driven the evolution of intelligence in primates and other social species (Whiten & Byrne, 1997). One proposed mechanism of the relationship between sociality and cognitive ability is that as members of a species become more cohesive, possessing greater amounts of self-control becomes an increasingly adaptive trait. It

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enables individuals to forgo immediate reinforcement to attain a greater delayed reward. Perhaps more importantly for group living species, self-control allows animals to abstain from immediately gratifying behaviors (such as taking another animal's food) likely to result in aversive consequences (Rosati, Stevens, Hare, & Hauser, 2007).

Studies demonstrating advanced social intelligence and cooperative problem solving abilities in spotted hyenas have generally provided support for the social intelligence hypothesis (Drea & Carter, 2009; Holekamp et al., 2007a). These studies provide great insights into the convergent evolution of problem solving abilities in distantly related social species, but it is also useful to study more genetically similar species living in diverse environments. This comparison will allow for the clarification of relationships between the cognitive capabilities of different species and the similar and dissimilar characteristics of their environments (MacLean et al., 2014).

The *Lutrinae* subfamily (in the *Mustilidae* family of the *Carnivora* order comprises the 13 extant species of otters. This group is ideally suited for studies of cognitive similarities and differences in a genetically similar but environmentally and socially diverse group of species. The diversity of social structures observed in different otter species when compared to their problem solving abilities can provide insight into what social variables are more or less related to the development of novel problem solving abilities. The study of the *Lutrinae* subfamily also allows comparison of the cognitive capacities related to tool-mediated problem solving in primates and the most prolific nonprimate mammalian tool-user: the sea otter (*Enhydra lutris*) (Byrne, 1995; Hall & Schaller, 1964).

Byrne (1995) suggests that of all non-primate mammalian tool-users, sea otters show the most sophisticated and human-like tool use in a due to their use of stones of specific sizes and

shapes to open different hard-shelled prey species. Additionally, Sea otters have been observed prying abalones off rocks using stones (Miller, Geibel, & Houk, 1974) or other available objects such as glass bottles (Riedman & Estes, 1990). Byrne (1995) claimed that primates are exceptional tool users because they use a single tool for multiple purposes, so sea otters using stones to dislodge clams as well as break them open lends credence to the suggestion that sea otters are similarly capable. Byrne also claimed that some species of primates exhibit tool-using behavior indicative of "real intelligence" because they use different and distinct tools for a variety of tasks. Observations of sea otter mothers wrapping pups in kelp to prevent them from drifting away while the mother dives (Talbot, 2012) and of them wrapping live crabs in kelp for containment while other prey is being eaten (Riedman et al., 1988 in Riedman, 1990) indicate that sea otters may possess problem-solving capacities comparable to those of primates.

Interestingly, the sea otter is the only confirmed native tool-user in the *Lutrinae* subfamily (Kruuk, 2006), although there is an unconfirmed report of African clawless otters (*Aonyx capensis*) using stones as anvils to crack open mussel shells during a drought that made their normal prey scarce and exposed the mussels (Donnelly & Grober, 1976). The sea otter's retractable claws and the specialized somatic sensory projections in their forelimbs are believed to be adaptations for improved object manipulation and tool-use (Radinsky, 1968). This proclivity for tool use is thought to have been driven by the sea otter's reliance on hard-shelled abalones which are plentiful in large portions of the sea otter's natural range (Estes, Riedman, Staedler, Tinker, & Lyon, 2003; Tinker, Bentall, & Estes, 2008). The relative rarity of hard-shelled prey species in the habitats of other species of otters that do not use tools further supports this explanation (Kruuk, 2006). However, sea otters may never have needed to utilize such an energetically expensive prey species had it not been for the intraspecific competition created by

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the size and density of their pre-fur trade population, along with the steep metabolic requirements associated with ranging as far north as Alaska while being the only major aquatic mammal without blubber for insulation (Kruuk, 2006). Sea otters' penchant for tool use allowed them to utilize an otherwise unobtainable food source that they rely on in many parts of their range. This raises the question of whether this crucial adaptation evolved in response to heavy selection pressures as a domain-specific cognitive ability performed as a rote series of behaviors or if it the species already possessed a more flexible domain-general cognitive ability which facilitated rapid behavioral adaptability leading to the unique seemingly intelligent behaviors for which the species is known.

The most recent common ancestor the sea otter shares with any other extant otter speciated approximately 4.9 million years ago and they are believed to have come to inhabit its current range roughly three million years ago (Koepfli et al., 2008). Given this phylogeny, if the sea otter's cognitive capabilities allowing tool-use are domain-general in origin and were present before they could have been shaped by the abundance of hard-shelled prey in its current habitat, then one could expect to find comparable cognitive capabilities in other otter species that are not native tool users. However, if it is a domain-specific cognitive function, having evolved in response to the unique characteristics of the sea otter's environment, then comparable cognitive capabilities would not be expected to be present in the other species of otter.

The Asian small-clawed otter (ASCO) may have the greatest potential to prove capable of completing tasks requiring object manipulation because the genus *Aonyx* to which they belong possess somatic sensory adaptations of the forelimbs similar to those of the sea otter which enhance object manipulation capabilities (Radinsky, 1968). As their name suggests, the claws on ASCOs' forelimbs are much smaller than is typical in most other otter species, which allows

them to manipulate small objects much more efficiently than their large-clawed relatives. It is believed this adaptation evolved to allow ASCOs to more easily catch and handle the terrestrial crabs that make up a larger portion of their diet compared to most other species of otter (Kruuk, 2006). This feeding pattern indicates that this adaptation evolved to facilitate object manipulation in much the same way that the sea otter's retractable claws are believed to (Radinsky, 1968). They have also been shown to possess a well-developed spatial memory (Perdue, Snyder, & Maple, 2013) that may suggest the presence of a similarly developed spatial reasoning ability. While the ASCO is considered a social species, it is worth noting that of the three species in the present study they are considered the least social because they often forage independently of each other even when living in groups (Kruuk, 2006).

In stark contrast to the ASCO, the giant river otter (GRO) is considered by many to be the most gregarious species of otter. They typically live in large interfamilial groups and cooperate in raising and defending their young (Kruuk, 2006). GROs are one of the rare species that care for each other's young (Rosas, Cabral, de Mattos, & Silva, 2009). They also appear to have the most complex and varied system of communication of any species of otter (Mumm, Urrutia, & Knörnschild, 2014). While the sociality of the GRO is well documented, a search of the literature failed to reveal any existing studies specifically addressing cognition in the species. However, it must be noted that their natural habitat is the Amazon River basin, which provides no shortage of impediments to researchers wanting to extensively observe them in the wild. Their low levels of neophobia (fear of new things) mean they have a tendency to approach novel objects and stimuli which when paired with the high value of their furs also causes individuals living near large human settlements to have very low survival rates, further hindering the study of their behavior. Although individuals cooperate on some tasks, such as predator defense, they have never been

observed cooperatively foraging for food, which may indicate that they might not perform as well on the cooperative problem solving task as their otherwise exceptional sociality might predict (Kruuk, 2006).

Although North American river otters (NAROs) are typically considered marginally less social than GROs (Kruuk, 2006), they are also the only otter species to have been directly observed to forage cooperatively (Blundell, Ben-David, & Bowyer, 2002; Serfass, 1995). Despite the distribution of NAROs throughout most of North America, there is a dearth of research concerning their cognition. NAROs have also been known to display neophilic reactions to nonthreatening novel objects (Tennessee Aquarium otter keepers, personal communication, January 11, 2014), which may suggest that they will perform well on problem solving tasks given that neophobia has been negatively correlated with success rates on problem solving tasks in other social carnivorans (Benson-Amram & Holekamp, 2012).

Even though GROs, NAROs, and ASCOs are not native tool-users it is possible that they are capable of using tools under experimental conditions where there is sufficient motivation and opportunity to do so. Such a phenomenon has been observed in the rook (*Corvus frugilegus*), a social species that has never been observed using tools in the wild but has proven to be a highly skilled tool user under captive conditions (Bird & Emery, 2009a, 2009b). Rooks are closely related to the New Caledonian crows (*Corvus moneduloides*), the tool use of which rivals that of many primates (Taylor, Elliffe, Hunt, & Gray, 2010). New Caledonian crows have been shown to manufacture hook tools out of both natural and manmade materials (Weir, Chappell, & Kacelnik, 2002), exhibit metatool use surpassing that of many primates (Hunt & Gray, 2004; Taylor et al., 2010), and use sticks as exploratory probes to investigate potentially dangerous novel objects (Wimpenny, Weir, & Kacelnik, 2011).

When captive rooks are presented with cognitively demanding tasks such as manufacturing hooks to retrieve otherwise inaccessible food they have consistently outperformed most species that are native tool users (Bird & Emery, 2009a). Most interesting is the rook's performance on Bird and Emery's (2009b) problem solving task inspired by Aesop's Fable, wherein a crow is said to have dropped stones into a pot of water to raise the water level to the point where it could drink. The researchers allowed rooks access to a clear vertical open-topped tube one-third filled with water in which there was an out of reach floating worm and a variety of stones of appropriate sizes to fit in the tube. All four rooks acquired the worm by dropping stones into the tube until the water level was high enough for them to reach the worm despite no previous exposure to this particular task. The spontaneous solving of the task is indicative of insight which is further supported by the lack of trial-and-error problem solving and the absence of any known species typical behaviors that would account for their success on the task.

The beauty of the Aesop's Fable stone dropping task is that it is usable across a variety of species (Jelbert, Taylor, & Gray, 2015) because it does not require fine manual dexterity in the species being studied. Animals not able to hold and manipulate sticks or stick-like objects may be cognitively capable of similar feats of problem solving but typical experimental conditions assessing tool use may not be conducive to them successfully completing tasks requiring the dexterous maneuvering of sticks or other objects. The stone dropping task developed by Bird and Emery (2009b) may provide a workaround for this problem since picking up and dropping appropriately sized stones may be more relevant to the physical affordances and behavioral repertoires of many species.

Because of the utility of the Aesop's Fable task, I modified it for use with otters. Two additional types of tool were presented with the stones: a probe tool that could be used to

manually retrieve the fish and water that could be spit into the tube to bring the fish within reach by raising the water level. The water was considered a tool that could potentially be used to retrieve the fish, because it meets Shumaker, Walkup, and Beck's (2011) previously mentioned definition of a tool.

I hypothesized that each species would be able to solve this task using at least one of the available tools. Each species is at least moderately social and as such would be predicted to possess enhanced cognitive capacities based on the social brain hypothesis. While only the ASCOs possess adaptations specifically related to object manipulation, both NAROs and GROs have been reported to possess a proclivity for manipulating and playing with almost any available objects (Kruuk, 2006). This tendency to spontaneously manipulate objects, along with the lower levels of manual dexterity required to pick up stones compared to the higher levels required for orienting the stick tool, led to my prediction that all species were equally likely to use the stones but the ASCOs' greater manual dexterity would make them more likely to use the stick tool. Since all subject species are aquatic and morphologically similar (Kruuk, 2006), I also hypothesized that they would be equally likely to solve the task using the available water.

CHAPTER II

METHOD

Subjects

Three species of otter were used as subjects. Two NAROs, a male (Slim, age 3.5) and female (Lenora, age 12), were tested at the Birmingham Zoo. Two female ASCOs (Harry and Nava Lee, ages 10 and 15 respectively) were tested along with two GROs, a female (Yzma, age 6) and male (Bakari, age 4.5) at Zoo Atlanta. Characteristics of each species are summarized in Table 2.1.

Table 2.1 Comparison of Species Characteristics (Kruuk, 2006)

	North American River Otters	Asian Small-Clawed Otters	Giant River Otters
Average Weight	9kg	3.5kg	28kg
Average Length	125cm	80cm	190cm
Claw Type	Full	Small	Full
Sociality	High	Moderate	Very High
Group Size	3-18	5-15	8-20
Group Foraging	Often	Rarely	Often
Cooperative Hunting	Yes	No	No

Adapted from *Otters: ecology, behaviour and conservation* by Hans Kruuk

Materials

The subjects were presented with an open topped transparent vertical plastic cylinder, partially filled with water and containing an out of reach floating food item. There were three types of tool available for each otter to potentially use to solve the problem: stones, sticks, and water. The stones were placed near the tube and were of a size that allowed the food item to come within reach by raising the water level after approximately three were dropped in the tube. The stick was of sufficient length to easily reach the floating food item. Water was provided in a bowl if it was not already present and was also considered a potential tool.
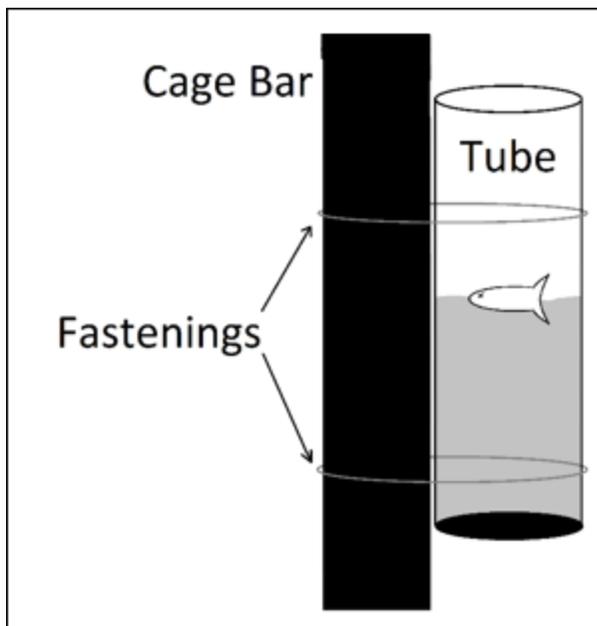

Figure 2.1 Experimental Apparatus

All sessions were video recorded with a Canon HFR400 camcorder set up on a tripod. Additionally, there was a Go Pro Hero 3+ video camera secured several feet directly above the apparatus providing a top down perspective. The Go Pro wirelessly streamed a live video feed to an iPad Mini allowing ongoing observation of the experiment while keeping subject distraction to a minimum.

Housing

Each species was tested in their indoor enclosure. For both the NAROs and GROs it was possible to close off a smaller subsection as the testing area. The NARO testing area was 1.5 meters by 1.5 meters and was empty except for the experimental apparatus and potential tools. The GROs were tested in a section of their indoor housing measuring three by three meters. The GRO testing area contained bedding, crates, a plastic tub filled with water and large enough for them to completely submerge, and a large plastic children's castle.

It was not possible to keep the ASCOs in a smaller area during testing. The physical affordances of their enclosure required the otter being tested to have access to the entire indoor portion of their environment, excluding a switching area where the otter not being tested was kept. The main area of the ASCO's enclosure where they were tested consisted of a raised concrete area (approximately three by four meters) and a recessed pool area (approximately 2.5 meters by 3 meters). Their indoor enclosure contained two otter shelters, logs, large rocks, and the same kind of children's play castle previously mentioned for the GROs.

Procedure

The apparatus was placed in a screened off or separate area of the enclosure, a food item was placed in the empty tube, and water was poured into the tube. The stones and stick tool were placed near the apparatus and a container of water was provided. Once the apparatus and tools were set up, the subject to be tested was brought in individually.

Day one of the experiment served as a habituation and orientation trial for each subject. The apparatus was set up in the same manner as subsequent trials except that the stick tool and stones were not present and the tube was nearly filled so that the food was easily reachable by the otter. In subsequent sessions the water level was lowered until the food was out of the otter's reach. If this distance was misjudged and the otter manually retrieved the food, the session timer was paused, the otter was shifted out of the testing area, the water level was lowered further, more food was added, the otter was shifted back into the testing area, and the session timer was restarted.

As planned, the NAROs completed ten sessions of 30 minutes each, however due to limited keeper availability and apprehensions regarding isolation during testing, the ASCOs and GROs were tested using 12 minute sessions. At least one of the otters' regular keepers was always present during testing. At the end of each session the otter was returned to its home enclosure, the apparatus was reset, and the next otter brought in. The otters' median number of seconds to first contact with, mean numbers of approaches to, and mean numbers of reaches into the apparatus were coded from the recorded videos and analyzed.

CHAPTER IV

RESULTS

Comparisons of Species

None of the six otters successfully completed the task. Only one otter interacted with the stones. Yzma, the female GRO, purposefully pushed around one of the stones with her forepaw on three occasions but never interacting with the tube. In sessions five and six the male NARO, Slim, interacted with the provided sticks by chewing their ends. Slim's stick oriented behavior never progressed beyond species typical gnawing behavior so it was determined to be unrelated to the experimental task. Only five of the planned ten sessions were completed with the GROs due to keeper concerns about stress caused by the isolation of the testing procedure. Because a session length of 30 minutes was used for the NAROs while 12 minutes sessions were used for the ASCOs and GROs, only the first 12 minutes of the NARO sessions were used in the analysis of the data concerning reaches and approaches in order to allow species comparisons. Data concerning each otter's median latency to first contact with, mean number of approaches to, and mean number of reaches into the apparatus are summarized in Table 3.1.

Data analyses were conducted using the IBM SPSS 22.0 software package. The data did not meet the assumptions necessary for parametric tests so species comparisons were made using the Kruskal-Wallace H test. Mann-Whitney U tests were then run to follow up on statistically significant group differences. Additional analyses were carried out using SPSS's linear

regression procedure in order to tease out factors contributing to the overall results and observed interspecies differences.

Table 3.1 Summary Statistics

Species	Name	Sessions	Age (years)	Median Latency (SD) (seconds)	Mean Number of Approaches (SD)	Mean Number of Reaches (SD)
NARO (First 12min)	Slim	10	3.5	12.0 (46.20)	6.6 (3.92)	3.5 (3.10)
	Lenora	10	12	58.0 (90.35)	4.5 (3.03)	1.4 (1.35)
	Average		*7.75*	*27.5 (75.04)*	*5.55 (3.58)*	*2.45 (2.56)*
ASCO (12min)	Harry	10	10	30.5 (98.28)	4.7 (1.83)	3.1 (2.13)
	Nava Lee	10	15	140.0 (124.03)	2.8 (1.32)	0.6 (0.70)
	Average		*12.5*	*46.5 (117.09)*	*3.75 (1.83)*	*1.85 (2.01)*
GRO (12min)	Yzma	5/10	6	2.0 (0.71)	8.8 (2.77)	3.0 (1.58)
	Bakari	5/10	4.5	5.0 (3.16)	7.0 (2.74)	3.0 (1.87)
	Average		*5.25*	*3.0 (3.02)*	*7.9 (2.77)*	*3.0 (1.63)*
All	*Average*		*8.5*	*24.5 (94.94)*	*5.32 (3.15)*	*2.26 (2.24)*

The distributions of each species' latency, approach, and reach scores were analyzed for interspecies differences. Levene's test of homogeneity of variances indicated statistically significant differences between the variances of the individual species' latency distributions ($W = 11.30$, $p < .001$) as well as the variances of the distributions of their approaches ($W = 3.673$, $p = .034$). Kruskal-Wallace H tests revealed statistically significant differences between the species' latencies ($\chi^2 (2) = 21.29$, $p < .001$) and number of approaches ($\chi^2 (2) = 12.11$, $p = .002$) but not their number of reaches ($\chi^2 (2) = 3.52$, $p = .172$).

To follow-up on the statistically significant Kruskal-Wallace results, three Mann-Whitney U tests were conducted to analyze both the latency and approach variables (see Tables

3.1 and 3.2). The distribution of GRO latencies were significantly shorter than the distributions of NARO latencies ($U = 10.5$, $p < .001$) and ASCO latencies ($U = 6.0$, $p < .001$). The series of tests conducted on the approach variable indicated that the GROs made significantly more approaches compared to the ASCOs ($U = 20.0$, $p < .001$). Differences in the NARO and GRO approach distributions verged on significance ($U = 56.5$, $p = .054$) while the differences between the distributions of NARO and ASCO approaches did not ($U = 139.0$, $p = .096$).

Note. The median number of seconds until first contact with the apparatus for each species is displayed with Mann-Whitney U tests of group differences. Medians were used due to the statisticaly significant positive skew of each species' latencies as determined by a Shapiro-Wilk test of normality ($W = .735$, $p < .01$; $W = .823$, $p < .01$; $W = .834$, $p < .05$ for NAROs, ASCOs, and GROs respectively). Because of the skew, error bars represent the 95% confidence interval. $**p < .01$.
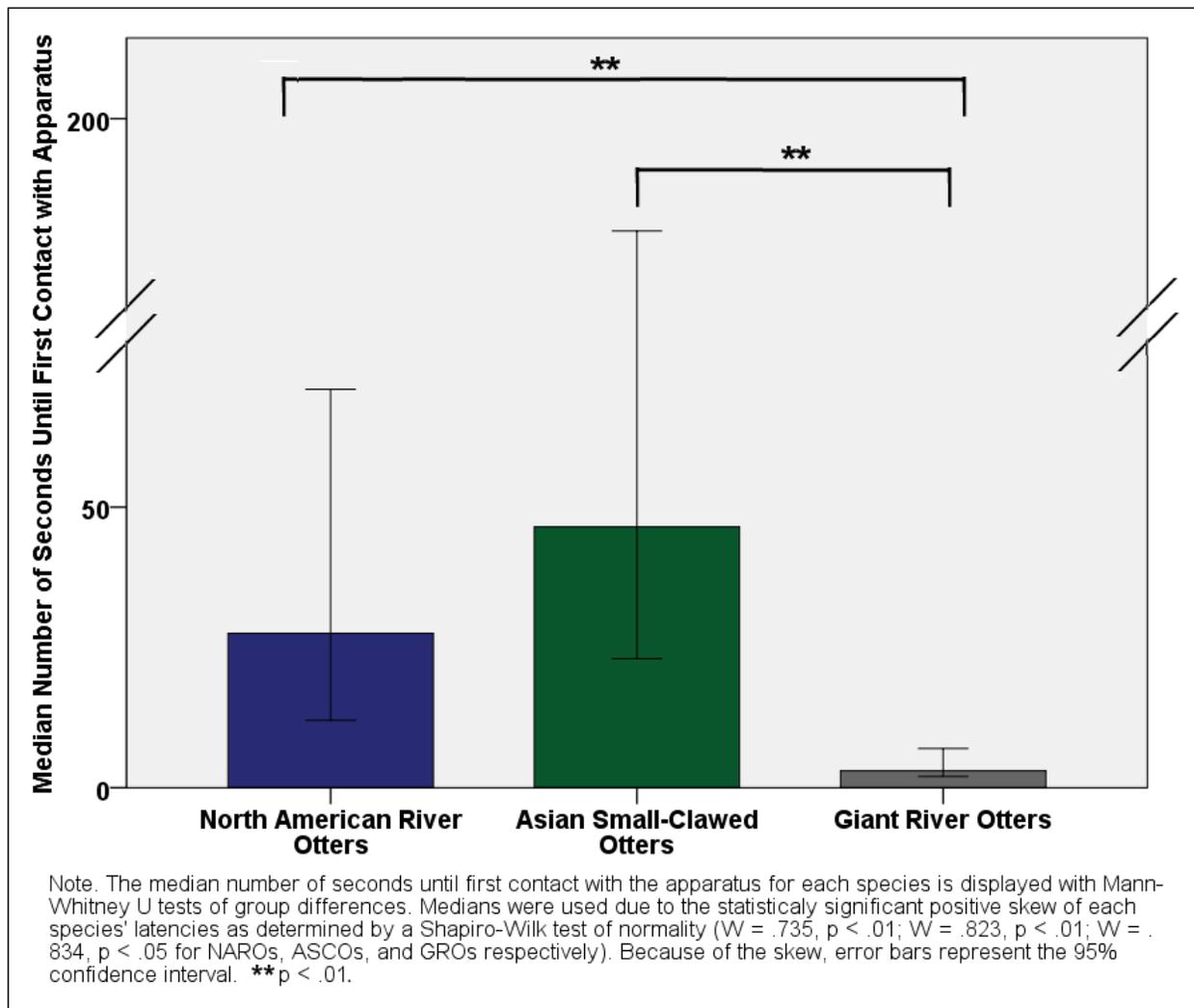
Figure 3.1 Mann-Whitney U Tests for Interspecific Differences in Latencies
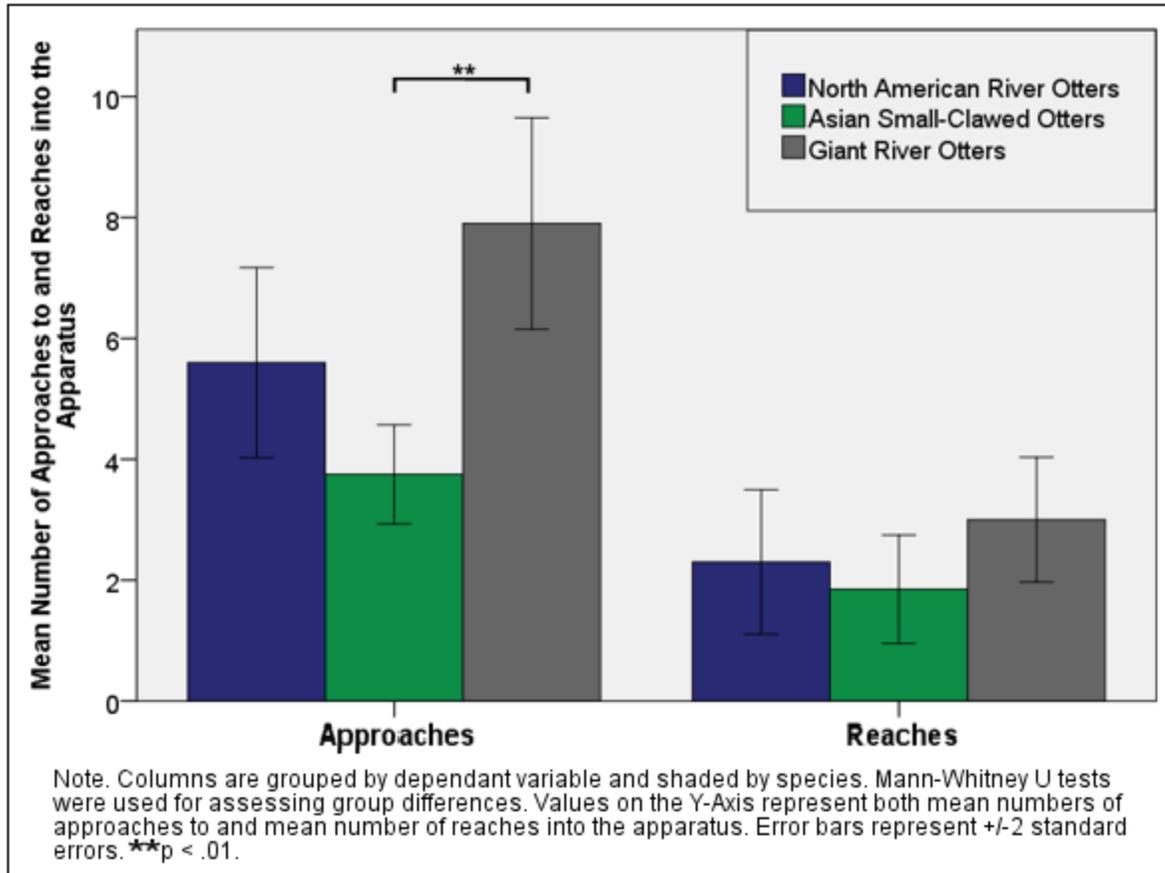
Figure 3.2 Mann-Whitney U Tests for Interspecific Differences in Approaches and Reaches

The amount of time elapsed from the start of the session to the otter's first approach tended to be positively correlated with session number. This relationship was statistically significant for the ASCOs ($p = .039$) and but not for the NAROs ($p = .062$). This relationship was reversed (see Figure 3.3) for the five sessions completed by the GROs but this negative relationship was not significant ($p = .203$). Despite one GRO, Yzma, decreasing her latency across the five sessions the GROs completed, age was still an exceptionally strong predictor of latency, with R^2 equaling 0.80 ($p = .001$) when median latencies were regressed onto each otters' age. Even though Yzma was faster to approach the apparatus as sessions went on, this only

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constituted a drop from her longest latency of three seconds to a median latency of two seconds and one session with a one second latency. In contrast, the ASCOs and NAROs sometimes took five minutes or more to approach the apparatus.
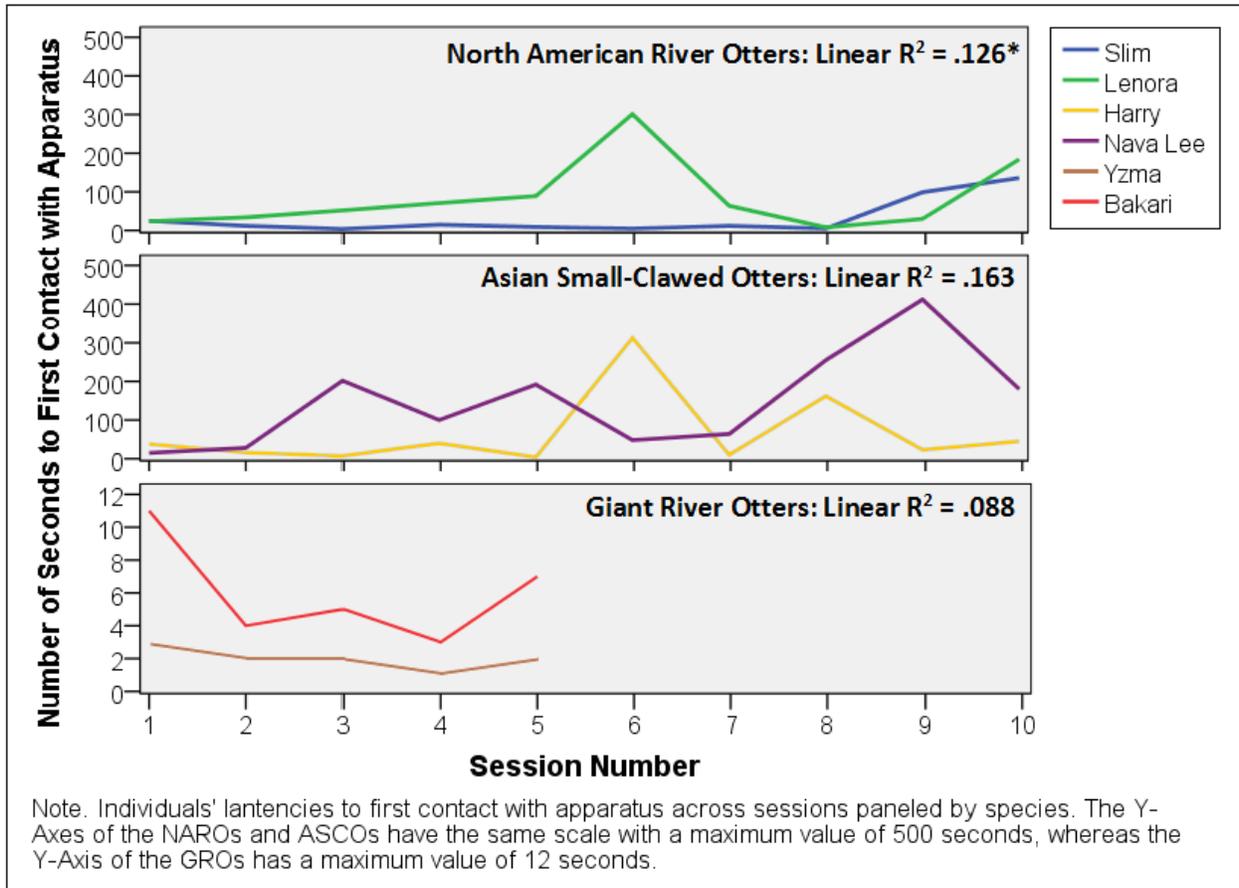

Figure 3.3 Latencies across Sessions Paneled by Species

The NAROs made significantly fewer approaches to the apparatus as sessions progressed ($p < .001$). The same negative relationship was evident in the ASCO's, however it was not

statistically significant ($p = .062$). In contrast, the correlations between session number and number of approaches was nonsignificant ($p = .250$) for the GROs (see Figure 3.4).
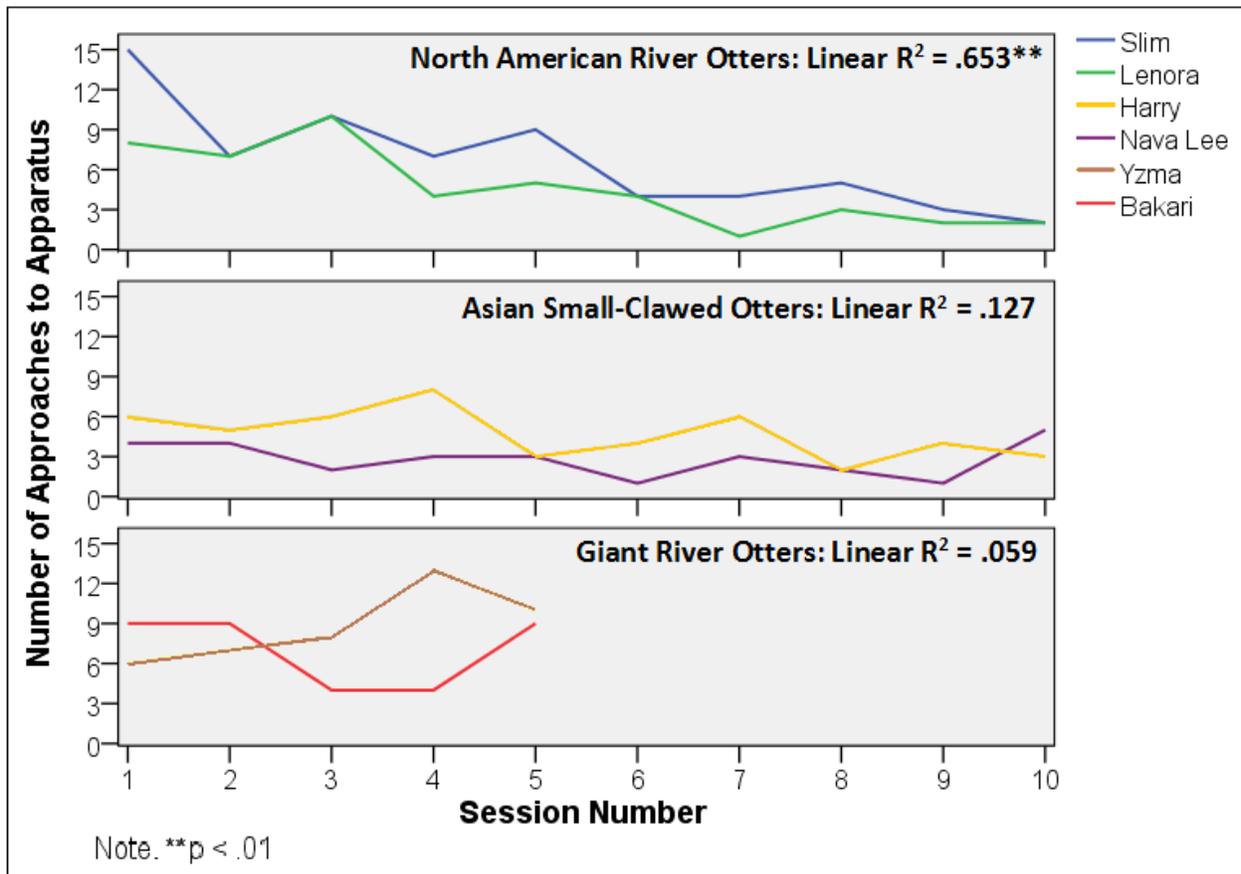

Figure 3.4 Approaches across Sessions Paneled by Species

The NAROs made significantly fewer reaches into the apparatus as sessions went on ($p = .007$). The number of reaches made by the ASCOs was highly variable (see Figure 3.4) and seemed to be relatively unaffected by session number ($p = .320$). The two GROs showed opposite trends from one another. Figure 3.5 shows that Bakari's results were similar to those of

the ASCOs and NAROs in that his number of reaches regressed onto session number was not significant ($p = .071$), whereas Yzma exhibited a significant ($p < .001$) linear increase in reaches into the apparatus across sessions.
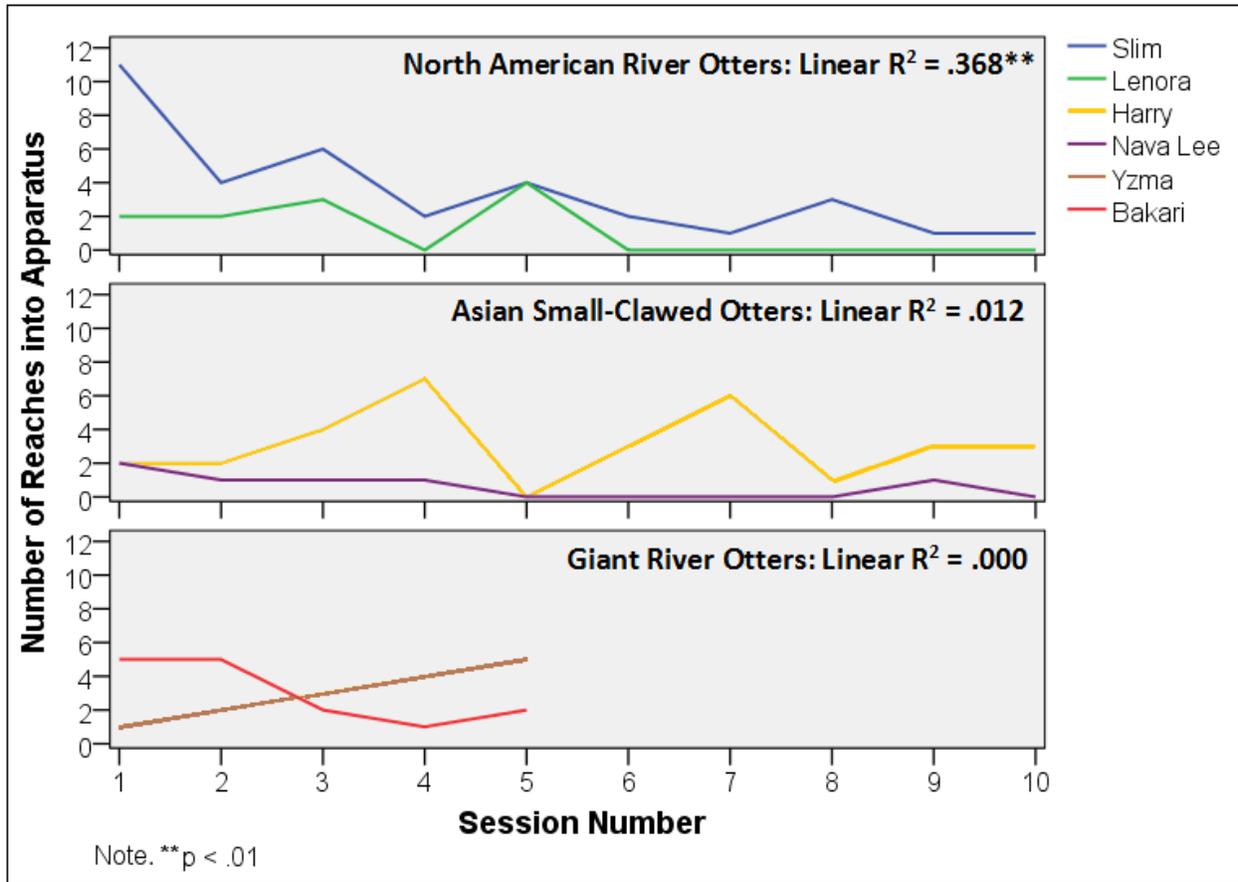

Figure 3.5 Reaches across Sessions Paneled by Species

Age Regressions

There was a strong tendency for latency to first contact with the apparatus to increase as a function of age. Regressing each otter's median latency to first contact onto their age yielded a

statistically significant ($p = .008$) linear model (see Figure 3.6). Additionally, there was a strong and significant ($p = .027$) negative relationship between the mean number of times each otter approached the tube and its age (see Figure 3.7). There was a similarly strong and significant ($p = .018$) negative relationship between each otter's age and the mean number of times it reached into the tube (see Figure 3.8).
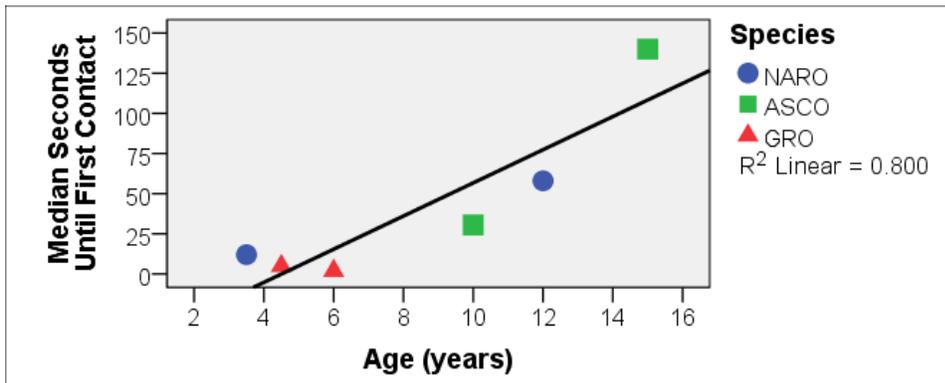

Figure 3.6 Median Latency to First Contact with the Apparatus Regressed onto Otter Age
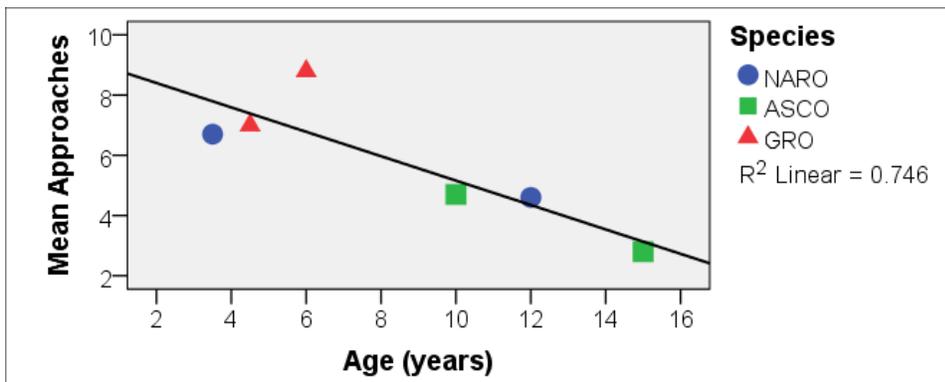

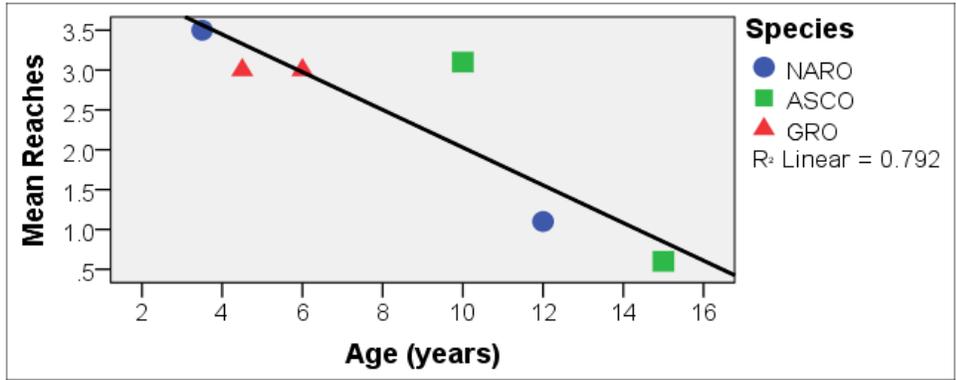Figure 3.7 Mean Number of Approaches to the Apparatus Regressed onto Otter Age

Figure 3.8 Mean Number of Reaches into the Apparatus Regressed onto Otter Age

CHAPTER V

DISCUSSION

The results of this study do not provide evidence for any of the three subject species being able to use tools to solve a novel problem. However, given the small sample size of the study ($n = 2$ for each species) these results should not be taken as definitive evidence that such abilities are completely absent in these species. Testing was stopped after the fifth session for GROs due to concerns regarding separation anxiety. This made the results particularly inconclusive, given similar studies in which subjects have succeeded in more than five sessions (Foerder et al., 2011). The high degree of sociality that made otters such interesting test subjects ironically prevented the test from being completed. The inability to complete testing with the GROs is particularly disappointing because Yzma was the only otter to increase her interactions with the apparatus over time and purposefully interact with any of the potential tools when she batted a rock around on three occasions.

There was a strong tendency for the otters to lose interest in the apparatus over time as demonstrated by the positive correlation between session number and latency to first contact and the negative correlations between session number and number of approaches and reaches. Although keepers tried not feed them directly prior to testing, the otters were not deprived of food for any set amount of time before testing. This may have reduced the motivation for the otters to work for a food reward. However, Yzma was once again unique in that she did not seem to lose interest in the apparatus over time. She was the only otter who steadily increased the

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number of times she reached into the tube across sessions. Yzma's unique increase of interest in the apparatus across sessions and manipulation of the rocks is another indicator that she might have solved the problem given a longer testing period or more sessions.

There were significant group differences between the three species' latencies to first contact with and numbers of approaches to the apparatus. The GROs had significantly shorter latencies than both the NAROs and ASCOs. The GROs also made significantly more approaches to the apparatus than the ASCOs. It is possible that these differences along with the instances in which the GRO Yzma batted around a stone are indicative of GROs being more neophilic in that they possessed a greater proclivity for interacting with and manipulating novel objects as measured by latencies, approaches, and reaches.

However, these group differences are also potentially attributable to differences in the environments the species were tested in as well as the effect of subject age on neophilia. The most striking difference in the testing environments is the discrepancy in their sizes. The ASCOs' testing area was roughly twice the size of the GROs' testing area which was itself approximately four times the square footage of the testing area used for the NAROs. ASCOs are also less than half the size of GROs, making the relative functional sizes of their testing areas even more discrepant. In light of these differences it is unsurprising that the ASCOs had the longest latencies to first contact since it could have simply taken them longer to reach the apparatus. If enclosure size was the predominant predictor of latency, then one would expect to see the NAROs, who were tested in the smallest area, have the shortest latencies. However, since the GROs had significantly shorter latencies than the NAROs despite being in a larger enclosure it seems unlikely that testing area size alone accounts for the aforementioned group differences

in latencies. The GRO's also made significantly more approaches to the apparatus than did the ASCOs, further supporting the idea that they possessed greater levels of neophilia.

Even though the GROs demonstrated more neophilia towards the apparatus than the NAROs and ASCOs it is still possible that this effect was not caused by true interspecific differences. Otter age was a particularly strong predictor of all three measures of neophilia: median latency, mean number of approaches, and mean number of reaches. Previous studies have shown that neophilia decreases/neophobia increases with age (Krueger, Farmer, & Heinze, 2014; Misanin, Blatt, & Hinderliter, 1985), so it is not surprising that an otter's age was a significant predictor of these variables. The effect of neophilia declining with age is important when considering the GROs' results. They were the youngest of the three groups, being 4.5 and 6 years old compared to the ASCOs 10 and 15 years of age and ages of 3.5 and 12 for the NAROs. The effect of age on neophilia was particularly evident in the NAROs, given the wide difference in their ages. Lenora was nearly four times older, and had a median latency (58 seconds) over four times longer than Slim (12 seconds), as well as fewer approaches to and reaches into the apparatus, as seen in Table 3.1. One can thus reasonably make the claim that the observed group differences in neophilia are at least in part due to the differences in the ages of the otters belonging to each species. However, the small sample size of this study makes it impossible to determine whether the variation of the neophilia measures is best explained by age, group membership, or a combination of the two. To make this determination, future studies would need an adequate sample size to run the age-neophilia regressions separately for each species so that species membership could be assessed for its potential unique contribution to neophilia.

Limitations

Only finishing half of the sessions that had been planned with the GROs was a major limitation of this study. The generalizability of the results is also limited by the sample size of two otters for each species. The three species that were studied were chosen as a sample of convenience based on their availability for study. Inclusion of sea otters in this study could have provided interesting comparisons between native and nonnative tool-using otters. Studying spotted-necked otters (*Hyricitis maculicollis*) would have been particularly informative given that their evolutionary divergence occurred roughly 4.9 million years ago, making the spotted-necked otter the sea otter's closest relative (Koepfli et al., 2008). It also would have been ideal to include a group of marine otters (*Lontra felina*) because of all extant otter species their predominantly aquatic lifestyle is the most similar to the sea otter's (Kruuk, 2006). As the arguably least social species of otter because of their lack of group living other than mating pairs (Kruuk, 2006), inclusion of the marine otter would also have provided a greater breadth of data concerning social intelligence. While the inclusion of these species would have provided the most additional insight, the inclusion of any of the ten members of the subfamily Lutrinae not currently being tested would provide a more complete picture of the cognitive capabilities related to problem solving and tool use in otters. Additional subjects in the species already represented would provide more power for the analyses conducted.

Implications

The findings of this study did not demonstrate a capacity for tool use in the three species that were tested. However, the small sample size of the study means that these results may not be indicative of the abilities possessed by members of the three respective species. Future studies

should include wild subjects to increase external validity given that differences in problem solving often exist in wild versus captive populations (Benson-Amram, Weldele, & Holekamp, 2013).

An environmental threat common to all riparian otter species is the construction of hydroelectric dams. These dams drastically alter the otters' aquatic habitat as well as the migration and distribution of many species of fish that otters prey on (Carter & Rosas, 1997). A better understanding of the novel problem solving skills of these otter species will also be informative regarding their abilities to adapt to these novel environmental characteristics. Otters being opportunistic predators (Kruuk, 2006) often causes them to adapt to human proximity by taking advantage of opportunities it provides, such as access to fish farms (Trindade, 1991). These dense and immobile fish populations consistently provide wild otters with sufficient motivation to gain access to these areas despite fish farmers' best efforts to keep them out (Kucerová, 1999). When humans and otters have conflicts, humans are unfortunately not always as creative at keeping the otters out as the otters are at getting in. These circumstances often result in the shooting or poisoning of the otters (Václavíková, Václavík, & Kostkan, 2011). Greater knowledge concerning the exploratory behavior and problem solving abilities of otters may lead to more effective and less harmful methods of deterring them from raiding fish farms. A fuller understanding of the problem solving abilities of otter species in general and of the differences between species may be informative in preventing otter-human conflicts from occurring as well as foreseeing impacts of environmental changes.

Conclusions

No evidence of tool using behavior was found in the three species of otter that were tested. All but one of the otters lost interest in the apparatus as sessions went on, indicating that further testing would have been unlikely to be beneficial. Age was shown to have a strong negative effect on the amount of neophilia displayed toward the testing apparatus. The small sample size of the study limited the generalizability of the findings. Further research with a larger sample size may provide more significant results which will be helpful in the conservation of otter species.

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