



12-2018

Determinants of Social Behavior in Captive North American River Otters (*Lontra canadensis*)

Olivia R. Beasley

Winthrop University, Beasleyo2@winthrop.edu

Follow this and additional works at: <https://digitalcommons.winthrop.edu/graduatetheses>



Part of the [Biology Commons](#)

Recommended Citation

Beasley, Olivia R., "Determinants of Social Behavior in Captive North American River Otters (*Lontra canadensis*)" (2018). *Graduate Theses*. 97.

<https://digitalcommons.winthrop.edu/graduatetheses/97>

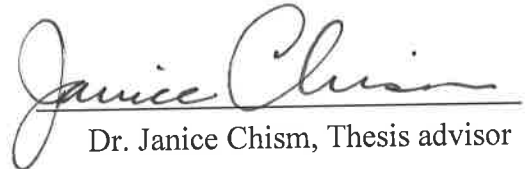
This Thesis is brought to you for free and open access by the The Graduate School at Digital Commons @ Winthrop University. It has been accepted for inclusion in Graduate Theses by an authorized administrator of Digital Commons @ Winthrop University. For more information, please contact digitalcommons@mailbox.winthrop.edu.

December 2018

To the Dean of the Graduate School:

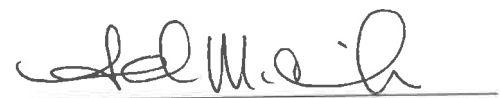
We are submitting a thesis written by Olivia R. Beasley entitled "Determinants of Social Behavior in Captive North American River Otters (*Lontra canadensis*)."

We recommend acceptance in partial fulfillment of the requirements for the degree of Master of Science.


Dr. Janice Chism, Thesis advisor


Dr. Bill Rogers, Committee Member


Dr. Kristi Westover, Committee Member


Dr. Adrienne McCormick, Dean
College of Arts and Sciences

Dr. Jack DeRochi, Dean
Graduate School

DETERMINANTS OF SOCIAL BEHAVIOR IN CAPTIVE NORTH AMERICAN
RIVER OTTERS (*Lontra canadensis*)

A Thesis

Presented to the Faculty

Of the

College of Science

In Partial Fulfillment

Of the

Requirements for the Degree

Of

Master of Science

In Biology

Winthrop University

December, 2018

By

Olivia R. Beasley

ABSTRACT

Field Studies of North American River Otters (*Lontra canadensis*), documented social behavior atypical among its mustelid relatives. In the wild, river otters are most active during crepuscular hours and males have been shown to be more social than females, as they cooperatively forage within bachelor groups (Blundell et al. 2002). Most social behavior occurs at latrine sites, where feces act as a means of communication between conspecifics (Blundell et al. 2005). While scientists have conducted some behavioral research on wild river otters, detailed studies of interactions are difficult for a species that ranges widely. A full understanding of river otter social patterns requires captive studies, however, as yet few such studies have been done. To help fill this gap we carried out a study of the social behavior of a group of captive river otters. We tested three hypotheses: first, that male otters would engage in more social behavior than females; second, that most social behavior among conspecifics would occur during the early evening; and third, that most social behavior would occur in the terrestrial portion of the exhibit (analogous to latrine sites). Data were collected at the Tennessee Aquarium in Chattanooga, TN, over 8 weeks in June-July 2017. An ANOVA revealed that our first hypothesis was rejected, and that there was no difference in sociality based on the sex of the animal ($F=0.746$, $df=1,4$, $p=0.437$). Our second hypothesis, that most social behavior among otters would occur during the early evening, was supported (ANOVA, $F=5.79$, $df=3,20$, $p=0.005$). Based on a Wilcoxon Signed Rank Test, our third hypothesis, that

river otter social behavior would occur more often in terrestrial areas, was rejected (\bar{x} =0.418, $sd=0.077$). Our data suggest, in a captive setting, that river otter sociality is not dependent upon the sex of the animal. River otter sociality occurred more frequently during the early evening hours, and was exhibited more often in the aquatic portion of the exhibit.

ACKNOWLEDGEMENTS

I would like to thank the Winthrop University Research Council. This project would not have been possible if it weren't for their gracious funding. Thank you, Dr. Janice Chism for being the most amazing and supportive advisor throughout my graduate career. You have provided me with an immense amount of guidance, knowledge, and sound advice throughout my many challenging moments. Thank you, Dr. Bill Rogers for assisting with the statistics and for your constant support and encouragement. Thank you, Dr. Kristi Westover for serving as a committee member, for your encouragement and advice. A personal thank you to Sara Webb and Jennifer Wawra, whose knowledge of the otters, and willingness to help, went far beyond measure. Thank you, to the rest of the staff and volunteers at the Tennessee Aquarium for being simply amazing.

TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS	iv
LIST OF TABLES	vii
LIST OF FIGURES	viii
BACKGROUND	10
River Otter Behavioral Ecology	11
River Otter Life History	14
Social Organization	15
STUDY OBJECTIVES, QUESTIONS, AND HYPOTHESES	18
SIGNIFICANCE	18
METHODS & MATERIALS	19
Exhibit Design	19
Subjects	20
Data Collection	20
STATISTICAL ANALYSES	24
Sex Differences	25
Kinship Bias	25
Time of Day and Location	26
RESULTS	26
Sex Differences and Social Behavior	26
Sex Differences and Solitary Behavior	28
Kinship Bias	30
Time of Day	33
Location	34
Individual Behaviors	35
Allogrooming	36
Self-Grooming	38
Allogrooming and Self-Grooming	38
Cuddling	40

Vocalizing	40
Sleeping	40
Attack/Attacked By	41
Rubbing	41
Sniffing	43
Latrine Use	45
Foraging, Aquatic and Terrestrial	46
Swimming	48
Wrestling, Aquatic and Terrestrial	49
DISCUSSION	52
Social Determinants	52
Foraging	53
Kinship Bias	55
Time of Day	56
Communication	56
Affiliation and Aggression	58
IMPLICATIONS	60
CONCLUSION	60
LITERATURE CITED	62

LIST OF TABLES

Ethogram

23

LIST OF FIGURES

1. Overhead view of the exhibit	20
2. Grid locations	22
3. Tier locations	23
4. Female mean frequency of IC and ICP	27
5. Males mean frequency of IC and ICP	27
6. Males vs Maya mean frequency of social behavior	28
7. Males vs Maya mean frequency of solitary behavior	29
8. Female solitary vs social behavior	29
9. Males solitary vs social behavior	30
10. Kinship bias, Benny and all otters	31
11. Pairwise comparison, Benny and all otters	31
12. Kinship bias, Maya and all otters	32
13. Pairwise comparison, Maya and all otters	32
14. Social behavior over the course of the day	33
15. Solitary behavior over the course of the day	34
16. Pairwise comparison, social behavior and location	35
17. Allogrooming, mean rates of all otters	37
18. Allogrooming, pairwise comparison of all otters	37
19. Self-grooming, mean rates of all otters	39
20. Self-grooming, pairwise comparison of all otters	39
21. Sleeping, mean rates of all otters	41
22. Rubbing, mean rates of all otters	42
23. Rubbing, pairwise comparison of all otters	43
24. Sniffing, mean rates of all otters	44
25. Sniffing, pairwise comparison of all otters	44
26. Foraging-Aquatically mean rates of all otters	46
27. Foraging-Aquatically, pairwise comparison of all otters	47
28. Foraging-Terrestrially, mean rates of all otters	47

29. Foraging-Terrestrially, pairwise comparison of all otters	48
30. Swimming, mean rates of all otters	49
31. Wrestling-Aquatically, mean rates of all otters	50
32. Wrestling-Aquatically, pairwise comparison of all otters	51
33. Wrestling-Terrestrially, mean rates of all otters	51
34. Wrestling-Terrestrially, pairwise comparison of all otters	52

BACKGROUND

The North American river otter (*Lontra canadensis*) is a member of the mustelid family. Morphologically, this semi-aquatic mammal ranges from 5-14kg, with males weighing on average 1.1kg more than females (Lariviere & Walton 1998, Blundell et al. 2002). The North American river otter has short legs, and a tail that is roughly one-third of the animal's body length; body length does not vary by gender. Both the head and neck of the North American river otter are the same diameter. River otters are equipped with dense fur, short ears, webbed feet, and a long tail, features, which are ideal swimming (Lariviere & Walton 1998). This species of river otter can be found in most freshwater systems around the United States and Canada, but can also be found in marine, coastal regions as well (Blundell et al. 2005).

As a member of the largest family within order Carnivora, the North American river otter has many relatives which include: sea otters, badgers, weasels, mink, polecats, fishers, and wolverines. Members within this family are known for their slender bodies, skilled hunting capabilities, diverse habitats, and ability to scent mark. Mustelids habitats vary greatly, from terrestrial to aquatic, yet their diets are similar, consisting of small invertebrates and vertebrates (Nowak 1991). Although residing within a different genus, river otters are often mistaken for sea otters, or *Enhydra lutris*. Geographically, the sea otter is the closest relative to the North American river otter. They are often found coexisting in coastal habitats along the west coast of the United States, but morphologically they vary. The sea otter is the largest species within the mustelid family,

weighing on average 22-45kg. Comparatively, sea otters have denser hair than river otters, shorter tails, and larger vibrissae (Nowak 1991, Lariviere & Walton 1998).

Otter fur is morphologically equipped for a semi-aquatic lifestyle, having a dual layer of interlocking hairs known as guard hairs and under hairs. Once submerged, these hairs interlock and trap air, which creates a barrier between the water and the body of the otter. This barrier serves as a means of insulation for the river otter (Liwanag et al. 2012).

Insulation is vital for the survival of both otter species, therefore, it is extremely important that hairs are kept clean via grooming behaviors. Self-grooming enables an individual to re-align guard hairs with under hairs, while also removing dirt and stimulating oil production (Liwanag et al. 2012). In contrast, allogrooming is a social behavior with the same function, but also serves as a means of bonding between conspecifics (Green et al. 2002, Liwanag et al. 2012).

River Otter Behavioral Ecology

River otter population distributions are scattered and fragmented throughout most of the United States and Canada. Due to its dense fur, the North American river otter has been a popular item in the pelt trade since the 16th century, which has greatly impacted its species (Scognamillo 2005). The rate of population decline increased between the mid 1800s into the early 1900s, as the demand for fur increased. By the 1970s, the North American river otter was eliminated from 11 states, and their numbers greatly reduced in 9 states (Scognamillo 2005). In the late 70s, early 80s, reintroduction programs worked diligently to increase population numbers, using Louisiana river otters as the founding

stock (Latch et al. 2008). River otters are still considered a furbearing species, with nearly 3,300 otters being harvested each year (Day et al. 2013, Latch et al. 2008).

River otters occupy home ranges. These home ranges vary based on sex, season, elevation, and availability of resources. Home ranges tend to be smaller in lower lying habitats compared to habitats in higher elevations (Helon 2006). The shape of the home range also varies depending on the type of habitat that is occupied. For example, otters inhabiting coastal regions of the United States occupy home ranges that are in the shape of a polygon, whilst otters in open bodies of water have linear home ranges (Helon 2006). Due to intense foraging strategies, males often occupy larger home ranges than females (Blundell et al. 2002, Helon 2006). During their reproductive cycle, females occupy overlapping home ranges within restricted parameters (Helon 2006). This spatial proximity of female home ranges to latrine sites suggests that females are more territorial than males (Blundell et al. 2005).

Home ranges are also impacted by resource availability. Although, river otters forage for a wide variety of foods, they predominantly feed on fish. The abundance of fish depends on season, as well as the biodiversity of the resource shed, or the area where resources are foraged (Blundell et al. 2005). An important factor that plays a role in biodiversity within river otter home ranges are latrine sites. Latrine sites are riparian areas where river otters deposit feces, urine, and anal secretions. High levels of nitrates and phosphates can be found in these deposition sites, while anal secretions serve as a means

of olfactory communication. Deposition of feces and urine can inform other conspecifics of home range boundaries and resource availability (Blundell et al. 2005).

Biodiversity of the resource shed is affected by latrine sites. Because river otters deposit high levels of phosphates and nitrates at latrine sites, areas surrounding latrine sites are more nutrient dense than areas within the home range that are not surrounded by a latrine site. Plant growth surrounding latrine sites is more abundant than random areas within the home ranges. Latrine sites, compared to random sites, have more intertidal rocks, providing the otters with places to mark and deposit feces (Blundell et al. 2005). An increase in vegetation along coastal regions provide various species of schooling fish with sheltered habitats where river otters are able to hunt and capture prey (Blundell et al. 2005).

Latrine sites can provide scientists with much insight about the social behavior and spatial use of river otters (Gorman et al. 2006). Latrine sites serve as home range markers for river otters and females' ranges tend to be closer to latrines than males. Often, these sites will be used for scent marking to communicate with conspecifics, which is beneficial in solitary species with widely dispersed home ranges. River otters forage for fish in areas surrounding their home ranges, and deposit fish remains via feces at latrine sites. Deposition of fish parts informs other river otters of resource availability (Blundell et al. 2005, Gorman et al. 2006).

Through scent-marking and fecal deposition, otters are also able to determine the health or the degree of relatedness to another individual river otter (Allen et al. 2016).

Latrine site marking is done most-often by one individual river otter at a time. Otters will use rocks, logs, trees, and other debris found along riparian habitats (Oldham & Black 2009). In order to gather information from markings, otters will sniff, rub and taste feces and anal secretions. They will also rub their bodies alongside rocks and stomp their feet in places where other otters have left feces (Green et al. 2015). Female river otters will scent-mark more often at these sites in order to relay information to males during breeding season, which is when males will scent-mark more frequently as well (Allen et al. 2016). Latrine site marking is also used by females to identify territorial bounds, which explains why their home ranges are not far from latrine sites (Blundell et al. 2005).

River Otter Life History

Although, they show no overall kinship bias, river otters often form family groups. A family of otters is defined as one adult female and the offspring of that adult female. Adult male river otters are not included in these family groups due to their polygynous nature (Lariviere & Walton 1998). Male and female river otters will often be seen in small groups together during the mating season in late winter to early spring depending on geographic location. Both male and female river otters reach sexual maturation between 2-3 years old. Litter sizes range from 1 to 5 offspring, and offspring will stay alongside the mother for roughly a year until they are able to forage properly on their own (Lariviere & Walton 1998).

Social Organization

Mustelids are not considered social animals within the mammal class, yet the North American river otter shows atypical behavior within its family, having a complex social network (Green et al. 2015). River otter sociality is a compound system with many contributing factors: location, season, time of day, resource availability, gender, and degree of relatedness (Green et al. 2015).

According to recent studies, river otter males are considered to have a higher degree of sociality, compared to females. Therefore, I hypothesized that male river otters would exhibit more instances of social behavior than the female in the romp. Although males do not help rear offspring, they are found often in social groups, known as bachelor groups. (Lariviere & Walton 1998, Blundell et al. 2002). This behavior among males is atypical, because males within the mammalian class will often compete with conspecifics for mates. Otter males, however, are able to benefit from these male bachelor groups via cooperative foraging. These bachelor groups are composed of both kin and non-kin male river otters (Hansen et al. 2009). Sociality is not kinship based in river otters; a lack of kinship bias within this species has thus allowed for males to form said bachelor groups (Blundell et al. 2004). Therefore, I hypothesized that river otters would exhibit no kinship bias between individuals.

Cooperative foraging is defined as individuals of the same species that work together in order to obtain resources more efficiently. Formation of bachelor groups is dependent upon resource availability (Blundell et al. 2004). A river otter's diet consists

primarily of various types of fish and small vertebrates. In order to obtain higher quality resources, like pelagic fish (fish of open water columns in lakes or along the coast), male river otters form bachelor groups. Pelagic fish consist of salmon, herring, capelin, juvenile salmon, and sand lance. These fish use intense swimming strategies in order to avoid predation, therefore social otters have a better chance at herding and capturing pelagic fish (Blundell et al. 2002). Pelagic fish consumption is highest prior to mating season (Blundell et al. 2004). When pelagic fish are unavailable, river otters will prey opportunistically on intertidal and demersal fish (fish which occupy bottom habitats), as well as freshwater fish. Intertidal and demersal fish consist of cod, rockfish, prickly backs, gunnels, greenling, and sculpin. A diet consisting of more pelagic fish is considered a higher-quality diet, as opposed to one consisting of intertidal or demersal fish due to the presence of omega-three fatty acids found in these fish. River otters forage for lower quality fish independently rather than cooperatively, because they are easier to catch than pelagic fish (Blundell et al. 2002).

Visits to latrine sites also vary depending on the season, time of day, and geography of the location. Otter visits to latrine sites occur more often during winter months, prior to breeding season. Males visit latrine sites more frequently than females during this time of year (Green et al. 2015, Martin et al. 2010). Visits to latrine sites are also more common during crepuscular hours, which has been suggested to be attributed to more human activity surrounding river otter home ranges during the day (Green et al. 2015).

Location is another contributing factor to the social organization of river otters. Terrestrially, river otters spend less time in groups, with the exception of females and their offspring. However, latrine sites serve as a means of social interaction and communication via olfactory cues. There is variation in visitation among social and nonsocial otters. Social otters visit the same latrines more frequently than nonsocial otters. However, nonsocial animals visit a greater number of latrine sites than social otters (Blundell et al. 2005). Therefore, I hypothesized that river otters would exhibit a higher degree of sociality terrestrially than aquatically.

Tactile behavior has also been previously studied and recorded at latrine sites. Individual otters will take part in self-grooming at these sites, while members of a social group often engage in allogrooming. Allogrooming is an affiliative behavior among river otters, where one otter will clean another conspecific's fur (Green et al. 2015). This behavior is beneficial, because analogous to their sea otter relatives, grooming enables river otters to store pockets of air between layers of guard hairs and under hairs. These pockets of air provide warmth and insulation to river otters (Nowak 1991).

Wrestling and mounting are other forms of tactile social interaction seen amongst river otters. Wrestling, often a sign of aggression in most mammal species, is an act of play between river otters, and is also displayed during mating rituals between mature males and females (Green et al. 2015).

STUDY OBJECTIVES, QUESTIONS, AND HYPOTHESES

The objective of this study was to look at the effects of sex, location, and time of day on the sociality of captive North American river otters. Because previous studies on wild populations revealed that males were more social than females, I wanted to know whether this was the case in a captive population (Blundell et al. 2002). Therefore, I hypothesized that male otters would engage in more social behavior than females. I also wanted to know whether or not this captive romp was more social during specific times of day. By nature, river otters are crepuscular mammals, meaning they are more active during the early morning and early evening (Green et al. 2015). Therefore, I hypothesized that most social behavior among conspecifics would occur during the early evening. Lastly, because river otters communicate via olfactory cues at latrine sites, I hypothesized that most social behavior would occur in the terrestrial portion of the exhibit, analogous to these sites (Blundell et al. 2005, Gorman et al. 2006).

SIGNIFICANCE

Understanding a species' behavioral ecology is important to its conservation and preservation. Ethology, the study of animal behavior, has thus been able to provide scientists with a way to understanding complex systems of a particular species in order to contribute to conservation efforts (Mench 1998). The North American river otter (*Lontra canadensis*) has intrigued scientists due to its unusual social behavior and means of communication, as well as its significance to multiple ecosystems as an apex predator (Green et al. 2015).

As an apex predator, river otters have been used as biomarkers for the overall health of many watersheds and marine habitats. The health and distribution of river otters in North America have thus provided scientists with information regarding the quality of water, the distribution of fish populations, as well as the overall health of riparian habitats surrounding river otter home ranges. Due to an increase in human population numbers, urbanization, and development, river otters remain at risk from a number of environmental threats including pollution, habitat destruction, habitat fragmentation, and overharvesting of resources (Hamilton 2014).

Because of the very nature of the kinds of habitats occupied by river otters and their crepuscular behavior, it is difficult to carry out detailed studies of their social behavior in the wild. Captive settings, such as the Tennessee Aquarium, provide an opportunity to study the behavior of this species at a greater level of precision. In addition, this study will also provide zoos and aquaria with a better understanding of the social dynamics of captive river otters.

METHODS & MATERIALS

The study took place on a romp of size otters housed at the Tennessee Aquarium in Chattanooga, Tennessee, over an eight-week period in the summer of 2017.

Exhibit Design

The otters were housed in an exhibit called River Otter Falls; a 136meter, multi-tiered exhibit which contained multiple logs and rocks, as well as three separate pools and a rock waterfall (Figure 1).



Figure 1 Overhead view of the exhibit

Subjects

The subjects of study were six North American river otters, five males and one female. Benny and Maya, both four years of age, were orphaned siblings that were rescued from the pelt trade. Delmar, twelve years old, was the eldest of the romp and was born in captivity at the Pittsburgh Zoo. Louie, Hunter, and Digger were estimated at being between eight and twelve years old and were from Louisiana. Maya was bred for the first time between March and May of 2017.

Data Collection

Focal animal samples were used to collect data over 60 day period beginning June, 2017 and concluding July, 2017. Each otter was given a numerical identification throughout the duration of the study Benny (1), Delmar (2), Digger (3), Hunter (4), Louie (5), and Maya (6). Male and female numerical representations were as follows: Female

(1), Male (2). Subjects were released into the exhibit in groups of 2, 3, and 4 individuals at a time, for roughly two hours starting at 10:00am every day. Otters were released into these groups in no specific order or fashion. The amount of time each group was on exhibit fluctuated from the 2-hour guideline depending on feeding schedules and release times. The first group was released into the exhibit from 10:00am to 12:00pm, the second group from 12:30pm-2:00pm, the third from 2:00pm-4:00pm, and the fourth from 4:00pm-6:00pm. Each 2-hour time period was considered a group of otters, and the time period for which the group of otters was on exhibit was given a numerical representation: 10:00am-12:00pm (1), 12:30-2:00pm (2), 2:00pm-4:00pm (3), 4:00pm-6:00pm (4). When not in the public exhibit, river otters were held in a separate exhibit with small pools, enrichment items, and latrine areas (Carlson 2016). For each time period, the identification numbers of otters on exhibit were entered into a generator which randomly chose which otter would be sampled, to prevent bias. The focal animal was sampled continuously for 10 minutes and all behaviors, and frequency of behaviors were recorded (Altman 1974) .

In order to determine sociality across all otters, all behaviors of focal animals were recorded as either solitary (S), in contact with (IC), or in close proximity (ICP) to another conspecific. Both IC and ICP were considered forms of social behavior. In order for an individual to be considered ICP, it was within roughly 91cm, the average body length of an otter, proximity to another otter. An otter which was IC with another otter was directly touching a conspecific for more than 3 seconds.

In order to determine the location of an individual the exhibit was sectioned into 5 grids, which were separated by concrete divider (Figure 2). The locations of all behaviors were also recorded as aquatic or terrestrial. Terrestrial behavior was recorded as T, while aquatic behavior was recorded as A. Tier location was also specified as either top tier (tt), middle tier (tm), or lower tier (tl) of the terrestrial portion of the exhibit (Figure 3). Latrine sites were located at the top tier in Grid 1, at the top tier in Grid 3, and at the lower tier in Grid 3. For aquatic behavior, there were three indicators of location: A-G0 which was any individual within the pool in the area that ranged from grid 1 to grid 3, A-G4 which was any individual in the grid 4 pool, and A-G5 which was any individual in the grid 5 pool.

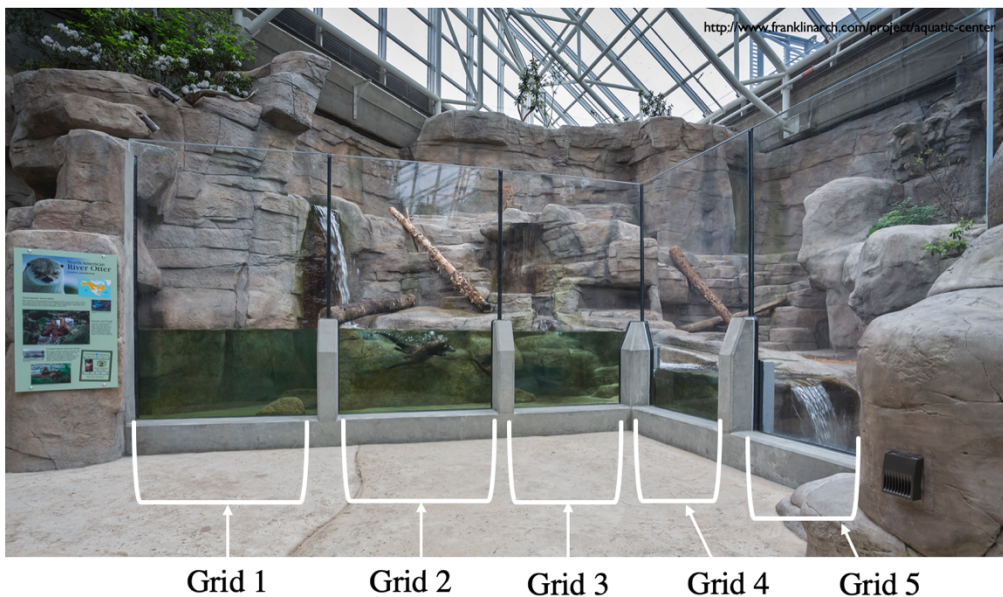


Figure 2 Grid locations



Figure 3 Tier locations. Top tier (TT), middle tier (TM), and lower tier (TL).

Affiliative Social Behaviors		
Behavior:	Code:	Defined as:
Allogrooming	AG	Licking or scratching another otter's fur with paws
Cuddle	C	Lying next to another conspecific, while awake or asleep
Vocalizing	V	Chirping, squeaking, or calling
Swim-wrestling	SW	wrestling underwater with one or more conspecifics
Wrestling	W	One or more otter jumping on, or biting another conspecific
Aggressive Social Behaviors		
Attacked By	AT	One or more conspecifics directing physical aggression to the focal animal
Attack	AK	directing physical aggression to one or more conspecifics
Behaviors that were performed solitarily, in contact with, or in close proximity to another otter		
Inactive	IA	Awake, but not interacting with another conspecific, or eliciting responses

Asleep	AS	sleeping
Self-grooming	SG	Licking or scratching at one's fur
Swimming	S	Swimming, diving
Foraging	F	Eating, cleaning food
Sniffing	SNF	Smelling an object, area, or another conspecific
Sniffing and Walking	SNWK	Smelling an object, area, or another conspecific while walking
Rubbing	R	rubbing or scent marking an object
Scratching	SC	Scratching at an object with one's claws
Foraging while Swimming	SF	Eating, cleaning food while swimming under water
Defecate	DEF	Defecating at a latrine site
Walk	WK	Traveling by foot

Table 1: Ethogram, influenced by Green et al. 2015

STATISTICAL ANALYSES

Frequencies of all behaviors were extracted from focal animal data and averaged for each animal over the course of the study. Differences in the number of males vs female was corrected for with each test. Whenever possible, parametric tests were used, but in some cases, the data were not normally distributed and could not be transformed into a normal distribution. In these cases, nonparametric tests were used (SPSS V24).

For all individual behaviors, an Independent-Samples Kruskal-Wallis Test was used to test for differences in frequency of time spent performing said behavior across all individuals, and the figures represent over distributions of data. When a significant effect of the variable was found, subsequent pairwise comparisons were based on the Mann-

Whitney U Test with the Bonferroni correction. In those post-hoc tests, any pair of animals connected by a yellow line are significantly different.

Sex Differences

An analysis of variance was used to detect differences in male solitary behavior and female solitary behavior. Differences in solitary and social behavior within the sexes were compared using a t-Test. Differences in contexts of sociality, whether it occurred in contact with (IC) or in close proximity to (ICP) another individual, were compared between the sexes using a Wilcoxon Signed Rank test. Because no difference was found in mean frequency of IC and ICP across sexes, IC and ICP were combined into a single measure, henceforth called sociality.

Mean rates of sociality between the males and the female were compared using an ANOVA for a single specimen against a sample (Sokal and Rohlf 1981). Because no significant effect of sex was found, female and male scores were combined for all further analyses (SPSS V24).

Kinship Bias

An Independent-Samples Kruskal-Wallis Test, with the Bonferroni correction, was used to compare mean time spent between Benny and all otters, as well as Maya and all otters to determine whether these individuals showed signs of kinship bias (SPSS V24).

Time of Day and Location

An analysis of variance was used to compare differences in sociality based on time of day, as well as differences in solitary behavior with time of day across all otters. A Wilcoxon Signed Ranks Test was used to compare both sociality and location, in addition to solitary behavior and location (SPSS V24).

RESULTS

Sex Differences and Social Behavior

Social behavior is defined as action patterns between an individual and one or more conspecifics (Altman 1974). Based on previous studies, river otter males are known to be more social than females due to cooperative foraging strategies (Blundell et al. 2002). Therefore, I hypothesized that male otters would be more social than female otters in captivity. A Wilcoxon Signed Rank Test showed the female's interactions were done more often while she was in close proximity (ICP) as opposed to in contact (IC) with another otter ($W=474.5$, $n=37$, $p<0.026$; Figure 4). In contrast, male sociality mean rates of being in contact with versus being in close proximity to another otter did not differ significantly (t-Test, $t=0.814$, $df=4$; $p=0.461$, $\bar{x}_{IC}=0.5720$, $\bar{x}_{ICP}=0.5140$; Figure 5). Despite the difference between the female and males as a group, when mean rates of IC and ICP are combined into a single measure called "sociality", there was no difference in frequency based on the sex of the animal, and therefore both sexes were equally social in both contexts (ANOVA, $F=0.746$, $df=1,4$; $p=0.437$; Figure 6).

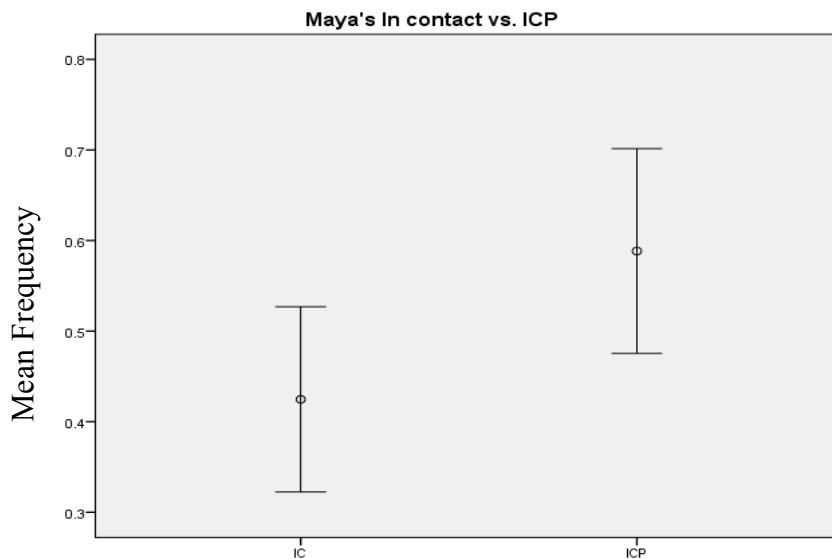


Figure 4 Confidence intervals and mean frequency of IC (in contact with) vs. mean frequency of ICP (in close proximity to) for the female. Means differ, Wilcoxon Signed Ranks Test, $W=475.5$, $n=37$, $p<0.026$. Maya was ICP more often than IC with another conspecific.

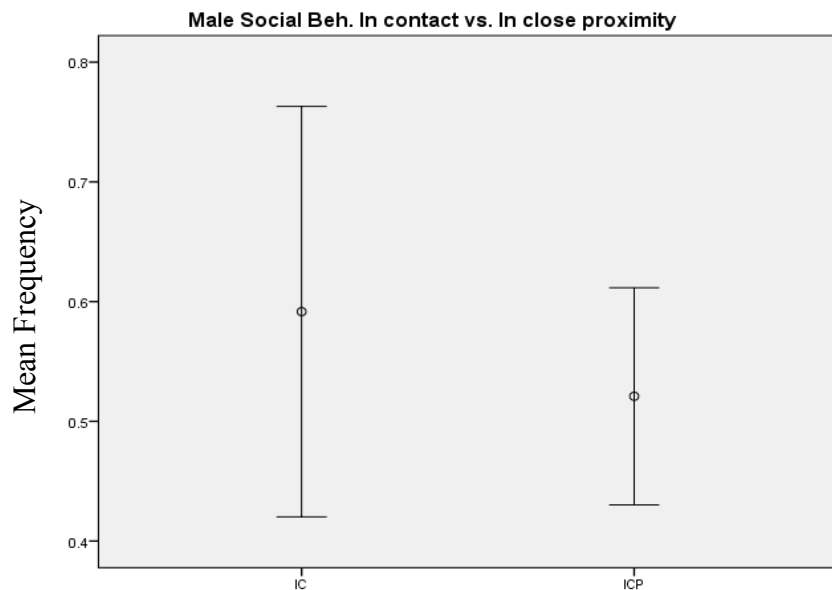


Figure 5 Confidence intervals and mean frequencies of IC (in contact with) vs. ICP (in close proximity to) for all males. Means of IC do not differ from ICP, t-Test, $t=0.814$, $df=4$; $p=0.461$, $\bar{x}_{IC}=0.5720$, $\bar{x}_{ICP}=0.5140$. Males were IC and ICP equally as often.

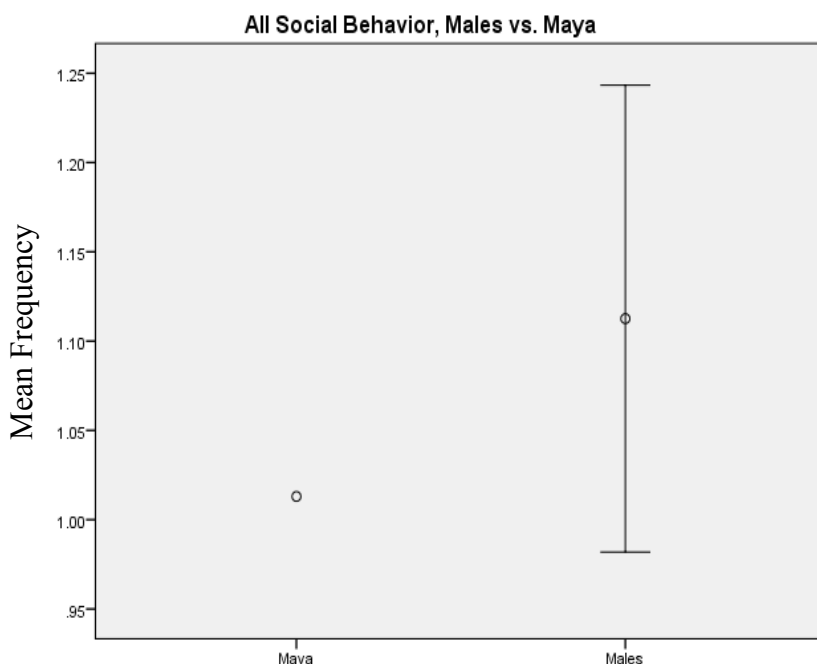


Figure 6 Confidence intervals and mean frequency of sociality between males and Maya. Means did not differ, ANOVA, $F=0.746$, $df=1,4$; $p=0.437$. Males and female were equally social.

Sex Differences and Solitary Behavior

Solitary behavior is defined as an action pattern performed by an individual that is not near, in-contact with, or towards another conspecific. I hypothesized that the female would exhibit more solitary behavior than the males, because males are more social than females (Blundell et al. 2002). An analysis of variance showed that there was no statistical difference in male and female solitary behavior ($F=0.405$, $df=1,4$, $p=0.559$; Figure 7). Therefore, they were equally solitary. However, there was a significant difference between the female, Maya's frequencies of social and solitary behavior; she exhibited social behavior more often than solitary behavior (t-Test, $t= -5.251$, $df=23$, $p<0.000$; $\bar{x}_{\text{social}}=1.095$, $\bar{x}_{\text{solitary}}=0.493$; Figure 8). Males exhibited a similar result having

higher mean frequencies of social behavior than solitary behavior (t-Test, $t = -8.774$, $df=4$, $p < 0.001$; $\bar{x}_{social} = 1.113$, $\bar{x}_{solitary} = 0.443$; Figure 9). Thus, both sexes were more frequently engaged in social behavior than in solitary behavior.

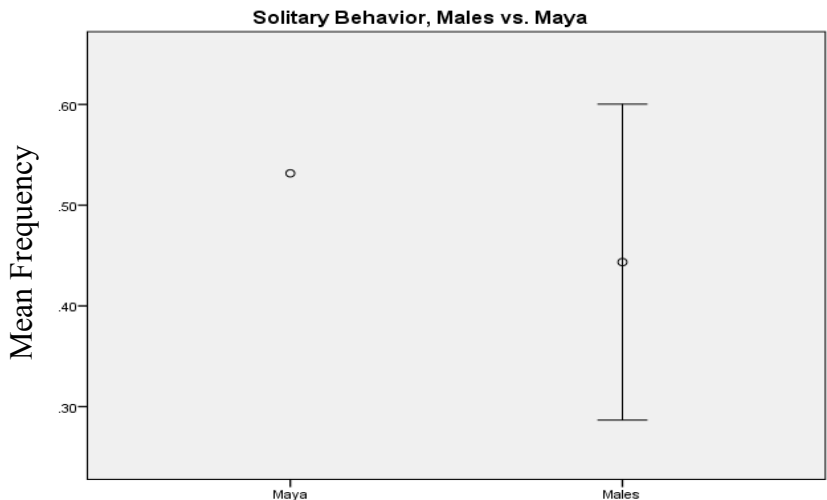


Figure 7 Confidence intervals and mean frequency of solitary behavior between males and the female Maya. Means did not differ, $F = 0.405$, $df = 1, 4$, $p = 0.559$. Males and female were equally solitary.

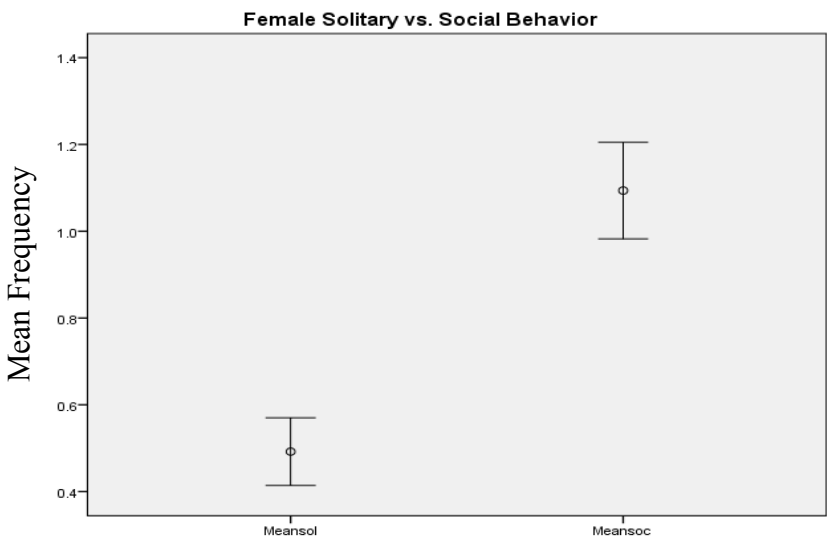


Figure 8 Confidence interval and mean frequency of solitary vs. mean frequency of social behavior for the female. Means differ, $t = -5.251$, $df = 23$, $p < 0.000$; $\bar{x}_{social} = 1.095$, $\bar{x}_{solitary} = 0.493$. The female was more often social than solitary.

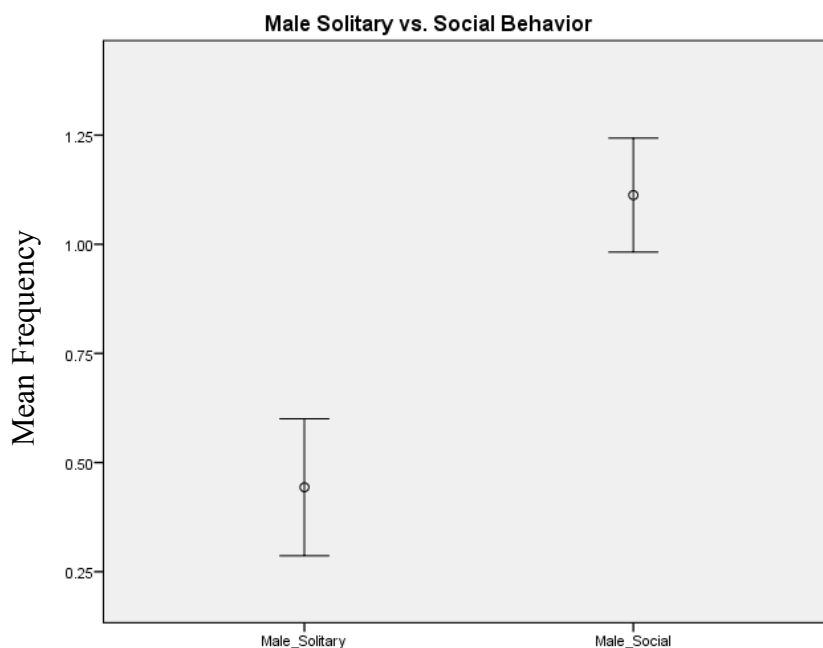


Figure 9 Confidence intervals and mean frequency of solitary vs. mean frequency of social behavior for all males. Means differ, t-Test, $t = -8.774$, $df=4$, $p < 0.001$; $\bar{x}_{\text{social}} = 1.113$, $\bar{x}_{\text{solitary}} = 0.443$. Males are more often social than solitary.

Kinship Bias

Benny and Maya were siblings housed together as adults in the Tennessee Aquarium, which is unlikely to occur in the wild, because males disperse from the natal group once able to forage on their own (Hansen et al. 2009). An Independent-Samples Kruskal-Wallis Test revealed that the male Benny spent significantly more time with Maya, his sister, than he did with all other otters suggesting that Benny was exhibiting a kinship bias, which was also supported by a pairwise comparison of his interactions with all otters ($H = 18.118$, $df=4$, $p = .001$; Figure 10, Figure 11). A Kruskal-Wallis Test further supported kinship bias between Maya and Benny and revealed that Maya interacted with Benny more often than with any other otter ($H = 28.337$, $df=4$, $p = 0.000$; Figure 12). A

post-hoc pairwise comparison between Maya and each otter revealed that she spent significantly more time interacting with Benny compared to Louie, Digger, and Hunter (Figure 13).

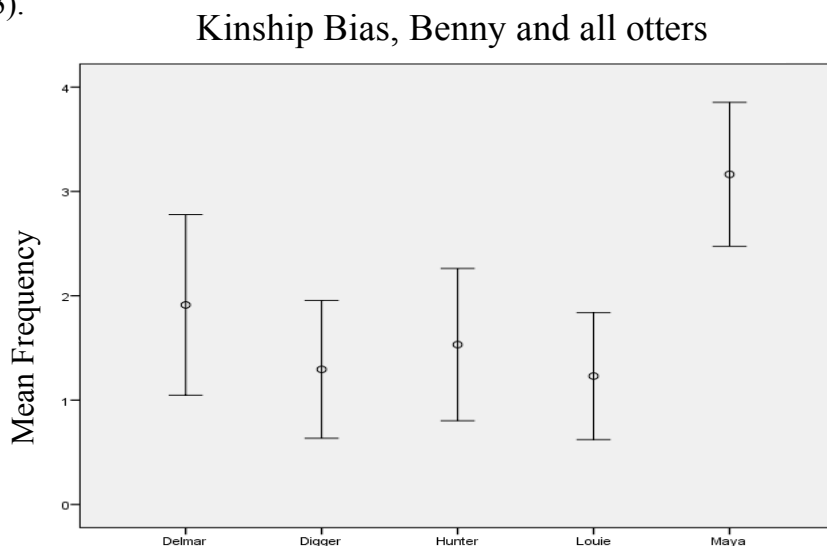


Figure 10 Confidence intervals and mean frequency of Benny's interaction rates with all otters. Means differ, $H = 18.118$, $df = 4$, $p = 0.001$. Benny interacted with Maya more often than with any other otter.

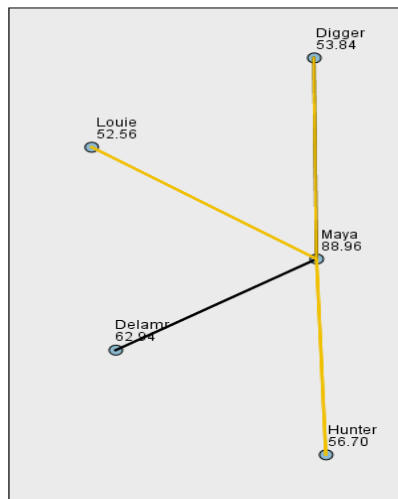


Figure 11 Pairwise comparison of mean interaction rates between Benny and all otters. Yellow lines signify significant differences between individuals and their interaction rates with Benny. Benny spent significantly more time interacting with Maya than he did with Louie, Digger, and Hunter.

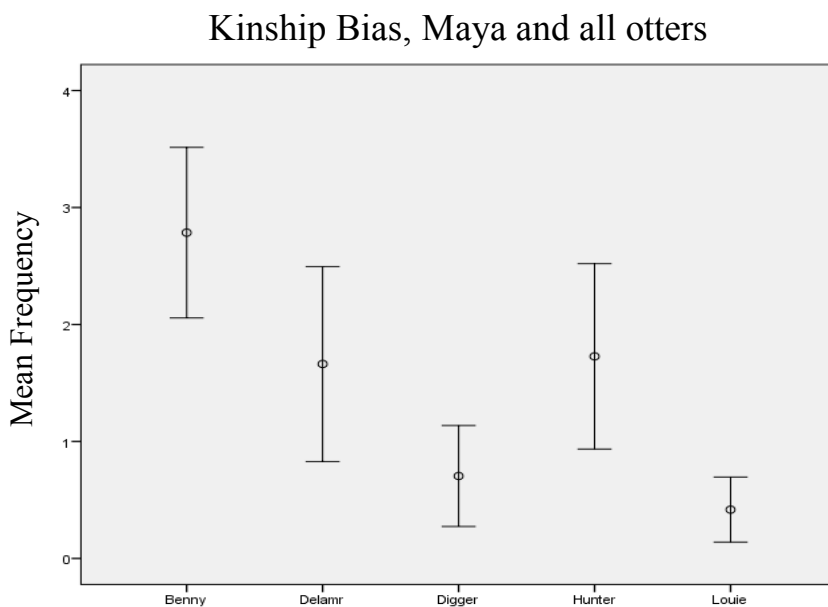


Figure 12 Confidence interval and Maya's mean interaction rates with all otters. Means differ, $H=28.337$, $df=4$, $p=0.000$. Maya spent significantly more time with Benny than with all other otters.

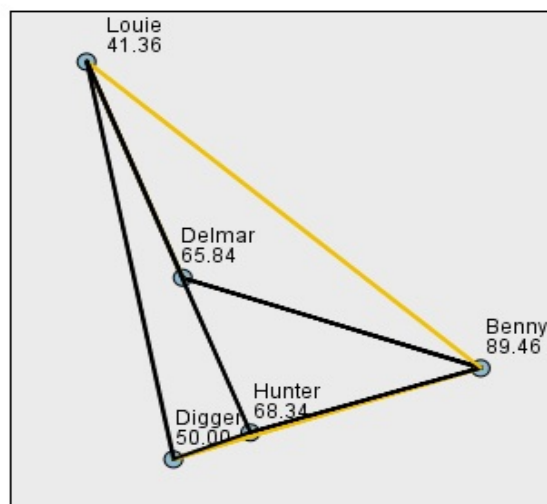


Figure 13 Pairwise comparison of mean interaction rates between Maya and all otters. Yellow lines signify significant differences between individuals and their interaction rates with Maya. Maya spent significantly more time interacting with Benny compared to Louie, Digger, and Hunter.

Time of Day

Wild river otters are crepuscular by nature (Green et al. 2005). Therefore, I predicted that the captive romp would be more social during the early evening period. Because there was no difference between overall male and female sociality rates, both male and female rates were combined to compare sociality across the course of the day. An analysis of variance showed differences in sociality over various times of day (ANOVA, $F=5.79$, $df=3,20$, $p=0.005$; Figure 14). Time period 4 (4:00pm-6:00pm) differed from time period 1(10:00am-12:00pm) and 2 (12:30pm-2:00pm), but did not differ from time period 3 (2:00pm-4:00pm) (Figure 14), suggesting that the otters were more social during the early evening as opposed to other time periods. In contrast, the rate of solitary behavior did not change over the course of the day (ANOVA, $F=0.772$, $df=3,20$, $p=0.523$; Figure 15).

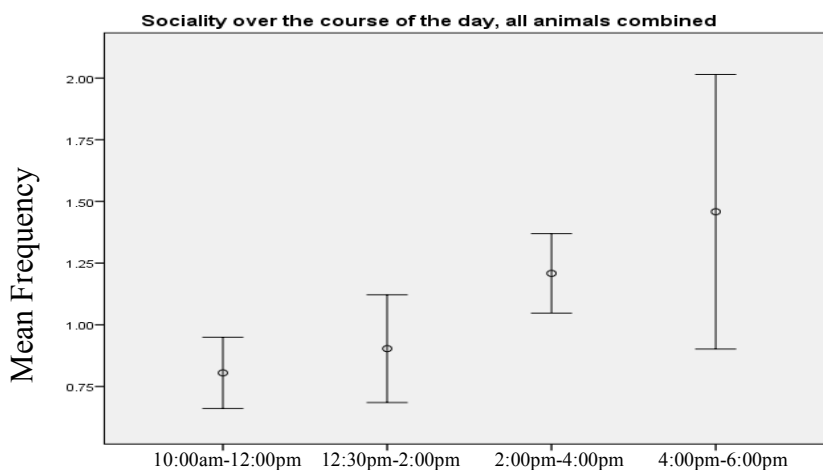


Figure 14 Confidence intervals and mean frequency of sociality across all otters during different time periods. Means differ $F=5.79$, $df=3,20$, $p=0.005$. The first three time periods did not differ from one another. Time period 4 (4:00pm-6:00pm) differed from time period 1(10:00am-12:00pm) and 2 (12:30pm-2:00pm), but did not differ from time period 3 (2:00pm-4:00pm).

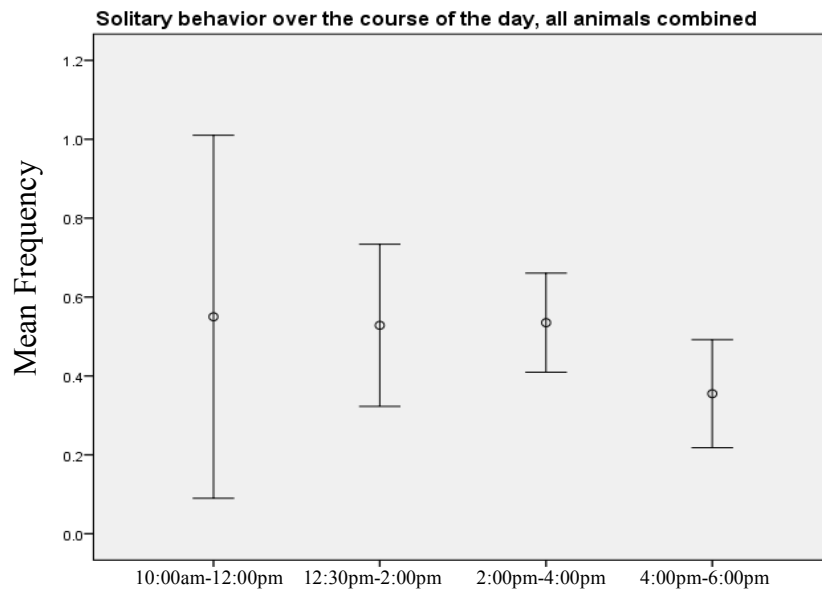


Figure 15 Confidence intervals, mean frequency of solitary behavior across all otters during different time periods. Means did not differ, $F=0.772$, $df=3,20$, $p=0.523$. Solitary behavior did not differ across various time periods.

Location

River otters are known to communicate via latrine sites (Blundell et al. 2005). TA related-samples Wilcoxon Signed Rank Test revealed that mean rates of social behaviors were significantly higher in the aquatic portion of the exhibit than in the terrestrial portion indicating that most of their social activity occurred in the water ($\bar{x}_{\text{aquatic}}=0.418$, $\bar{x}_{\text{terrestrial}}=0.204$, $W=2.201$, $n=6$, $p=0.028$). A related-samples Wilcoxon Signed Rank Test demonstrated higher frequencies of solitary behaviors on land as opposed to in the water ($\bar{x}_{\text{sol aq}}=0.177$, $\bar{x}_{\text{sol terr}}=0.333$, $W=2.207$, $N=6$, $p=0.027$). Significant differences between individuals are exhibited in the pairwise comparison; combined social behaviors

occurred more often aquatically than terrestrially, and combined aquatic behaviors also occurred more often than solitary aquatic behaviors (Figure 16).

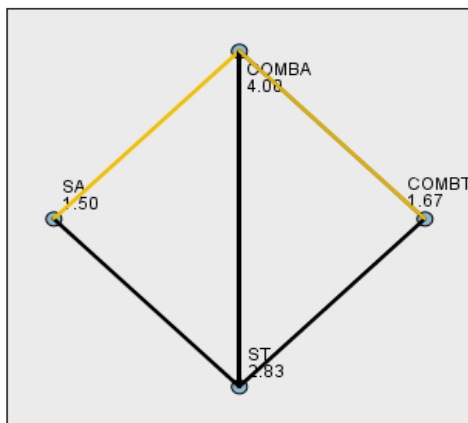


Figure 16 Pairwise comparison indicating the relationship between social behavior and location. SA=Solitary Aquatic, ST=Solitary Terrestrial, COMBA=All Social Aquatic, COMBT=All Social Terrestrial. Yellow lines signify significant differences between each node. Combined social behaviors occurred more often aquatically than terrestrially. Combined aquatic behaviors also occurred more often than solitary aquatic behaviors.

Individual Behaviors

Some otter behaviors were either social or solitary by nature. Social behaviors were separated into two categories, affiliation and aggression. Behaviors that occurred in an affiliative context included: allogrooming (AG), cuddling (C), Swimming-wrestling (SW), Vocalizing (V), and Wrestling (W). Behaviors that occurred in the context of aggression included attacking (AK) and being attacked by (AT) by another otter (Table 1). Behaviors that occurred in-contact with, or in close proximity to another otter, but that were not classified as social in nature included: Sleeping (AS), Foraging (F), Inactive

(IA), Rubbing (R), Self-grooming (SG), Swimming (S), Sniffing (SNF), Sniff-walking (SNWK), and Walking (WK) (Table 1).

Allogrooming

Allogrooming is an affiliative behavior performed by river otters and is defined as one river otter licking or pawing at another conspecific's fur. Allogrooming was performed by all otters, but there appeared to be a slight variation between the frequency of allogrooming among them (Figure 17).

A residual analysis showed that males allogroomed more often than the female ($X^2=7.982$, $z_{\text{males}}=1.15$, $z_{\text{female}}=-2.58$, $df=1$, $p=0.0047$). An Independent-Samples Kruskal-Wallis Test revealed statistical differences in allogrooming frequencies of individuals ($H=18.119$, $df=5$, $p=0.003$; Figure 17). A post-hoc pairwise comparison showed that Digger allogroomed more often than Maya, and Maya less often than Louie (Figure 18).

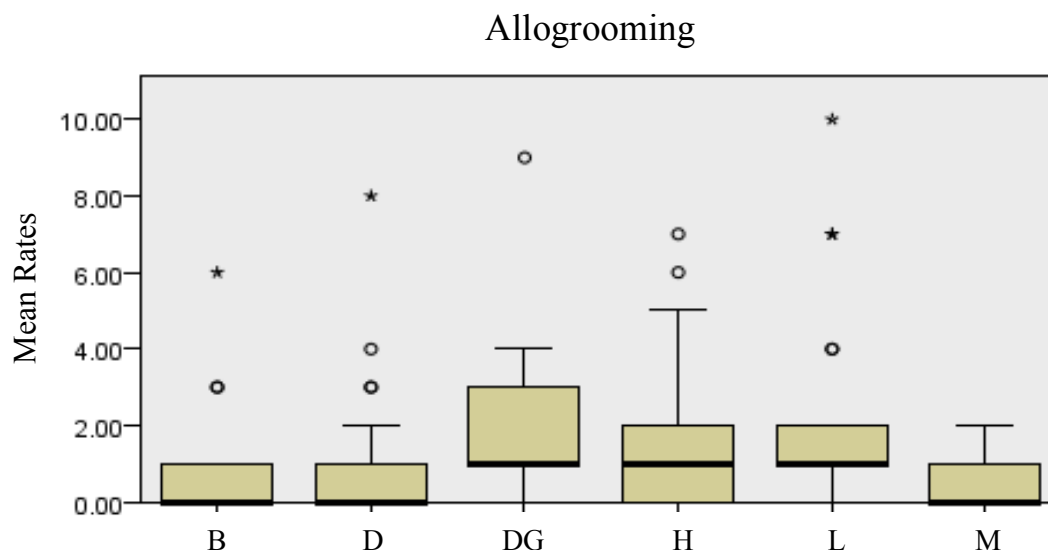


Figure 17 Independent-Samples Kruskal-Wallis Test compared mean time spent allogrooming by each individual. $H=18.119$, $df=5$, $p=0.003$. Digger, Hunter, and Louie spent more time allogrooming than all other individuals. Circles represent outliers approaching the 95% confidence level; asterisks indicate values outside those expected of a normal distribution.

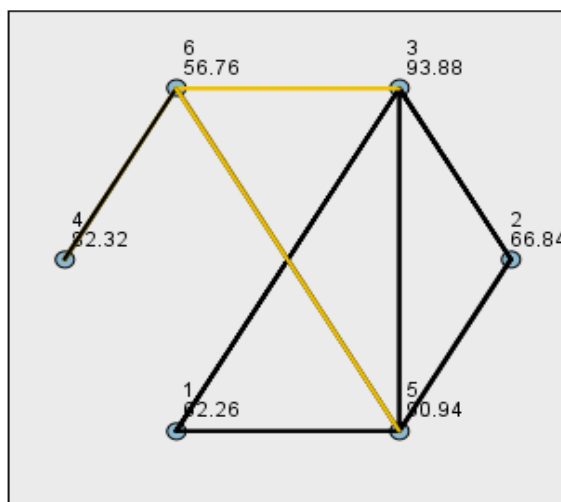


Figure 18 Pairwise comparison of mean allogrooming rates of all otters. Yellow lines signify significant differences in time spent allogrooming. 1=Benny, 2=Delmar, 3=Digger, 4=Hunter, 5=Louie, and 6=Maya. Maya spent significantly less time allogrooming than both Digger and Louie.

Self-Grooming

Self-grooming was recorded when a focal animal would lick or paw at one's own fur. An Independent-Samples Kruskal-Wallis Test revealed statistical differences in self-grooming frequencies of individuals ($H=40.106$, $df=5$, $p<0.000$; Figure 19). A post-hoc pairwise comparison revealed that Delmar spent more time self-grooming than both Maya and Digger. Hunter spent more time self-grooming than Maya, but less time self-grooming than Louie. Louie spent more time self-grooming than Benny, Digger, Hunter, and Maya. Digger spent more time self-grooming than Maya, but less time self-grooming than Delmar and Louie (Figure 20). A residual analysis revealed that, overall, males self-groom more often than the female ($X^2=45.70$, $z_{\text{males}}=2.12$, $z_{\text{female}}=-4.73$, $df=1$, $p=0.001$).

Allogrooming vs Self-Grooming

A residual analysis revealed that allogrooming happened significantly more often than self-grooming across all otters ($X^2=8.768$, $z_{\text{ag}}=2.09$, $z_{\text{sg}}=-2.09$, $df=1$, $p=0.0031$). Therefore, allogrooming more often than expected, and self-grooming occurred less than expected by chance.

Self-Grooming

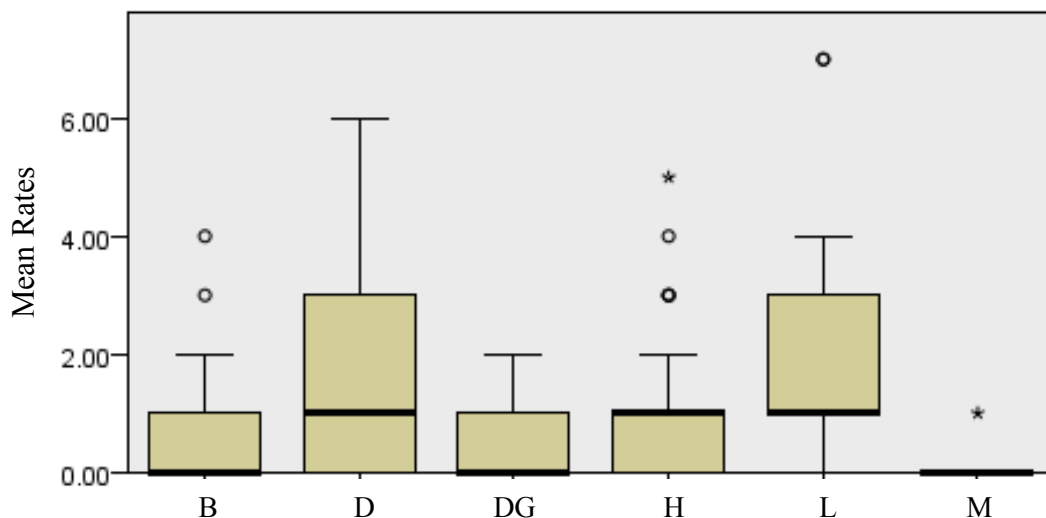


Figure 19 Independent-Samples Kruskal-Wallis Test compared mean time spent self-grooming by each individual. $H=40.106$, $df=5$, $p<0.000$. There was a significant difference in time spent self-grooming. Circles represent outliers approaching the 95% confidence level; asterisks indicate values outside those expected of a normal distribution.

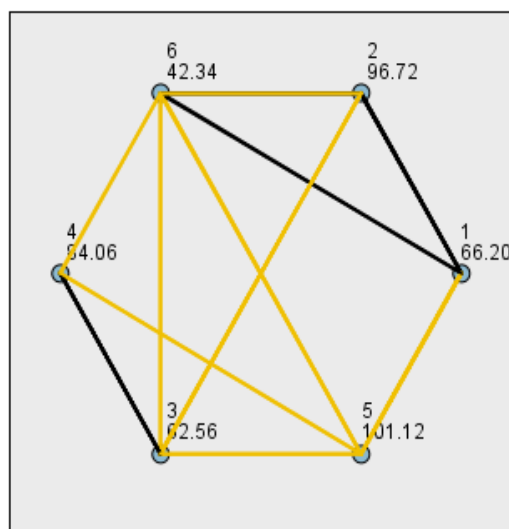


Figure 20 Pairwise comparison of mean self-grooming rates of all otters. Yellow lines signify significant differences in time spent self-grooming. Delmar spent more time self-grooming than both Maya and Digger. Hunter spent significantly more time self-grooming than Maya, but less time self-grooming than Louie. Louie spent significantly more time self-grooming than Benny, Digger, Hunter, and Maya. Digger spent significantly more time self-grooming than Maya, but significantly less time self-grooming than Delmar and Louie.

Cuddling

Cuddling is an affiliative behavior and was recorded when the focal animal was seen lying next to another conspecific, either awake or asleep. Few instances of cuddling were documented across all otters; it occurred only between Delmar and Hunter a total of three times. The only area where cuddling was recorded was in the substrate pit on the lower tier in grid 4.

Vocalizing

Vocalizations were recorded when a focal animal would call, and a conspecific would respond and walk towards the focal animal within five seconds of the initial call. Digger was recorded vocalizing a total of 10 times, and Delmar was the conspecific who walked towards him. Delmar was recorded vocalizing a total of 13 times, with Delmar and Louie responding. Hunter was recorded vocalizing a total of 2 times, with Digger and Delmar responding to his calls. This behavior was also performed by both Maya prior to attacking Louie 3 times. Benny also performed this behavior prior to attacking Louie a total of 3 times. Louie did not perform vocalizations.

Sleeping

As expected, given their crepuscular nature, it appeared that river otters were sleeping more often during the middle of the day. It also appeared that the otters were spending more time sleeping solitarily than socially. Hunter seemed to spend more time sleeping compared to other individuals, while Maya slept the least. It also seemed as though Digger slept more often socially, than any other individual (Figure 21).

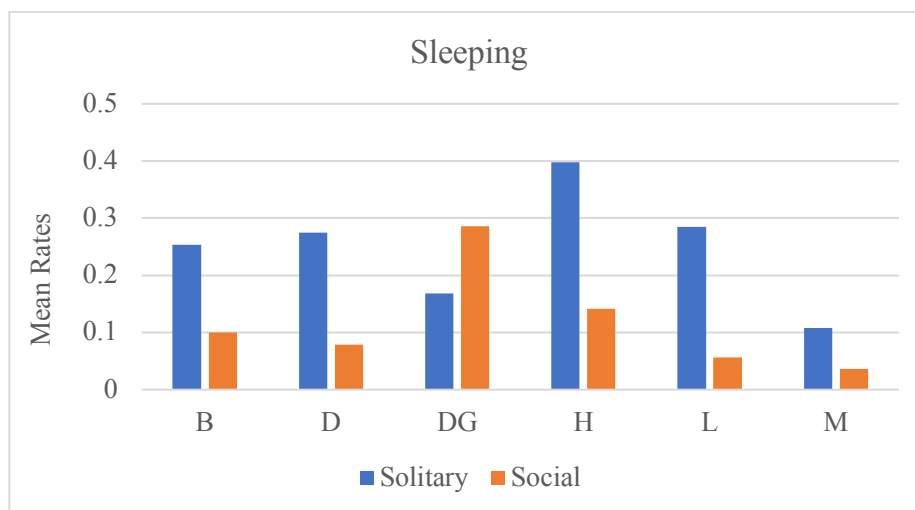


Figure 21 Mean rates of sleeping by each otter

Attack/Attacked By

Aggressive behavior included harsh vocalizations and biting while the otter being attacked would flee from the aggressor. Instances of aggression were rare, having been recorded a total of 6 times during the study and were only performed by Maya and Benny towards Louie. Events leading up to an attack were not atypical in that all individuals involved would be walking around the terrestrial portion of the exhibit. Attacks lasted no more than 5 seconds and were accompanied by harsh vocalizations of the attackers. Louie was rarely seen in an affiliative context with either Maya or Benny.

Rubbing

Rubbing behavior in river otters is used as a means of scent marking and communication. In this study, rubbing was infrequent, and even less so in the social context. An Independent-Samples Kruskal-Wallis Test revealed statistical differences in

rubbing frequencies of individuals ($H=17.183$, $df=5$, $p=0.004$; Figure 22). A post-hoc pairwise comparison revealed relationships between individuals, showing that Louie spent significantly more time rubbing than did Maya or Digger (Figure 23).

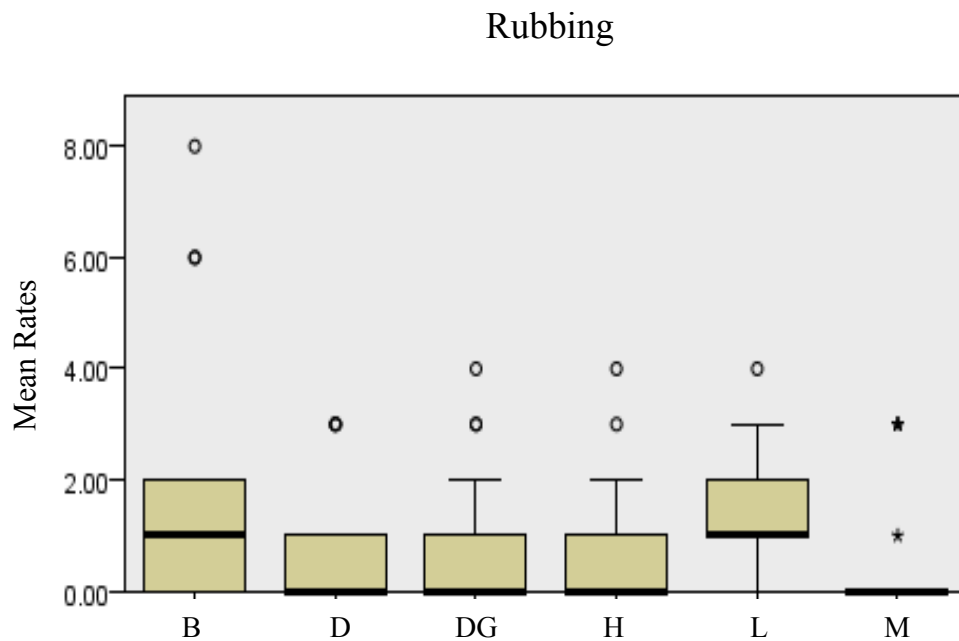


Figure 22 An Independent-Samples-Kruskal Wallis Test revealed significant differences in rubbing by individuals. $H=17.183$, $df=5$, $p=0.004$. Circles represent outliers approaching the 95% confidence level; asterisks indicate values outside those expected of a normal distribution.

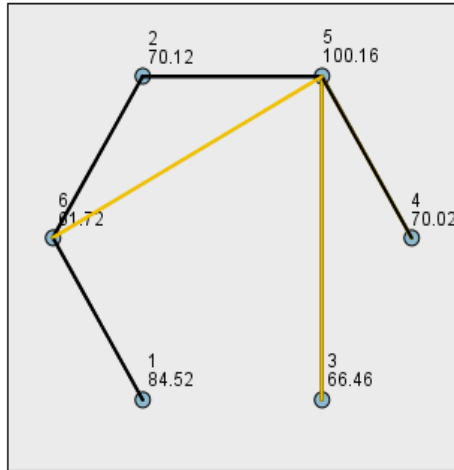


Figure 23 Pairwise comparison of mean rubbing rates of all otters. Yellow lines signify significant differences in time spent rubbing. 1=Benny, 2=Delmar, 3=Digger, 4=Hunter, 5=Louie, and 6=Maya. Louie spent significantly more time rubbing than did Digger and Maya.

Sniffing

Sniffing is a form of receiving information by river otters (Gorman et al. 2006).

An Independent-Samples Kruskal-Wallis Test revealed statistical differences in sniffing frequencies of individuals ($H=16.280$, $df=5$, $p=0.006$; Figure 24). A post-hoc pairwise

comparison confirmed significant differences between individuals. Louie sniffed

significantly more often than Digger, while there was little differentiation among all other individuals (Figure 25).

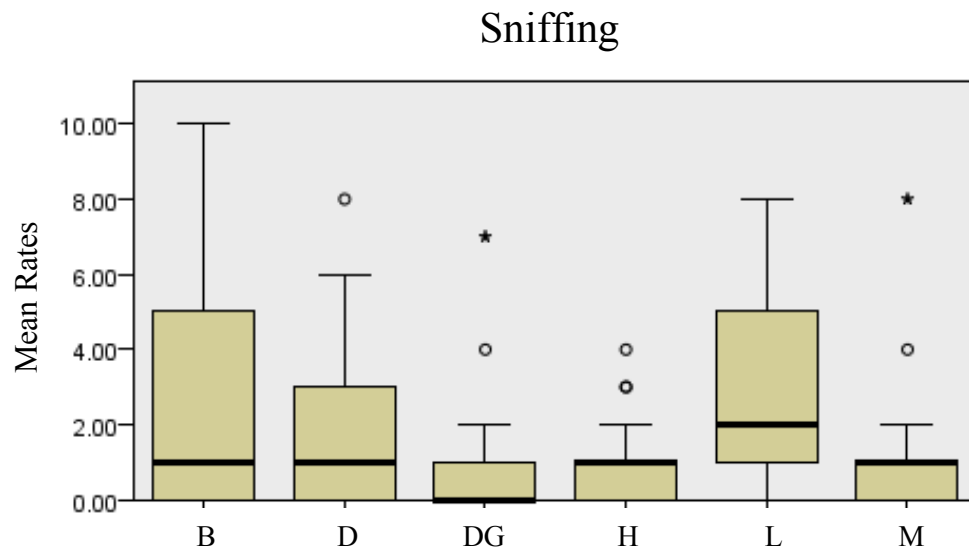


Figure 24 An Independent-Samples-Kruskal Wallis Test revealed significant differences in sniffing by individuals. $H=16.280$, $df=5$, $p=0.006$. Circles represent outliers approaching the 95% confidence level; asterisks indicate values outside those expected of a normal distribution.

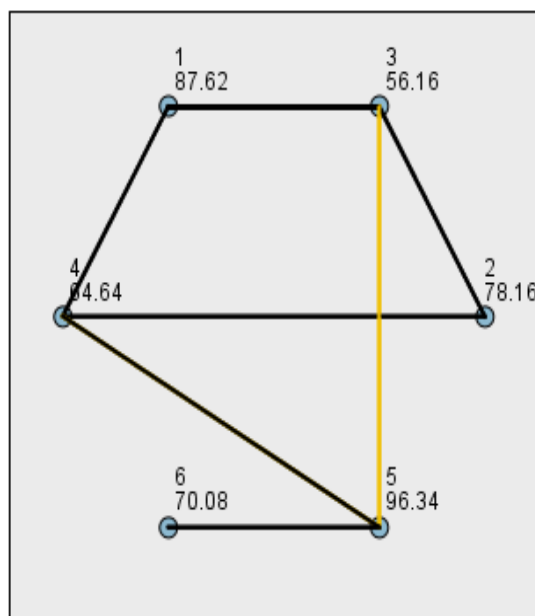


Figure 25 Pairwise comparison of mean sniffing rates of all otters. Yellow lines signify significant differences in time spent sniffing. 1=Benny, 2=Delmar, 3=Digger, 4=Hunter, 5=Louie, and 6=Maya. Louie spent significantly more time sniffing compared to Digger.

Latrine Use

Because of the importance of latrine sites to communication, and as an area where social behavior occurs, I expected to see higher rates of social activity occur more often terrestrially than aquatically. However, Maya and Benny were the only otters seen using latrine sites on exhibit. Defecation was performed a total of 12 times during the study and in two specific locations in the exhibit: grid 1-tier 4, and grid 3-tier 4. Maya and Benny sniffed defecation sites prior to, and after defecating.

Foraging, Aquatic and Terrestrial

In the wild, male river otters will cooperatively forage in order to catch higher quality resources (Blundell et al. 2002). In captivity, foraging occurred both aquatically and terrestrially by males and the female. Overall, the otters spent more time foraging in the water than they did on land ($X^2=56.926$, $z_{aq}=5.36$, $z_{tr}=-5.33$, $df= 1$, $p<0.00001$).

An Independent-Samples Kruskal-Wallis Test compared time spent by each individual foraging in the water and revealed that there was a significant difference in time spent foraging in the water ($H=11.391$, $df=5$, $p=0.044$; Figure 26). Although, it appeared as though Delmar spent the most time foraging in the water, a post-hoc pairwise comparison showed that there were no differences found in rank among individuals (Figure 27).

Terrestrial foraging occurred when food items were released at random into the exhibit. An Independent-Samples Kruskal-Wallis Test revealed significant differences in

terrestrial foraging behaviors ($H=26.75$, $df=5$, $p=0.000$; Figure 28). A post-hoc pairwise comparison revealed that Benny spent significantly more time foraging terrestrially than Digger, Hunter, and Maya, but showed little variation between Louie and Delmar (Figure 29).

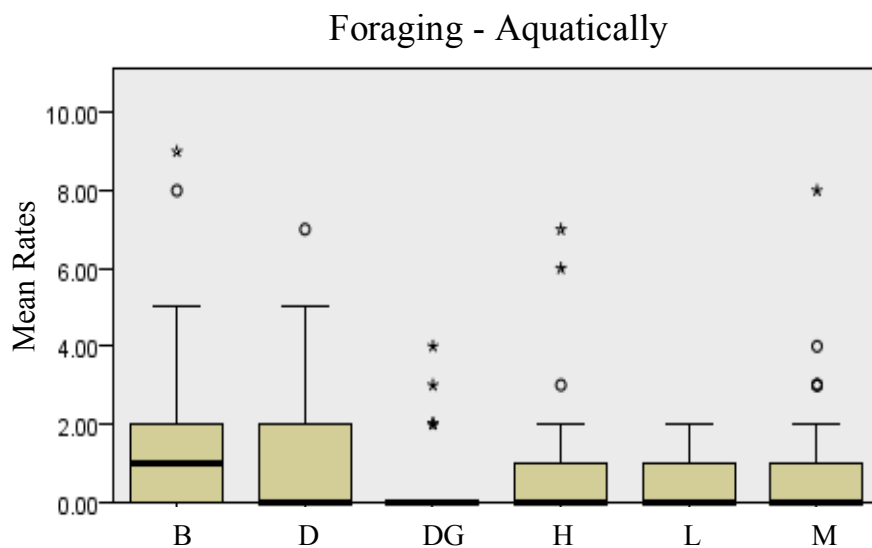


Figure 26 An Independent-Samples Kruskal-Wallis Test compared time spent by each individual foraging in the water. $H=11.391$, $df=5$, $p=0.044$. Circles represent outliers approaching the 95% confidence level; asterisks indicate values outside those expected of a normal distribution.

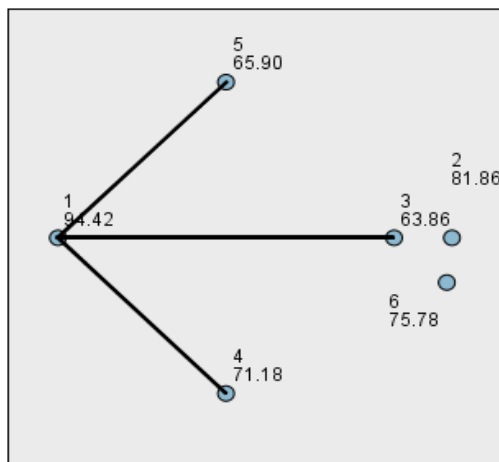


Figure 27 Pairwise comparison of mean aquatic foraging rates revealed that there is more variation in individual rates, and that no two pairs of values showed significant differences.

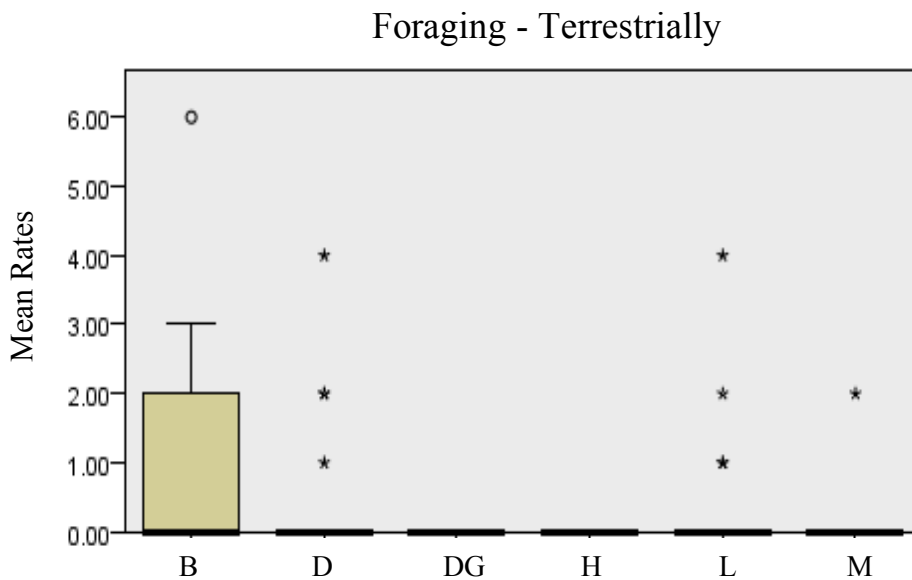


Figure 28 An Independent-Samples-Kruskal Wallis Test revealed significant differences in terrestrial foraging by individuals. $H=26.75$, $df=5$, $p=0.000$. Benny spent significantly more time foraging terrestrially than other otters. Circles represent outliers approaching the 95% confidence level; asterisks indicate values outside those expected of a normal distribution.

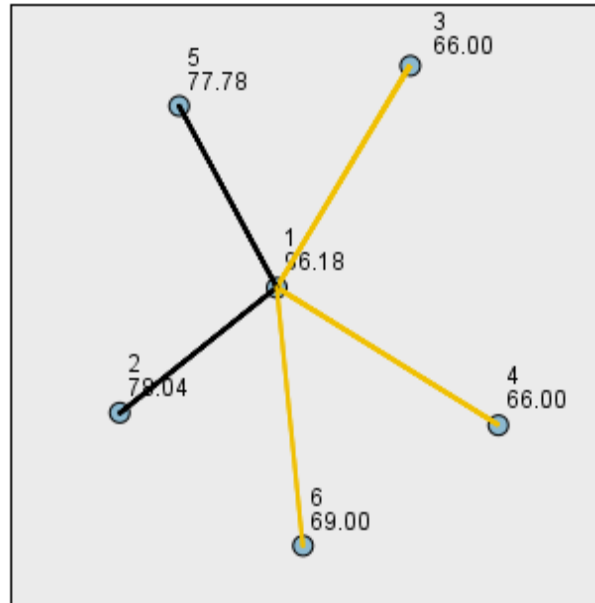


Figure 29 Pairwise comparison of mean terrestrial foraging rates of all otters. Yellow lines signify significant differences in time spent foraging terrestrially. 1=Benny, 2=Delmar, 3=Digger, 4=Hunter, 5=Louie, and 6=Maya. Benny spent significantly more time foraging terrestrially than Digger, Hunter, and Maya, but showed little variation between Louie and Delmar.

Swimming

Although, swimming was performed both solitarily and socially, it appeared that most swimming was social. Solitary swimming appeared to be performed most often by Maya, Louie and Benny (Figure 30). Maya and Benny were often recorded performing stereotypical swimming patterns in grid 0-3. They were also seemed to be swimming in contact with or in close proximity to other individuals more often than any other otter (Figure 30). Hunter and Digger appeared to perform swimming behaviors the least often.

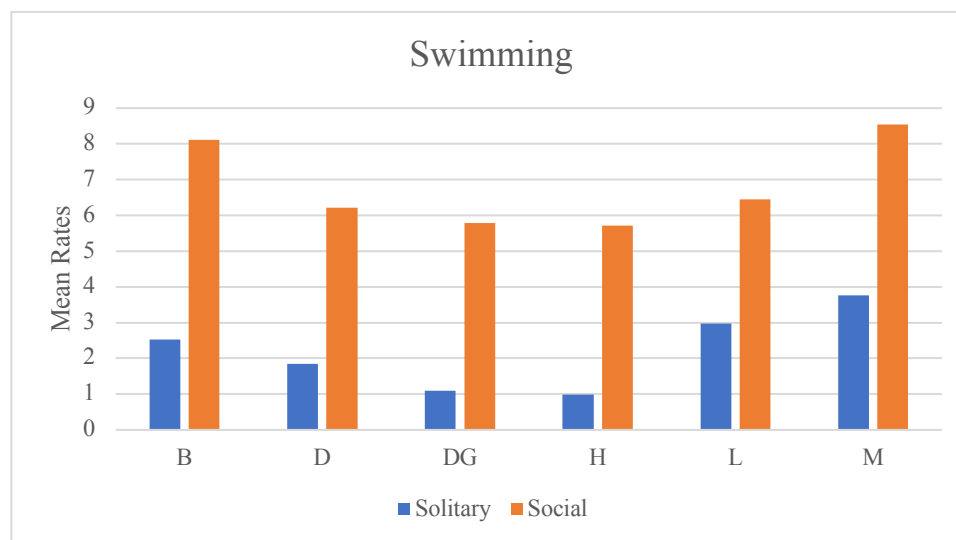


Figure 30 Mean rates of solitary and social swimming by each otter

Wrestling, Aquatic and Terrestrial

Wrestling was an affiliative behavior performed between river otters and occurred terrestrially and aquatically. A residual analysis revealed that the otters mean rates of wrestling bouts were higher in water than on land ($X^2=793.651$, $z_{aq}= 19.92$, $z_{tr}= -19.92$, $p<0.00001$). An Independent-Samples Kruskal-Wallis Test revealed that there was a significant difference in aquatic wrestling behaviors among individuals ($H=12.131$, $df=5$, $p=0.033$; Figure 31). Digger performed aquatic wrestling behaviors more often than any other individual. Despite this overall difference, a post-hoc pairwise comparison showed that no two otters differed significantly from each other (Figure 32).

Terrestrially, this behavior was recorded when the focal animal would mount and roll with one or more individuals on land. An Independent-Samples Kruskal-Wallis Test compared rates of terrestrial wrestling and found significant differences ($H=20.110$, $df=5$,

$p=0.001$; Figure 33). A post-hoc pairwise comparison revealed a difference in ranks; Louie performed terrestrial wrestling behaviors more often than Delmar, Digger, and Maya (Figure 34).

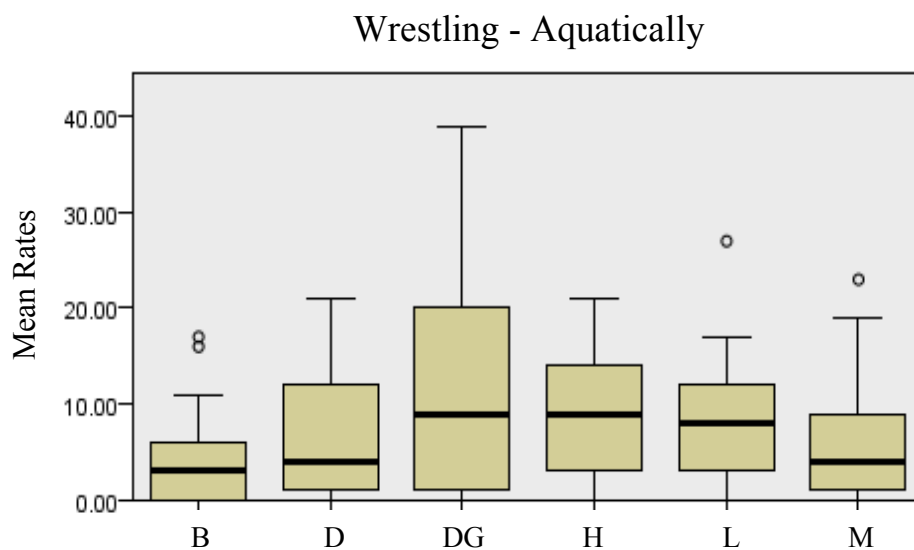


Figure 31 An Independent-Samples Kruskal-Wallis Test revealed that there was a significant difference in aquatic wrestling behaviors among individuals. $H=12.131$, $df=5$, $p=0.033$. Digger wrestled aquatically significantly more than Benny, Delmar, and Maya. Circles represent outliers approaching the 95% confidence level; asterisks indicate values outside those expected of a normal distribution.

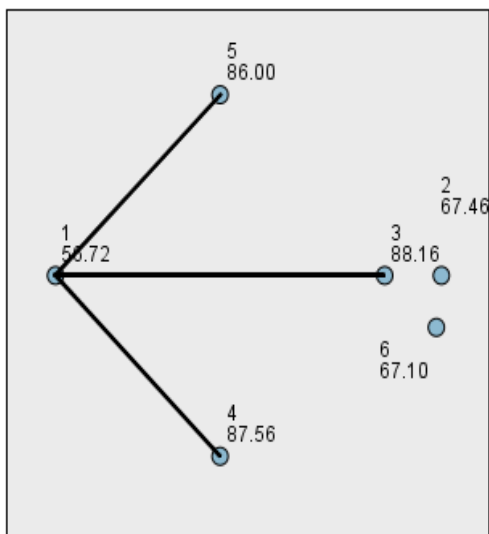


Figure 32 Pairwise comparison of mean wrestling rates of all otters in water. 1=Benny, 2=Delmar, 3=Digger, 4=Hunter, 5=Louie, and 6=Maya. Otters did not show significant differences in ranks.

Wrestling - Terrestrially

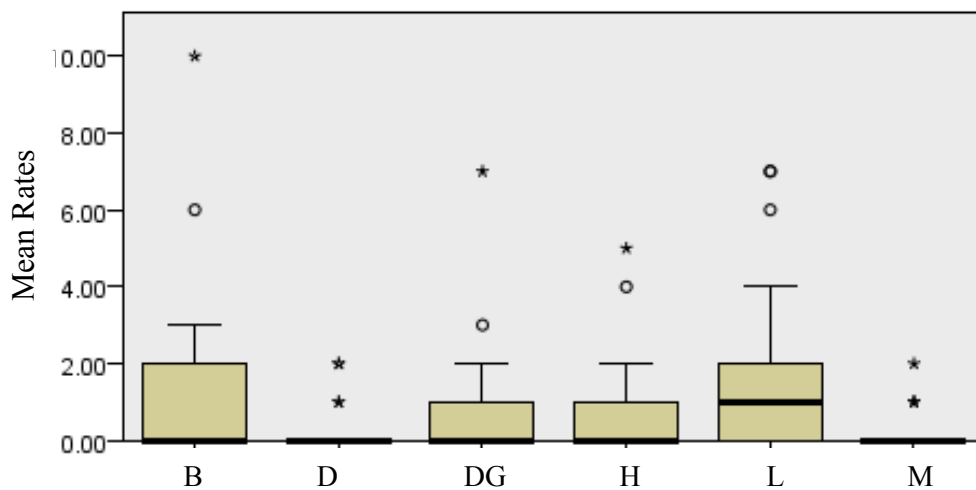


Figure 33 An Independent-Samples Kruskal-Wallis Test revealed that there was a significant difference in terrestrial wrestling behaviors among individuals. $H=20.110$, $df=5$, $p=0.001$. Louie spent more time wrestling, terrestrially, than any other otter. Circles represent outliers approaching the 95% confidence level; asterisks indicate values outside those expected of a normal distribution.

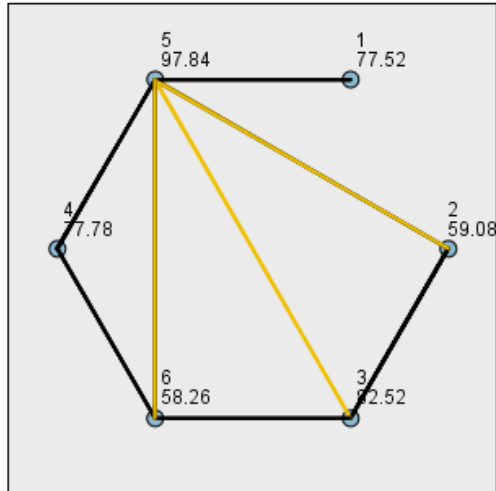


Figure 34 Pairwise comparison of mean wrestling rates of all otters on land. Yellow lines signify significant differences in time spent wrestling. 1=Benny, 2=Delmar, 3=Digger, 4=Hunter, 5=Louie, and 6=Maya. Louie spent more time wrestling on land than Delmar, Digger, and Maya.

DISCUSSION

Social Determinants

The mustelid family is the largest family within order Carnivora. Members of the mustelid family are born hunters, asocial, and known for their diverse habitats, being found all over the world (Nowak 1991). Among the mustelids is the North American river otter, *Lontra canadensis*. The North American river otter lives in various water systems around the United States and serves as an apex predator and biomarker in riparian habitats (Blundell et al. 2005). Among its relatives is *Enhydra lutris*, the sea otter, which is often found coexisting alongside the North American river otter in coastal habitats (Nowak 1991).

Mustelids are not considered social animals within the mammal class, yet the North American river otter and sea otter both show atypical behavior within the mustelid family, having complex social networks (Green et al. 2015, Riedman & Estes 1990). In both species of otters, males are known to be more social than females, and this sociality mostly takes the form of cooperative foraging (Blundell et al. 2002, Riedman & Estes 1990). Females of both species are considered asocial, with the exception of association with males during the breeding season and within their family units, which include the mother and her offspring. Thus, resource availability and foraging behaviors influence sexual segregation in wild populations of river otters.

Foraging

From previous studies, we know that male river otters are more social than females for foraging purposes (Lariviere & Walton 1998, Blundell et al. 2002). Males in wild populations are able to capture higher quality resources with the help of male conspecifics in bachelor groups (Blundell et al. 2004). In contrast, females with offspring have been known to forage solitarily to evade infanticide, resource theft, or while teaching their young to forage (Albeke et al. 2015, Riedman & Estes 1990). However, on occasion, lone females have been known to join small mix-sexed foraging groups to acquire higher quality fish (Blundell et al. 2002).

Foraging, as a social determinant, is also present in male sea otters, *Enhydra lutris*, as well. Nearly 98% of foraging behavior in sea otters is performed solitarily, with the exception of small male bachelor groups, which cooperatively forage like the male

river otter (Blundell et al. 2002, Riedman & Estes 1990). Male sea otters will also exploit females by performing hostage behavior, holding a female's young underwater until she trades over her food source (Riedman & Estes 1990). Although this kind of hostage behavior has not yet been documented in wild river otter populations, but is an apparent factor as to why females with offspring avoid males during foraging events.

Although, foraging groups exemplify sexual segregation in wild river otter populations, my observations of a captive group showed that sociality was equal across both sexes, thus rejecting the first hypothesis, that males in the group would show higher rates of sociality than the female, Maya. Overall, foraging, both aquatically and terrestrially, occurred most often solitarily in captivity. This suggests that little-to-no cooperative foraging occurred within this captive setting, terrestrially or aquatically. This difference in behavior between wild otters and the captive group is probably because resource availability was not a limiting factor in captivity; the captive otters were fed by their keepers, mostly while off-exhibit, and had few opportunities to forage during the periods when I observed them.

Part of the explanation for why I did not find a difference in sociality between the males and female may be that while the female, Maya, was an adult and had been bred once, she was not pregnant during the time of the study, nor was she raising young. Although, gender did not influence sociality in captivity, sociality was influenced by degree of relatedness between individuals, time of day, and location.

Kinship Bias

Although, neither species is known to exhibit kinship bias towards conspecifics, we did find that (Blundell et al. 2002, Riedman & Estes 1990), I did find that, in captivity there was kinship bias being exhibited between the siblings, Maya and Benny. I found that Maya and Benny both spent more time interacting with one another than with any other individuals in the romp, which could be attributed to their age and limited habitat range.

Maya and Benny were both between 3-4 years of age at the time of the study, and therefore adults as most river and sea otters reach sexual maturation between 2 and 3 years (Stenson 1985, Riedman & Estes 1990). However, Benny had not yet had an opportunity to mate. In contrast, Maya was bred for the first time prior to the study. Signs of a successful implantation would not be apparent until 9-12 months later, due to delayed implantation (Reed-Smith 2001, Riedman & Estes 1990). However, a year later, Maya had not produced a litter of kits, suggesting a failed reproduction. Being in captivity may have had an impact on her reproduction, given that there is a 48% probability of success rate in reproduction of many captive species (Farquharson et al. 2018).

This unsuccessful reproduction, as well as the continuing close relationship between Maya and Benny, could also be attributed to home range size. In wild river otter populations, sexually mature females will stay within close-knit home ranges away from males, while males will disperse from the natal group at or around 12-13 months of age

(Blundell et al. 2005). Similarly, in wild sea otter populations, females with young offspring will often evade males, because dominant males have been known to coerce lactating females into forced copulation, resulting in physical damage to the female or death to her offspring (Riedman & Estes 1990). Maya's failure to reproduce could be attributed to her limited space to evade males within captivity and could also explain her aggressive behavior towards Louie.

Time of Day

In the wild, river otters are more active during crepuscular hours due to human activity near home ranges (Green et al. 2015). Water pollution from human urbanization and development has been shown to cause a reduction in the presence of river otter populations (Potter et al. 2017, Godwin et al. 2015). Sea otters exhibit similar activity patterns, often seen resting during the day, and foraging in the early morning and early evening (Riedman & Estes 1990). Previous studies found that variation in fish availability caused noticeable spikes in sea otter activity levels during crepuscular periods (Riedman & Estes 1990). Similarly, the captive group of river otters were more social during the early evening period, thus supporting my second hypothesis. This was the case even though the otter keepers at the Tennessee Aquarium introduced food items during the middle of the day to keep the captive group active.

Communication

The captive romp of otters performed a variety of behaviors on land. Many of these behaviors were social. An important factor in social behavior is communication.

River otters use vocalizations and olfactory cues as means of communication (Blundell et al. 2005, Mcshane et al. 1995). Thus, in the wild, latrine sites serve as an important area where information can be exchanged between individuals (Gorman et al. 2006).

Therefore, I hypothesized that captive otters would perform a higher frequency of social behaviors, especially those involving communication, in the terrestrial portion of the exhibit with these areas functioning like latrine sites do for wild otters. My data contradicted my hypothesis. River otter sociality occurred more often in the aquatic area of the exhibit, as opposed to the terrestrial area.

A factor that may have contributed to a lower rate of social behavior on land was a lack of latrine use in captivity. Maya and Benny were the only two otters that were recorded using the latrine sites during the study. Combined, both otters used the latrine sites a total of 12 times. The captive romp also had access to an off-exhibit area, which provided them with another area to defecate.

In order to utilize latrine sites as an area of information exchange, rubbing and sniffing behaviors are performed at these sites (Gorman et al. 2006). Information received by latrine use could be resource availability, reproductive status, or the identification of an individual (Blundell et al. 2005). Again, the youngest otters and siblings, Maya and Benny were the only two to use latrine sites on exhibit. However, because Maya and Benny were related, it is possible that their utilization of latrine sites could be attributed to receiving information about resource. The captive group was often fed a variable diet, which included: melons, clams, fish, cat food, and the occasional block of ice. The

exhibit was also cleaned every two weeks, removing information from previously marked areas. Therefore, river otters are able to receive new information about resources fairly often.

Previous studies also indicate that sniffing, rubbing, and latrine use work synergistically in the exchange of information among river otters (Green et al. 2015). Thus, indicating that they may be receiving information from locations that were rubbed, or scent marked, outside of latrine sites. Rubbing one's body against a log, a rock, or the ground of the exhibit were an indication of scent marking. Male river otters have sexually dimorphic pedal glands, which when rubbed against an object, deposit secretions which relay information about sexual status (Green et al. 2015). Otters would often sniff prior to, and after, rubbing a specific item or location. This may also have been in part due to enrichment items set out by the aquarium keepers, which included objects that were sprayed in various scents to entice the otters.

Affiliation and Aggression

Although, latrine use was not frequent, there were other social behaviors that occurred terrestrially including allogrooming, wrestling, and vocalizations. Vocalizations occurred on multiple occasions in an affiliative, or neutral context. For example, in some cases the focal animal would make a vocalization which sounded like a bark, and a conspecific walked towards the focal animal within five seconds after the call was made. However, vocalizations also occurred in aggressive contexts. Prior to attacking Louie, the female, Maya, would make a loud screeching noise followed by charging at him. Benny

made the same vocalization prior to attacking Louie as well. Instances of aggression among otters is not uncommon in wild populations, because of limited resources and territory (Riedman & Estes 1990). However, instances of aggression were rare in captivity, which may be attributed to a plethora of resources and space, both on and off exhibit, for individuals to occupy.

I also recorded multiple bouts of grooming behaviors among individuals. Grooming enables river otters to rid hair of debris, realign hair shafts, distribute oils, and blow air into the hair (Liwanag et al. 2012). The overall status of river otter hair is vital to its survival in colder climates. Grooming can also be performed socially. Allogrooming is an important social behavior that enables bonds between individuals to be established and maintained (Liwanag et al. 2012). Allogrooming was performed most often by males in the captive group, specifically Digger and Louie. Allogrooming was performed more often than self-grooming, suggesting an important role in the maintenance of social bonds between individuals in the captive group. It is important to maintain social bonds in a captive group, because these individuals are housed in a smaller home range than they would be in the wild. Allogrooming as a means of bond maintenance could also explain the group's rare instances of aggression, overall.

Another affiliative behavior, which could have attributed to the group's lack of aggression, is wrestling. Wrestling is an affiliative behavior, which is considered an act of play between individuals. This behavior occurred most often in the water, which could explain the otters' high rates of sociality in the aquatic portion of the exhibit.

Overall, my study showed that, in captivity, North American river otter sociality appears to vary from that of wild river otters in terms of which sex is most social and in use of latrines, but is similar in how sociality varies by time of day. Individual behaviors contributed insight and support of the various social determinants of this captive group.

IMPLICATIONS

Overall, this study provided important information about the management of this captive river otter group. Much of the group's behavior was analogous to that of wild populations, which suggest the high level of maintenance and care dedicated to the well-being of this captive population. This study also provides important information about the social dynamics of mix-sexed groups of river otters in captivity. Despite wild populations showing high levels of aggression, due to sexual segregation, under the proper conditions, mix-sexed groups in captivity can thrive without there being high rates of aggression between individuals. It is important to note that high rates of aggression between mix-sexed groups are most likely when offspring are present, and when resources and space are limited. It would be interesting to test rates of aggression in the same population, had Maya been pregnant. However, this study was conducted in an exhibit, which provided the group with plenty of space to occupy, accompanied by an abundance of resources and enrichment items to keep the otters busy.

CONCLUSION

Overall, this study provides important insight into the complex social dynamics of the North American river otter in captivity and can contribute to the conservation efforts

of this species. The study began the process of filling a gap that wild studies had not yet reached. Further studies are needed to dissect affiliative, social behaviors outside of the realm of cooperative foraging in river otters. Little-to-no research on age and behavioral development has been done on the North American river otter. Captive studies such as these could provide further understanding into river otter behavior throughout different stages of development. Moving forward, more detailed, long-term studies are necessary to further understand the social determinants of the North American river otter both in the wild, and in captivity.

Literature Cited

- Albeke SE, Nibbelink NP, Ben-David M. 2015. Modeling Behavior by Coastal River Otter (*Lontra Canadensis*) in Response to Prey Availability in Prince William Sound, Alaska: A Spatially-Explicit Individual-Based Approach. *Plos One*. 10(6).
- Allen ML, Yovovich V, Wilmers CC. 2016 Evaluating the responses of a territorial solitary carnivore to potential mates and competitors. *Scientific Reports*. 6(1).
- Altman, J. 1974. Observational study of behavior: Sampling methods. *Behaviour*. 49(3-4): 227-266.
- Barocas A., Golden H.N., Harrington M.W., McDonald D.B., Ben-David M. 2016. Coastal latrine sites as social information hubs and drivers of river otter fission–fusion dynamics. *Animal Behaviour*, 120:103–114.
- Blundell, G.M., Ben-David, M., and Bowyer, R.T. 2002. Sociality in river otters: cooperative foraging or reproductive strategies? *Behavioral Ecology* 13 (1): 134-141.
- Blundell, G.M., Ben-David, M., Groves, P., Bowyer, R.T., and Geffen, E. 2004. Kinship and sociality in coastal river otters: are they related? *Behavioral Ecology*, 15 (5): 705-714
- Blundell, G.M., Ben-David, M., Kern, J.W., Maier, J.A.K., Brown, E.D., and Jewett, S.C. 2005. Communication in river otters: creation of variable resource sheds for terrestrial communities. *Ecology*, 86 (5): 1331-1345.

- Day C.C., Westover M.D., Mcmillan B.R. 2013. Factors influencing mortality associated with the translocation of northern river otters (*Lontra canadensis*) in Utah. *Western North American Naturalist*, 73(3):357–364.
- Dytham C. 2011. Choosing and Using Statistics. Oxford: Wiley-Blackwell.
- Farquharson KA, Hogg CJ, Grueber CE. 2018 A meta-analysis of birth-origin effects on reproduction in diverse captive environments. *Nature Communications*. 9(1).
- Green M.L., Monick K., Manjerovic M.B., Novakofski J., Mateus-Pinilla N. 2015. Communication stations: cameras reveal river otter (*Lontra canadensis*) behavior and activity patterns at latrines. *Journal of Ethology*, 33(3):225–234.
- Godwin B, Albeke S, Bergman H, Walters A, Ben-David M. 2015. Density of river otters (*Lontra canadensis*) in relation to energy development in the Green River Basin, Wyoming. *Science of The Total Environment*. 532:780–790.
- Gorman T.A., Erb J.D., Mcmillan B.R., Martin D.J. 2006. Space use and sociality of river otters (*Lontra canadensis*) in Minnesota. *Journal of Mammalogy*, 87(4):740–747.
- Hamilton, C.F. 2014. Habitat and seasonal distribution of the North American river otter (*Lontra canadensis*) and vertebrate species assemblages in two protected areas of the Florida everglades. Nova Southeastern University.
- Hansen H., McDonald D.B., Groves P., Maier J.A.K., Ben-David M. 2009. Social networks and the formation and maintenance of river otter groups. *Ethology*, 115(4):384–396.

- Helon D., 2006. Summer Home Range, Habitat Use, Movements, and Activity Patterns of River Otters (*Lontra canadensis*) in the Killbuck Watershed, Northeastern Ohio [dissertation]. West Virginia University. 101 p.
- Lariviere S., Walton L.R. 1998. *Lontra canadensis*. *Mammalian Species*, (587):1.
- Latch EK, Scognamillo DG, Fike JA, Chamberlain MJ, Rhodes OE. 2008. Deciphering ecological barriers to North American river otter (*Lontra canadensis*) gene flow in the Louisiana landscape. *Journal of Heredity*. 99(3):265–274.
- Liwanag HEM, Berta A, Costa DP, Abney M, Williams TM. 2012. Morphological and thermal properties of mammalian insulation: the evolution of fur for aquatic living. *Biological Journal of the Linnean Society*,. 106(4):926–939.
- Martin DJ, Mcmillan BR, Erb JD, Gorman TA, Walsh DP. 2010. Diel activity patterns of river otters (*Lontra canadensis*) in southeastern Minnesota. *Journal of Mammalogy*, 91(5):1213–1224.
- Mcshane LJ, Estes JA, Riedman ML, Staedler MM. 1995. Repertoire, Structure, and Individual Variation of Vocalizations in the Sea Otter. *Journal of Mammalogy*. 76(2):414–427.
- Mench J. 1998. Why it is important to understand animal behavior. *ILAR Journal*, 39(1):20–26.
- Nowak, R. 1991. Carnivora: family Mustelidae. Pp. 1104-1105 in *Walker's Mammals of the World*, Vol. 2, 5th Edition. Baltimore: Johns Hopkins University Press.

- Oldham AR, Black JM. Experimental Tests of Latrine Use and Communication by River Otters. *Northwestern Naturalist*. 2009;90(3):207–211.
- Potter TM, Hanna JA, Freer L. 2017. Human North American River Otter (*Lontra canadensis*) Attack. *Wilderness & Environmental Medicine*. 18(1):41–44.
- Reed-Smith J. 2001. North American river otter: *Lontra canadensis*: husbandry notebook. Grand Rapids, MI: John Ball Zoological Garden.
- Riedman ML, Estes JA. 1990. The Sea Otter (*Enhydra lutris*): Behavior, Ecology, and Natural History. 14th ed. Washington: Fish and Wildlife Services; p. 1–117.
- Scognamillo DG. 2005. Temporal and spatial harvest patterns of river otter in Louisiana and its potential use as a bioindicator species of water quality.
- Sokal R, Rohlf F.J. 1981. Biometry, 2nd ed. San Francisco: Freeman and Co.
- Stenson GB. 1985. The reproductive cycle of the river otter, *Lutra canadensis* in the marine environment of Southwestern British Columbia [dissertation].
- Valiela I. 2001. Doing science: design, analysis, and communication of scientific research. 2nd ed. Oxford: Oxford University Press.
- Weisel JW, Nagaswami C, Peterson RO. 2005. River otter hair structure facilitates interlocking to impede penetration of water and allow trapping of air. *Canadian Journal of Zoology*, 83(5):649–655.