The Vocal Behaviors of North American River Otters

(Lontra Canadensis)

Individual Differences and Shared Repertoires

by

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Abstract

The Vocal Repertoire of Captive North American River Otters *(Lontra canadensis).* Individual Differences and Shared Repertoires

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The current information on the vocal repertoire of the North American River Otter is very limited. To date there have been no direct studies conducted on their repertories. In this study, I examined the vocal behavior of 12 captive river otters. The discriminant function analysis suggests that river otters have 4 distinct call types with 7 sub-call types and one call the *whistle* is unique to one group of pups. The results of the Kruskal-Wallis comparing acoustical structures shows strong evidence for the presence of individuality with some individuals showing greater differences in comparison to the others. I also examined the differences in sexes and age groups, and the results show that unique calls are present, and there are significant differences across groups when comparing acoustical structures. Finally, I examined the uses of vocalizations, and the results show a positive correlation between the duration, max frequency, and max power of the call and the arousal state of the individual producing the call. Specific call types also showed tendencies to be produced when the individual was in a particular interaction (asocial or social) and when in a particular arousal state.

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Bear Mountain Zoo (Palisades Park Conservancy): Edwin McGowan (Director) & Melissa Gilmer (Head Trainer)

Atlantis Aquarium: Ann Yauillo (Head Curator) & Candyce Paparo (Head Trainer)

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Vocalizations and their uses in otters

Introduction

Communication can be defined as a 'behavior involving signals" with a signal being something that has evolved by natural selection to transmit information. Vocal communication studies focus on highly social species because auditory communication generally requires two or more individuals. Analyzing the structure and context of vocal systems has helped reveal how members of a social group maintain cohesiveness. In British Columbia Killer Whales within pods there are unique dialects developed to assist in distinguishing between pod and non-pod members *(Deecke, 2000)*. Sperm whales use cultural transmission and learning to create the unique dialects seen in their clans (*Rendell, 2003).* Vocal individuality in harp seal pups is an important factor that assists the mother to correctly identify and locate her offspring (*Van Opzeeland, 2004).* These studies have identified important factors shaping social behaviors. It is also important to extend these studies to asocial and semi-social species to develop further insights into the function of their behaviors.

I studied the vocalizations of North American River Otters because what is known about their social and vocal system is limited and often incorrect. River otters have highly variable social structures and examining their vocal communication can illuminate our understanding of their social systems. Otters have been observed living various lifestyles: solitary, temporary cohesions, or more permanent family groups. Solitary otters have been observed interacting with their environment, or playing with live prey. In temporary cohesions otters work together to increase their prey capture, or engage in synchronized behaviors. In permanent family groups females assist one another in the rearing of young. Since there are such great differences in social behaviors within river otters, it would be expected that vocal communication would vary greatly. In studying their vocal system we can begin to get a better and more accurate understanding of their social behaviors.

I studied river otters in a captive setting in order to (a) observe behaviors of individuals in various interactions (b) describe a vocal repertoire (c) measure variation in vocal structure among animals (d) determine the vocal differences across sexes and between adults and pups (e) identify the association between vocalizations and the arousal state of the otter**.**

Background-Related Species

Of all the species of otters the Giant Otter (*Pteronura brasiliensis)* is the most social, and also the most vocal. They form large family units with up to 16 members and communicate extensively. Giant otters use various forms of communication, such as: visual, tactile, olfactory, and vocalization to maintain group cohesiveness. The vocal repertoire of the Giant Otter in Igapo forests has shown that their repertoire consists of four call types: the *HAH, Purr, Scream, and Snort (Bezzera, 2009).* The authors suggest that calls vary with the individual's behaviors, social rank and age. Giant Otters have an elaborate vocal system, and use scent communication as well to relay information on social status, sexual status, and for territorial purposes *(Leuchtenber, 2008).*

Sea Otters *(Enhydra lutris)* are variable in their social structures. They can live solitary lifestyles, but have been observed forming "rafts" as large as 2000 members. This social behavior may be an anti-predation strategy *(Kruuk, 2006),* as Sea otters are highly susceptible to killer whales and this may reduce predation risk. Although, the sea otter has its vulnerabilities, evidence suggests that it copes via complex behaviors. They have been observed showing affection by clasping paws, and studies confirm that they use tools, which are both behaviors normally considered 'cognitive' in primates and other animals.

Sea otter vocal systems are adapted for short-range communication *(McShane, 1995).* The calls are generally low in frequency and amplitude, and commonly used in close contact interactions. The repertoire is made up of 10 vocal categories, and calls unique to the adults and pups are present. For instance, the scream was emitted by the mother and pup and was used frequently when they were separated.

The European (Eurasian) otter *(Lutra lutra)* inhabits vast areas of Europe and Asia. They live a predominant solitary lifestyle. The European otter vocalizes in close contact with con-specifics *(Gnoli, 1995).* Seven calls have been identified in their repertoire, and two calls (blow and cry) may relay aggression, since they are made during defensive or threatening situations.

The Asian small-clawed otter *(Aonyx cinerea)* is gregarious and docile making it an excellent candidate for zoo exhibits. Deborah Fripp worked with two groups of Asian small-clawed otters in Dallas Zoo. In the preliminary studies seven call types were identified, based on the visual appearance of the spectral analysis. Vocal rate varied extensively, and the vocals can be distinguished using duration and frequency characteristics.

Otter phylogeny suggests that the Giant Otter and the Sea Otter's lineages split early contributing to the morphological and behavioral differences they exhibit in comparison to other otter species *(Kruuk, 2006)*. Preliminary comparisons of their vocal repertories indicate that the scream of the sea otter and the snort of the giant otter elicit behavioral responses from receivers.

Natural History of North American River Otters

There are 13 species of otters that make up the Subfamily *Lutrinae* of the Family *Mustilidae* and the distribution, ecology, and behavior vary among the groups. Otters can be found throughout the world, so they are highly adaptive to various environments. The North American River Otter *(Lontra canadensis)* is found throughout North America, Alaska and Canada. River Otters are versatile in both terrestrial and aquatic environments, they use the aquatic environment to hunt and play, all other activities occur on the land. The otter although well adapted to aquatic environments, still resemble the terrestrial weasel and they physically have the characteristics that Mustelids are known for. Chanin *(1985)* describes otters "as animals that have long torpedoed shaped body with short legs, and they walk with the humpbacked gait that is typical to the family".

They are sexually dimorphic. Males and females generally are similar in length weighing about 11-40lbs, but the males have a higher body mass. However, other species like the Eurasian Otter exhibit greater sexual dimorphism *(Kruuk, 2006)*. The fur color is usually dark brown, or some variation of it. The face is round with small ears and a short snout. Their nose is wide and adapted for scent communication. River otters have short legs that are efficient in both terrestrial environments and aquatic environments *(Williams, 2002).* The hind legs are strong allowing the otter to stand up to get a better view of its surroundings.

The life expectancy in the wild is 15 years, but the oldest otter in captivity died at 25 years old. Predation is not a great threat but their known predators are coyotes, bobcats and wolves, with the pups being very vulnerable to eagles and other birds of prey. Their greatest threats are pollutants, and fur trappers. During the mid-20th century they disappeared from many areas due to these factors, but their numbers have increased with the help of re-introduction phases and trapping regulations.

Feeding

River otters feed in fresh waters and can be found by lakes, streams and of course, rivers. River otters have teeth that are adapted for gripping and slicing, and they hold their prey down with the paws when ingesting. Prey consists of various types of crustaceans, invertebrates, and fish. They have also been known to feed on frogs, small birds and mammals. River otters have adaptations that make them excellent hunters in the aquatic environment. Their feet are fully webbed and adapted for swimming reaching speeds of up to 7 mph. Otters can dive up to 60 feet to capture prey, and when diving flaps cover their ears and nostrils to prevent water intake. They can stay submerged for up to 4 minutes and have acute eyesight in the water to search for prey. The fur coat acts as an insulator keeping the skin virtually dry due to the thick hairs that crisscross each other making the coat waterproof.

Scent Communication

River otters have large home ranges that are usually found around shorelines. They are not migratory animals but cover large distances in a day. Males particularly travel long distances and their home ranges are approximately three times larger than that of the female (*IUCN Otter Specialist Group, 1992).* Large home ranges cause a lot of territorial overlapping between otters. Therefore, scent communication is vital in maintaining territorial space. Rostain *(2003)* suggests that otters scent mark (spraint) to relay species identity to con-specifics, establish and maintain territories, and in males it relays social status. River otters inhabiting coastal environments (*Ben-David, 1998)* visit latrine sites often and spend a lot of time depositing repeatedly. Kruuk *(2006)* describes, "the animals appeared to be very adept at avoiding confrontation, a phenomenon…in which scent communication must play a dominant role". These studies suggest that scent communication is vital in maintaining the spatial organization of home ranges, and the purpose is to avoid confrontation.

Social Behaviors

There is not a set description of the social behaviors of otters in the literature. Their social structures are as variable as the ecological niches they inhabit. On one extreme there is the solitary European Otter and on the other there is the highly social Giant Otter. The other species tend to follow a more flexible social structure. River otters fall into this type of social category. Various social groups have been observed including: bachelor groups, mixed adults groups, extended family groups, and groups with helper animals *(Rostain, 2003).* However, the dynamics of the groups can change seasonally and are not as cohesive as highly social species (i.e. marine mammals, primates).

Play is a common social interaction; both in the wild and in captivity otters spend a great deal of time playing. When otters play they wrestle, chase each other and vocalize. In the water they perform acrobatic wrestling and engage in synchronized swimming. They also can form large groups and engage in synchronized sliding down a mountain covered in snow *(Kruuk, 2006)*.

Mating and Reproduction

Females undergo delayed implantation, which allows them to mate but delay implantation until environmental conditions are optimal. After mating the males contribution to the offspring is complete. Females rear the young alone or with related females. They generally give birth annually to 1-5 altricial pups that may remain with the mother from 10 months to 2 years. The females are highly protective of their young, and may engage in physical confrontations with males that are potential threats.

Chapter Two

Data Collection: Methods & Analysis

I collected data in 5 zoos, housing captive North American River Otters. The zoos were located in Connecticut, New Jersey, and New York. Sessions were conducted under daytime and overnight conditions. Collecting data under both conditions allowed for a complete view of the otters behaviors over the entire day.

For 'Daytime' protocol a session consisted of 30 minutes of continuous recording of all the individuals at a given site. I conducted 1-2 sessions at random times and days per visit, however I avoided conducting sessions while trainers were cleaning the exhibit or back areas, which was usually early morning and late afternoon. I used a Handheld DV Camera with a microphone to capture daytime footage.

For 'Overnight' protocol a session consisted of 15-24 hours of continuous recording of all the individuals at a given site. I conducted the sessions when the zoo was closed and void of any visitors or staff. I randomized the days that sessions were conducted, but sessions occurred for 3-7 consecutive nights. The set up consisted of 1-3 infrared cameras (varied based on number of indoor dens), 1 Omni-directional microphone with 30ft diameter range, and 1 Digital Video Recorder (500GB).

Study Sites & Data Collection Set-ups:

TURTLE BACK ZOO*:* Turtle Back Zoo is located in West Orange, NJ. It housed 2 adult otters and 1 young otter. During the time of the study, the otters were undergoing introduction and reintroduction phases. Therefore, I spaced my sampling of these otters to span out throughout a year to ensure that enough sessions were conducted with all three otters present.

Remus: Adult Male, Born March 15, 1997 at Flag Acres Zoo in Hoosick Falls, NY. He was 11 years old at the time of the study. He was peer reared for the first 3 years until he was transferred in 2000 to Turtle Back Zoo In 2006 he was sent out for mating and sired 3 offspring. Remus passed away in September 2010 from complications caused by an abscess on his liver.

Leveau: Adult Female, Born ~Feb 15, 1990, she was ~18 at the time of the study. Leveau had a complete hysterectomy, and suffered from glaucoma. She was wild born and parent reared, but entered captivity early. She spent time at Bayon Otter Farm in Louisiana and Lincoln Park Zoo in Illinois. She was transferred to Jacksonville Zoo in Florida in 2003 and remained there until she was transferred to Turtle Back Zoo in Oct 2007. She remained at Turtle Back Zoo until her passing in May 2009 due to old age.

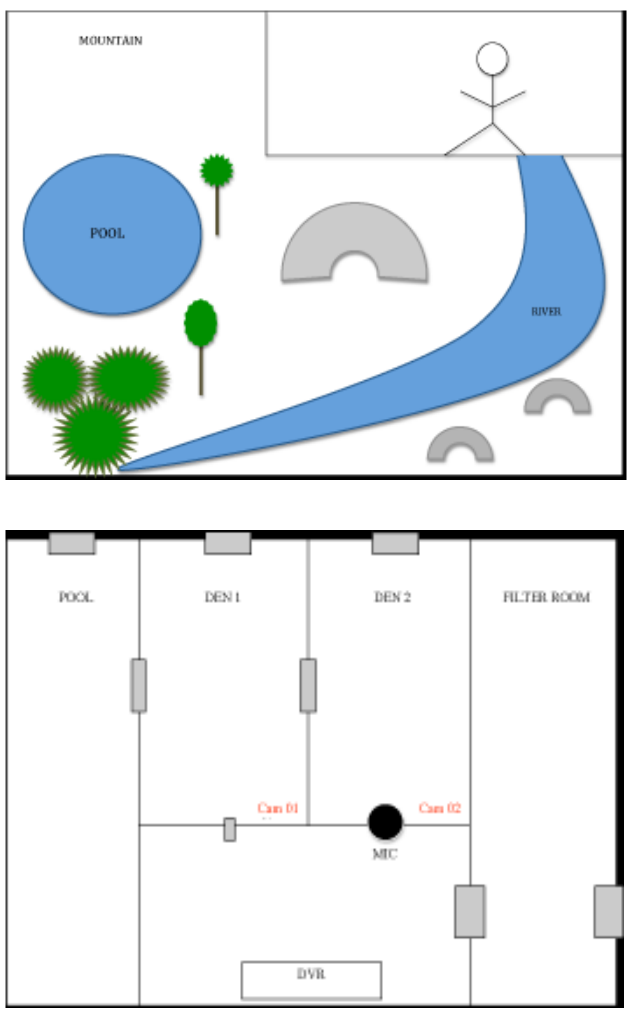
Kassie: Young female, Born March 2, 2007 at Beardsley Zoo, parent reared by Rizzo and Delaney. She was 10 months old at the beginning of the study. She spent the first 10 months in a family unit with her parents and 2 sister siblings. She was transferred to Turtle Back Zoo in January 2008.

When I first began the study Turtle Back Zoo only housed (1) male otter (Remus). Leveau was brought to Turtle Back shortly after but kept separate from Remus for 30 days. Introduction occurred around November 2007, but Remus was transferred out of the facility in January 2008 for approximately 3 months for mating purposes. Upon his return, he was isolated in the hospital at the zoo for a 30-day incubation period to ensure a clean health record. During the time that Remus was out for mating, Kassie was brought to Turtle Back, and the introduction phase began with Kassie and Leveau. It wasn't until May 2008 that all 3 otters were in the facility together and passed the introduction phases.

Daytime Set-up: (Figure 2.1a) I conducted one session per day; however, on a few occasions I randomly conducted a second session. One session was cut short due to construction work that was being done by the exhibit, and two sessions only consisted of a 10 minutes stimulus exercise conducted by the trainer.

Nighttime Setup: *(Figure 2.1.b)* Two infrared cameras were used since there were two dens. Because this was my first site, I ran the first 15 sessions (11/07-05/08) with the cameras placed outside of the dens to ensure that the otters were not destructive and it would not be too invasive to place them inside the dens. I then placed the cameras inside the corners of each den facing diagonally, which allowed for a completely non-obstructed view. There was a third den that was filled with water, which made access difficult so there was no camera placed in that den. Recordings made from 11/07-02/08 varied in length from 6 to 24 hours of non-stop recording. I used these sessions as a grace period to determine the actual storage capability of the DVR on various preferences. Every session thereafter entailed non-stop recording for 15 hours, from 4:00pm to 7:00am. However, the dates were always randomized.

Figure 2.1: (a) Depiction of outdoor exhibit (b) indoor exhibit at Turtle Back Zoo.



(a)

(b)

BEARDSLEY ZOO: Beardsley Zoo is located in Bridgeport, CT. It housed an adult mating pair. The female became pregnant therefore, I extended my collection to 9 months to include the birth and collect data on the vocal behaviors of the pups.

Rizzo: Adult male, captive born in 2001. He was approximately 7 years old at the time of the study. He is part of a mating pair with Delaney. Had sired 2 known litters at the beginning of the study. He sired one litter during the study and one after the study. He is also the father of Kassie.

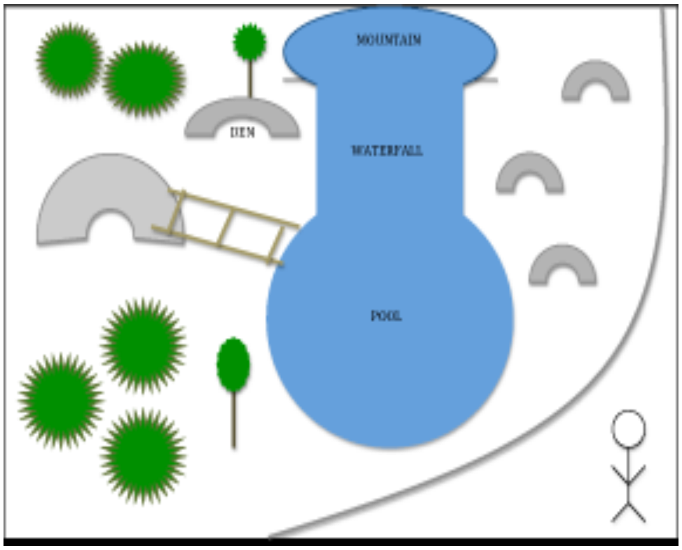
Delaney: Adult female, captive born in 2004. She was approximately 4 years old at the time of the study. She gave birth to three litters and her forth litter was born during the study. She is the mother of Kassie.

Pups 1: Litter of 4 pups born on March 5th 2009. All passed away by March 14th, 2009.

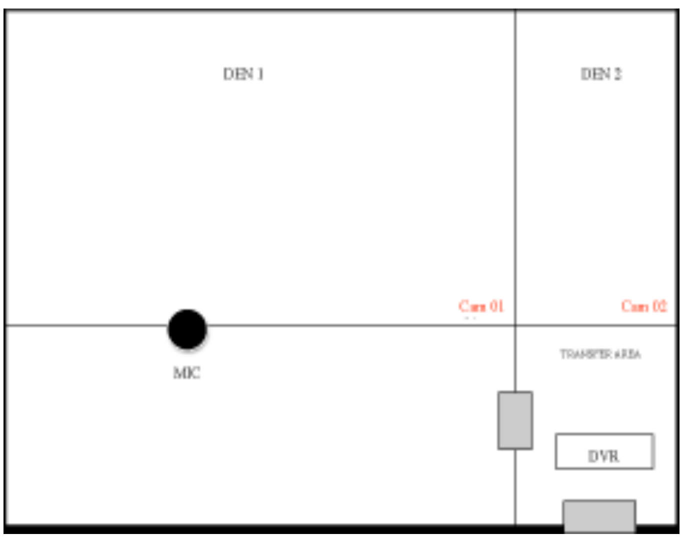
Daytime Setup: *(Figure 2.2a)* I conducted two randomized sessions per visit.

Nighttime Setup: *(Figure 2.2b)* The set up consisted of 2 infrared cameras. Sessions began in November 2008; I conducted sessions for 15-18 hours each night (4:00pm-10:00am). But, once the due date for Delaney's birth approached (1 week prior) I began recording for 24 hours non-stop to ensure that I would capture the birth. This occurred from March 5, 2009-March 17, 2009. The remaining sessions were conducted for 18 hours.

Figure 2.2: (a) Depiction of outdoor exhibit (b) indoor exhibit at Beardsley Zoo.



(a)



(b)

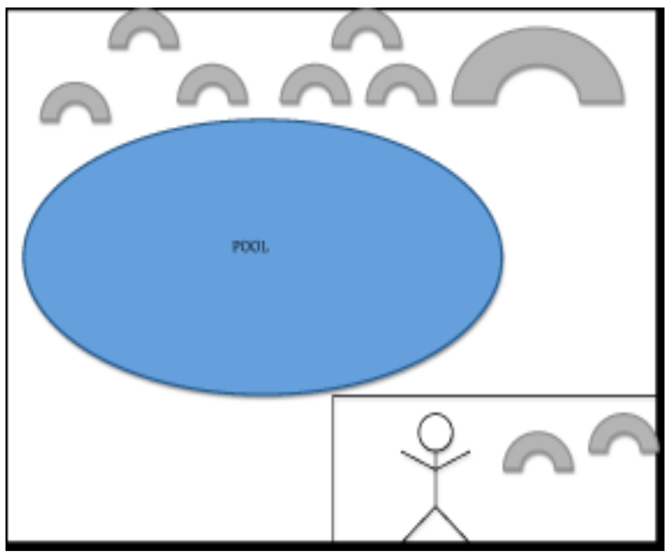
<u>PALISADES PARK CONSERVANCY:</u> PPC or Bear Mountain Zoo is located in Bear Mountain, NY. It housed a solitary adult male otter.

<u>Dell:</u> Adult male, wild born in 1995. He was 14 years old at the time of the study and is the only solitary otter in the study. Dell was orphaned as a pup and was human raised for the first year of his life. He was then donated to Bear Mountain Zoo at 1 year old and has remained there his whole life and has always been solitary.

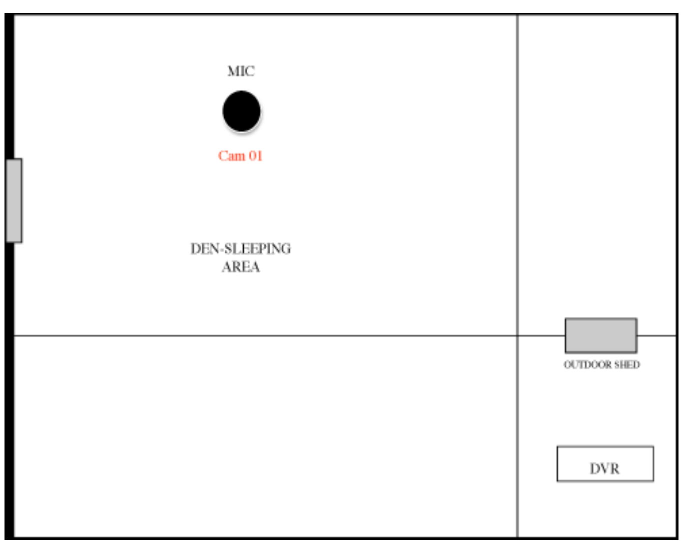
Daytime Setup: *(Figure 2.3a)* I conducted 2 sessions per visit.

Nighttime Setup: *(Figure 2.3b)* The set up consisted of 1 outdoor infrared camera. Dells den was outside and would be closed during the evening. I placed the camera and microphone directly above him giving a completely non-obstructed view. All sessions were conducted for 15 hours from 4:00pm-7:00am.

Figure 2.3: (a) Depiction of outdoor exhibit (b) indoor exhibit at Bear Mountain Zoo.



(a)



(b)

ATLANTIS AQUARIUM: Atlantis Aquarium is located in Riverhead, NY. It housed 2 adult otters that were the first otters ever at the aquarium. Due to the fact that the female gave birth during the study I extended my collection to include the pups.

Peanut Butter "PB": Adult male, wild-born. He was estimated to be approximately 7 years old at the time of the study. He was housed solitary for a short period at the Louisiana Zoo before he was transferred to Atlantis in July 2008. He was introduced to Jelly after a 30-day isolation period. They began mating in January 2009, and sired his first (known) litter in March 2010.

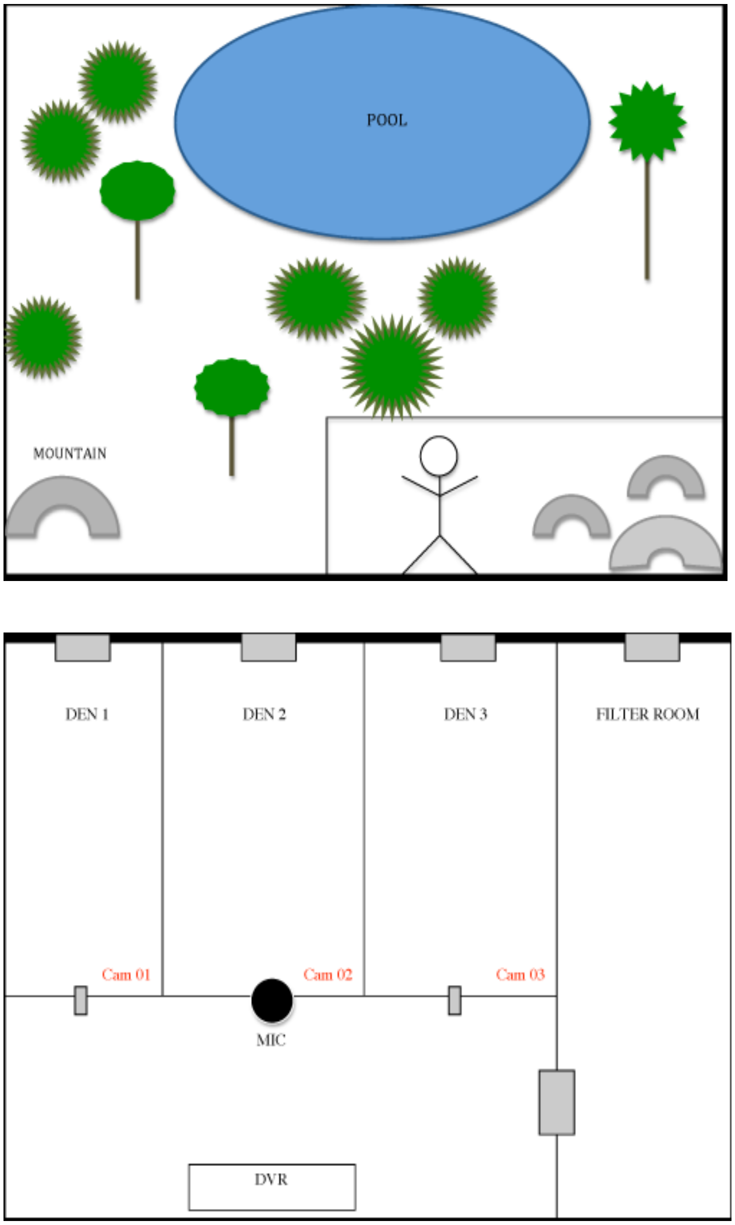
Jelly "J": Adult female, wild born. She was estimated to be approximately 5 years old at the time of the study. She was housed solitary for a short period before coming to Atlantis in July 2008. She gave birth to her first (known) litter in March 2010.

Pups 2: The pups were born on or around March 4, 2010. They were born outside in a closed off den were there was no camera. However, by three days old we were able to view them for short periods when Jelly would feed or swim. By two months old they were included in the study. They have all survived and continue to do well. All 3 pups were identified as males.

Daytime Setup: *(Figure 2.4a)* I conducted 2 sessions per visit.

Nighttime Setup: *(Figure 2.4b)* The set up consisted of 3 infrared cameras, and sessions were conducted for 18 hours from 4:00pm-10:00am. However, I conducted 24 hours sessions beginning one week (7 sessions) before her estimated delivery date (03.03.10-03.09.10).

Figure 2.4: (a) Depiction of outdoor exhibit (b) indoor exhibit at Atlantis Aquarium.



(a)

(b)

STAMFORD FARM: Stamford Farm and Museum is located in Stamford, CT. It housed 2 adult otters that are a non-mating pair.

Bert: Adult male, unknown where he was born. It is estimated that he was approximately 7 years old at the time of the study. He came to Stamford in May

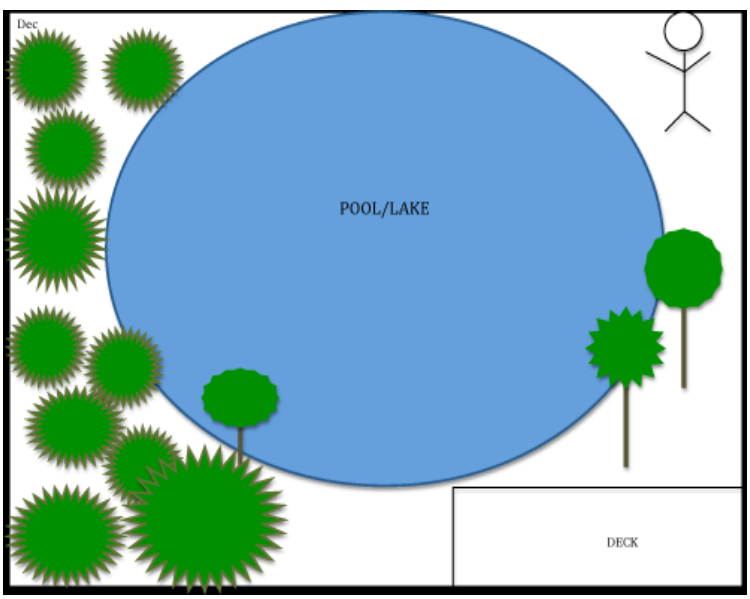
2008, from a facility in Miami. He has fathered previous litters but the number is unknown.

Edith: Adult female born in captivity. She was 4 years old at the time of the study. She was born in Louisiana, and was brought to Stamford Farm at 4 weeks old. She was hand-raised and spent the first 2 years alone. Bert was introduced in June 2008 with positive results. She has mated with Bert but there has never been any implantation.

Daytime Setup: *(Figure 2.5a)* I conducted 2 sessions per visit.

Nighttime Setup: *(Figure 2.5b)* The set up consisted of 3 infrared cameras, and all sessions were conducted for 18 hours from 4:00pm-10:00am.

Figure 2.5: (a) Depiction of outdoor exhibit (b) indoor exhibit at Stamford Farm and Museum.



(a)

Figure 2.5 continued: (a) Depiction of outdoor exhibit (b) indoor exhibit at Stamford Farm and Museum.

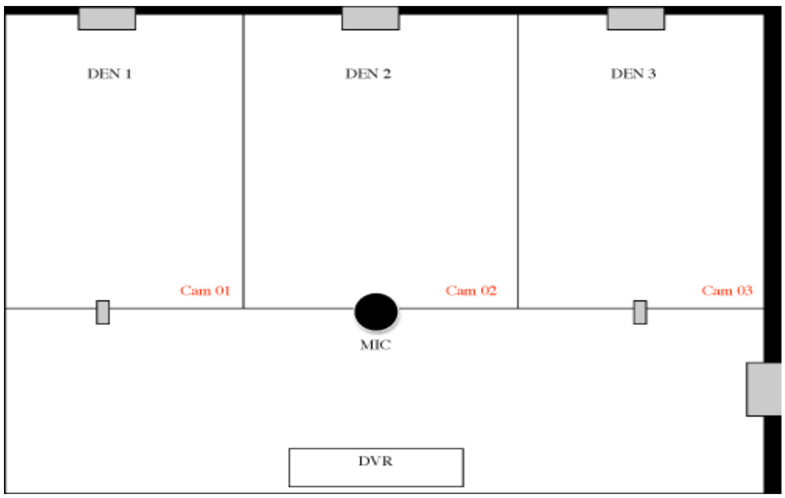
b) 

Table 2.1: Table showing the dates, number of sessions conducted during each condition, and the total hours observed.

Study Site	Condition	Dates*	# of sessions	Total # of hours
Turtle Back Zoo	Nighttime	11/13/07-10/06/08	31	470
	Daytime	01/28/08-12/17/08	35	16.2
*No Sessions were conducted in 4/08				
Beardsley Zoo	Daytime	06/02/08-01/21/09	21	10.5
	Nighttime	11/06/08-03/26/09	33 (29 analyzed)	569 (473 analyzed)
*No sessions were conducted in 10/09 for the daytime condition *No sessions were conducted in 2/09 for the nighttime condition				
Bear Mountain Zoo (PPC)	Daytime	11/18/08-10/08/09	15	7.3
	Nighttime	07/31/09-09/16/09	11	165
*No sessions were conducted in 04/09 and 06/09 under the daytime condition.				
Atlantis Aquarium	Daytime	07/17/09-06/01/10	21	10.45
	Nighttime	11/28/09-05/31/10	36	678
*No sessions were conducted in 10/09 for daytime sessions *No sessions were conducted in 02/10 for nighttime sessions				
Stamford Farm	Daytime	06/20/09-11/09/10	20	10
	Nighttime	08/19/10-09/27/10	14	288
*No sessions were conducted from 1/10-4/10 and 5/10-8/10 for daytime sessions.				
Total number of hours observed=2129 hours				

Analytical Methods

Video Analysis and Call Identification

The total sample size consisted of 12 individuals, (5) males, (5) females, and (2) litters of otter pups. The litters of pups are grouped collectively and count as one individual. Since all the otters in litter 1 passed away, there was no opportunity to determine the individuality and sex. The otters in litter 2 all survived and were determined to be males. However, by the end of my sessions they were not given individual 'names' and differentiation was not possible.

For daytime footage, the original footage was edited down to smaller clips that contained vocals, using Final Cut Pro. The time and sound(s) that were heard were recorded into an Excel sheet. For overnight footage data were stored on a Digital Video Recorder. After each series of sessions, the video from each night was transferred to DVD's in 6hr sets. I then viewed all the footage and recorded the time a sound was heard. The footage was then edited down to smaller files using Final Cut Pro. I viewed the edited footage again and recorded the time and sound(s) that were heard into an Excel Sheet.

Edited files were defined to be usable or non-usable. A usable file was a file that contained at least one usable call, and non-usable files contained no usable calls. A usable call was defined as a call isolated from other calls (non-overlapping) and identification of individual making the call was possible. For all edited clips I made an initial identification of the otter and the sound(s) being produced.

RAVEN analysis: Specific identifications of the otter and the call type could not be accomplished using only the video footage. So, usable files were imported into RAVEN to produce an audio and spectral image making it possible to hear and see the call at the same time. The RAVEN images allowed me to locate the time of a specific call in the edited file. I used this information that the spectral image provided to locate the usable vocal in the video footage to make specific identifications.

I used RAVEN to conduct a structural analysis of the calls. Each usable call (isolated calls) was analyzed by RAVEN for the following variables: High Frequency, Low Frequency, Maximum Frequency, Center Frequency, Max power, Average power, and Duration. The range and mean of the frequency were determined using Microsoft Excel. I included the number of harmonics bands, which was determined visually. *(Table 2.2)*

*Table 2.2***:** *Table of RAVEN's definition of the variables used in the vocal analysis*

Variable	**Type of Variable***	**Definition**
Structural Variables		
High Frequency (kHz)	Selection Bound	Point of highest frequency (pitch).
Low Frequency (kHz)	Selection Bound	Point of lowest frequency (pitch).
Range of Frequency (kHz)	Selection Bound	The difference between the High Frequency and Low Frequency, calculations were made by Microsoft Excel
Max Frequency (kHz)	Selection Bound	The frequency at which the greatest power (energy) occurs.
Max Power (dB)	Robust	The darkest point in the spectral analysis
Average Power (dB)	Robust	The summation of the spectral power density divided by the number of time-frequency bins.
Mean Frequency (kHz)	Selection Bound	Determined by Microsoft Excel; the average of the high and low frequency.
Center Frequency (kHz)	Robust	The frequency at the center time of the vocal.
Duration (s)	Selection Bound	The length of the call. Raven gives a begin time and an end time, the duration was determined by taking the difference.

Table 2.2 continued: Table of RAVEN's definition of the variables used in the vocal analysis

Harmonics (#)	Visually observed	A harmonic is defined as an integer of the fundamental frequency of the call. Fundamental frequency is the lowest frequency wave that exactly repeats over time
Static	Visually observed	Calls that do not contain harmonics. This was visually observed using the spectrogram produced by RAVEN

**Selection Bound: Variables (measurements) in RAVEN that are based on the aspects that are created by the box that is used to select a call. These can vary based on the size of the box.*

**Robust Measurements: Variables in RAVEN that are based on the selected item, will not vary much based on the selection box aspects.*

** Visually observed: Measurements or behaviors that I determined using visual characteristics that were viewed through a spectral analysis produced by RAVEN, or by observing video footage.*

Identification of otter: I utilized several techniques to identify the otter making the vocalization. In daytime footage identification was done easily, I was able to use fur color if they were at a distance, and unique markings when they were close to the camera. For overnight footage, identification was more difficult. The footage was black and white, and generally the angle was a skewed overhead view. Therefore, I used several factors to assist in identification such as: body size, body shape, size of the tail, shape of the tail, body language, visible physical displays (i.e. mouth opening) and the outdoor footage as a template. There were some interactions where identification of the otter was impossible, because the vocalizing otter was out of range of the camera, two or more otters were vocalizing simultaneously, or they were in a physical confrontation during the vocals making it difficult to view the otters.

Classification of call type: I classified all calls based on the sound that I heard produced. There were many calls that sounded similar however if there were any minor differences in the sound then the calls were not grouped together. This was to ensure that calls were identified based only on what was heard, not on their context or structure. Because identification of the otter for all the calls was not always possible some calls were rendered unusable. After I did my initial RAVEN analysis, I had several data points that contained two vocals (i.e. *Whine/Chirp*). I reanalyzed those data points and was able to separate all the data points that contained two vocal call types. Although, Dell had 5 calls that could not be separated, Delaney had 7 calls and Edith had 2 calls. These calls were recorded as two vocal call types, and would be grouped based on which call was dominant. (i.e. *Whine/Chirp* would be categorized as a *whine*).

2nd observer: In order ensure that the identification (otter and call type) was replicable I used a 2nd observer to check for inter-observer reliability. She was an inexperienced observer that made her unbiased observations based solely on the definitions that I established. She observed 50 video clips (10 clips from each study site) and 324 calls (10.7%) of the data set.

Table 2.3a: Inter-observer reliability results for otter and call identification

Otter Identification		Call Identification	
Agree	Disagree	Agree	Disagree
300	24	293	31
92.5%	7.4%	90.4	9.6%

Analysis of behavior(s): I included an analysis of the behaviors *(Table 2)* that occurred before, during and after a vocal occurred or a vocal interaction. This was to get some insight into when calls are heard. From the video footage, I recorded two variables that were visually observed: the type of interactions (asocial or social) and the emotional state of the otter (Non-agitated, Mildly Agitated, Moderately Agitated, Highly Agitated).

Table 2.3b: Definitions of behavior variables

Behavior Variables		
Type of interaction (Asocial or Social)	Visually observed	Asocial interaction: Otter is interacting with self, environment, or inanimate object Social interaction: Otter(s) is interacting with one or more otter, or human and otters distance away
Arousal State of Individual	Visually observed	Non-agitated: otter(s) exhibits 'friendly' or timid behaviors. (play, grooming) Mildly agitated: otter(s) exhibits behaviors associated with frustration (pacing) Moderately agitated: otter(s) exhibits behaviors associated with aggression, but is not physically violent (lower head, arching back) Highly agitated: otter(s) exhibits behaviors associated with aggression, and is physically violent (biting, scratching)

2nd observer: Because type of interaction and arousal state is subjective my 2nd observer made her unbiased observations for these variables. She observed 50 clips (10 clips from each study site) that contained 324 calls (10.7%). She categorized calls based on whether they were asocial or social and the arousal state the otter was in when producing the call.

Table 2.3c: Inter-observer reliability results for otter and call identification

Type of Interaction		Arousal State	
Agree	Disagree	Agree	Disagree
319	5	289	35
98.5%	1.5%	89.2%	10.8%

Coding: I created a coding system to use for all statistical analyses for the study.

Table 2.4: Table showing the coding system of the call types, individuals and arousal state.

Call Type	**Coding**	**Individual**	**Coding**	**Arousal State**	**Coding**
Whine	(1)	Kassie	(KS)	Non-agitated	0
Chirp	(2)	Bert	(BT)	Mildly agitated	1
Chatter	(3)	Delaney	(DE)	Moderately Agitated	2
Creek	(4)	Dell	(DL)	Highly Agitated	3
Squeak	(5)	Edith	(ED)		
Scream	(6)	Jelly	(JY)		
Grunt	(7)	Leveau	(LV)		
Swish	(8)	Peanut Butter	(PB)		
Hiss	(9)	Remus	(RM		
Blow	(10)	Rizzo	(RZ)		
Hiccup	(11)				

Ethogram: I created an ethogram to have a catalog of all the observed behaviors and which individuals exhibited the given behavior. The ethogram depicts the definitions of the behaviors and sub-behaviors that were exhibited *(Table 2.5).*

Table 2.5: Ethogram showing the behaviors and the definitions observed for all the individuals in the study.

Behavior	Sub-Behavior	Definition	Otters that exhibit behavior
Sleeping	Indoor	Period of rest in den for 30 minutes or more	ALL
	Outdoor	Period of rest for 30 minutes or more; occurs mainly by trees	ALL
	Social/Group	Sleeping with another otter(s) (within an otters distance away) for 30 minutes or more	RM, LV, KS, DE, RZ, PB, JY, BT, ED, P1, P2
Grooming	Self	Licking and biting of own skin, fur, or paws	ALL
	Others	Licking and biting of skin, fur, or paws of another otter	RM, LV, KS, DE, RZ, PB, JY, BT, ED
	Massaging	Rubbing body or back against a substrate (i.e. rock, log, wall)	ALL
Sprainting		Scent-marking; each otter sprains at their own site	ALL
Swimming	Submerged	Otter completely submerged in water or in pool and maneuvering through the water for more than 30 seconds	ALL
	Acrobatic	Underwater swimming involving acrobatic movements (i.e. spinning, back flips)	ALL
	Floating	Swimming on the back during floating	KS
Play	Toys	Grasping, manipulating, or playing with toys	ALL
	Climbing	Scaling a gate or wall	LV, KS, JY
	Plopping	Running forward and then laying body and head flat and spread out onto the ground	KS
	Water	Splashing water out of the pool with paws	KS
	Self	Playing with body parts, tail or feet	DL
	Otter	Physical contact with otter(s) that are docile, and playful; or more than one otter manipulating a toy(s)	RM, LV, KS, DE, RZ, PB, JY, BT, ED, P2
Nesting	Indoor	Collecting twigs in den and placing onto the ground in a pile in dens	ALL
	Outdoor	Collecting twigs and shrubbery and placing onto the ground in a pile on exhibit	ALL
Enrichment	Painting	Painting stimulated by the trainers	R;L
	Training	Other activities stimulated by trainers (tricks)	RM, KS, DL, DE, RZ
	Seeking	Searching behavior that results from enrichment (i.e. stashing food in toys)	LV, KS
Aggressive	Vocal	Vocalizations that occur within the 2 minutes before, during, or 2 minutes after a hostile physical confrontation or vocal quarrel	ALL
	Physical	Physical attack on another otter (biting, scratching), or violent wrestling	RM, LV, KS, DE, RZ, PB, JY, BT, ED
Non-Aggressive	Physical	Physical interaction that includes no hostile behavior, or submissive behavior	ALL
	Vocal	Vocalizations that occur within the 1 minute before, during, or 1 minute after a non-aggressive physical behavior	ALL
Submissive	Physical	Subordinate behavior (i.e. cowering, running away, giving up after quarrel or confrontation)	RM, LV, KS, PB, RZ
Stereotypical	Scratching	Scratching at gate or door with paws repeatedly more than 5 times in a row	RM, KS
	Pacing	Walking back and forth repeatedly in the same one area	RM, LV, KS, ED, DL
	Swimming	Swimming in circles	DL, RZ

Chapter Three

Behavioral Observations of captive North American River Otters

Introduction

At the time of my study all the otters had spent most of their life, if not their whole life, in captivity. But, PB and Jelly were both wild born and their first introduction occurred once they both had passed the isolation phase and were on exhibit. PB and Jelly were useful study subjects because they had minimal influences on their natural behaviors, at the time of the study they had only been in captivity for about a year. They had never been in captivity before coming to Atlantis, and even by the end of the study there was little change in their naturalistic behaviors (i.e. no stereotypical behaviors observed, such as pacing). When they first came to Atlantis Aquarium they spent most of their time outside but managed to remain inconspicuous by hiding under rocks, behind bushes or in the outside tree den. They only went inside for feedings. By the time that I began observing them they still showed more naturalistic behaviors than any of the other otters in the study, such as being shy and elusive. They were more hesitant to my presence; I would enter the back area, and would come in contact with PB. He would be curious about my presence, but never approached or made any vocalizations, which was very different from the behaviors of the other otters that would vocalize when I approached or would approach me with curiosity. Jelly had no interaction with me, either outside or inside. The only time that I came in contact with Jelly was when I was hand feeding one of her pups. She remained in the vicinity but never approached me.

The other otters in the study were more ‘human' friendly than PB and Jelly however they also exhibited many naturalistic behaviors that have been observed in the wild. Both Edith and Rizzo exhibited the sliding behavior while playing in the snow. I observed Dell and Kassie play when no otter or human was present. Kassie spent some time alone in the early introduction phases, and would play with various toys. I also observed her playing with water and splashing it out the pool with her paws.

Dell is solitary and he would utilize his tail as a toy. He would lie on his back with his tail between his legs and chew on it and make several different vocals (*grunts, whines, blows).*

The otters in my study varied greatly on the way they interacted with themselves, environment, other otters and humans. However, all the otters in the study vocalized and used this to communicate with others, as my studies will demonstrate.

Observations of a solitary lifestyle

Dell was the only otter who lived a solitary lifestyle. Due to his captive history he was very 'human' friendly. He would vocalize extensively, primarily exhibiting the chirp when visitors would approach his exhibit. He was very aware of my presence and often interacted with me when I got close to the exhibit. At times my presence appeared to frustrate him and he would lunge at the gate and exhibit *chatters*, and *squeaks*. Sometime he would enter the water and swim vigorously splashing water out of the pool. Overall, Dell exhibited very different behaviors from the otters that were socialized.

Observations of male-female social dynamics

In my observations of male-female dynamics the females were more aggressive, and less tolerant of the males. When physical confrontations ensued the females were often the aggressors. In two mating pairs I observed the females behavior before and after giving birth.

Delaney was observed from June 2008 to March 2009. At the beginning of the study Rizzo and Delaney produced 2 successful litters and one that was unsuccessful. For her forth litter Beardsley Zoo implemented fecal studies to determine time of implantation, which was estimated to be January 4, 2009. Based on her date of implantation we were able to estimate her delivery date to be the first week of March. I began a 24-hour monitoring period one-week before her expected delivery date. The two weeks prior to her delivery her behaviors grew increasingly aggressive towards the trainers, me, and especially Rizzo. Overnight footage showed that Rizzo spent most of his time outside and on the rare occasions that he entered inside Delaney would become aggressive, and exhibit screams, chatters, and whines. Many of the aggressive vocal interactions led to physical confrontations. This type of female aggression has been observed in the wild *(Chanin, 1995 & Kruuk, 2006).*

Delaney gave birth to 4 pups in March 2009, none survived. She was very protective of her pups and continued to be aggressive towards Rizzo. On a few occasions Rizzo would manage to get into the den, and Delaney would submit to his presence, but he never came in contact with the pups. After the second pup passed away Delaney began mating with Rizzo. She would leave the surviving 2 pups in the den while she mated. Female otters have been observed to mate immediately after the loss of a litter *(Kruuk, 2006)* but Delaney mated before she lost her complete litter. Although she mated with Rizzo she remained extremely aggressive towards him and protective of her surviving pups. Within one week of the last pup's passing Delaney returned to her original behaviors. She continued to mate with Rizzo and produced a 5^{th} litter in 2010 with one male surviving.

Other than the period of Delaney being pregnant and caring for her young, Rizzo and Delaney exhibited a friendly male/female dynamic. Their interactions were docile and were accompanied by *whines,* and *chirps*. I observed them swim together, and chase one another on exhibit. Overnight, Rizzo and Delaney spent a lot of time sleeping and at times there would be some calls that were exhibited when an otter appeared frustrated. For example, sometimes Delaney would disturb Rizzo while he was asleep and he would *whine* as a response, or vice versa. In October 2008, Delaney suffered from a seizure during an overnight session. Rizzo did not react but he did not leave her side. After her seizure she appeared disoriented, and Rizzo approached her and sniffed her until she stabilized. One of the trainers observed Delaney have a minor seizure on exhibit in the water. She became slightly disoriented and Rizzo in this case nudged her out of the water.

Jelly and PB began mating soon after their introduction, so Atlantis Aquarium implemented fecal studies to determine if and when Jelly would implant. It was determined that she implanted on December 15, 2009, and it was estimated that she would give birth at the end of February 2010. I began a 24-hour monitoring period a week before her due date, and observed behaviors similar to Delaney. She grew increasingly aggressive and remained in her outside tree den during the three days before she gave birth. She gave birth in the tree den (no camera present) on or about March 4th 2010.

Jelly gave birth to three male pups (sex was determined at 1 month). During the period after Jelly gave birth she would leave the tree den only at night. In overnight sessions I observed several physical confrontations, and PB was the submissive party with Jelly being the aggressor. It appeared the PB was attempting to avoid Jelly and maintain distance; I even observed him hiding behind large kennels that were placed inside the overnight dens. In these instances Jelly would appear to be seeking him out and once she located him the confrontation would be initiated.

Bert and Edith are a non-mating pair; they have mated in the past but it never led to implantation. Their dynamic was playful and sibling oriented. Edith was highly vocal and Bert's vocals often were in response to Edith's vocals or behaviors. Most of the vocals were observed during 'playful' interactions. Before their afternoon feed they would become rambunctious, and I would observe a lot of play. They also played and wrestled extensively overnight and would exhibit whines and chirps.

The keeper discovered Bert and Edith were engaging in cooperative behavior before he was almost attacked by Edith while he was in the exhibit and she was supposed to be locked up. I observed how they managed this; Edith would wiggle her nose under the transfer door, using the leeway that is on the door to lift it high enough so that Bert could fit his head under. Once he squeezed in far enough he would use his upper back to lift the door high enough for Edith to fit through. Edith also implemented this technique when Bert was separated from her in another den. This was a spontaneous behavior that was not influence by training.

Turtle Back Zoo housed 1 male and two females. Remus the male was first introduced to Leveau. Leveau was the eldest otter in the study she was 18 years old at the time. She was past her reproductive age and had a complete hysterectomy a few years prior to coming to Turtle Back Zoo. Therefore, there could be no mating between Leveau and Remus. The introduction was a very slow process that began in November 2007 and stalled in January 2008 when Remus was transferred out temporarily for mating purposes. During the three months they spent together the interactions were highly aggressive. In the beginning the trainers would alternate Remus and Leveau onto the exhibit during the day to gradually get them use to each other. But, overnight they were kept inside in different dens, with a transfer door keeping them apart. The first few nights they would both scratch at the transfer door and *whine* at one another. Leveau eventually managed to break through the transfer door, which led to their first physical confrontation. During these physical confrontations, many vocalizations were exhibited; various *whines*, and *chatters* were the most common. Leveau also exhibited her low raspy *hiss* but many times the calls were low and hard to hear over Remus' calls. All the aggressive confrontations were always accompanied by vocals and at times led to wounds. These interactions continued until Remus left in January 2008.

The introduction phase between Leveau and Kassie began in February 2008. The period while Remus was gone allowed for me to observe a female/female dynamic. Kassie and Leveau represented two different ages classes Leveau being the eldest in the study and Kassie being the youngest of the study (excluding the pups). They participated in physical confrontations during the early stages of introductions, but they did not lead to wounds.

When Remus returned to Turtle Back Zoo in May 2008 the introduction between Remus and Kassie began, which was a smooth transition. Once all 3 otters were together the social dynamic changed dramatically. Both Remus and Leveau formed a bond with Kassie and engaged in several 'friendly' interactions with her, such as play, and grooming. Low *whines* and *chirps* often accompanied these interactions. Many physical confrontations between Remus and Leveau occurred if one approached another while with Kassie. Remus and Leveau formed a tolerance for each other, but never formed a social bond.

Observing the dynamics from a mating standpoint shows that there were 2 mating pairs (Rizzo & Delaney and PB & Jelly), 2 potential, non-mating pairs (Remus & Kassie and Bert & Edith) and 1 no potential, non-mating pair (Remus and Leveau). In all the dynamics the males were submissive to the females, and the females were more aggressive and less tolerant of the males. However, Remus and Leveau did not exhibit this type of dynamic. Remus was highly aggressive towards Leveau and often instigated physical confrontations. Leveau was the only female past her reproductive age, and this likely affected Remus' behavior towards her. It is probable that males in captivity are submissive and less aggressive towards females for mating purposes.

Observations of adult-pup interactions

Delaney was the first otter to give birth during the study, and I captured the birth of her pups. At the time of the study Delaney had given birth to 3 previous litters. Her first litter was born in 2006 when she was only 2 years of age. Since Delaney was young and inexperienced and there were two males on exhibit the litter was hand raised by the keepers. Her second litter was born the following year (2007) and by this time Rizzo was the only male in the exhibit. This litter produced two females and one male whom all survived and remained as a family unit for one year until they were transferred out. Kassie was part of this litter and this was also the first litter that Delaney reared. Her third litter was born in March 2008 and they all passed away to unknown causes by April. The 2009 litter occurred during the study.

Delaney gave birth on March 5th 2009, the first pup was born at 7:08:28 p.m. it made its first call a *whine* at 7:09:13p.m about 30 seconds later. Delaney did not vocally respond to the calls, but she did immediately clean the pup and nuzzle it. The second pup was born at 7:23:24p.m and after it was born it chirped immediately. The last two pups were delivered with ease and Delaney cleaned them all immediately and all the pups vocalized within the first 30 seconds. The pups were sexed but all post-mortem, since they all passed within two weeks. During the deliver Rizzo did not enter the den.

Delaney exhibited normal maternal instincts, she groomed, nursed, and protected her young, but she also exhibited some odd behaviors that may have directly caused the death of the pups. The first pup to pass was on March 12th 2009 to unknown causes. The second pup that passed was a female and it occurred later that day, when Delaney sat on her causing her to suffocate. The last two pups one male, and one female both died on March 14th 2009 to unknown causes. However, I observed her incorrectly picking up the male by the stomach rather than by the nape to transport him. The male *whined* in pain when she did this, so this may have been a contributing factor. Furthermore, the male was found dead on exhibit the morning after I made this observation and he had puncture wounds. The behavior was peculiar for her especially since she was experienced and had successfully reared other pups. Delaney's health was a concern during her pregnancy and rearing period, because she was suffered from seizures potentially affecting her ability to properly nurture the young.

Jelly gave birth between March 3rd 2010 and March 5th 2010; I recorded 24hrs from March 3rd to March 8th 2010 and then returned to recording for 18hrs. The first recording I obtained of the pups was on May 20, 2010. During the 2 months prior the pups were almost inconspicuous. They remained in the den underneath a rubber mat for approximately the first month of their life. The first time the pups were observed outside the den was April 25th 2010. The trainers describe coming into the indoor den for the first feed and Jelly had all her pups with her. Once she noticed their presence she immediately moved them. On April 25th she was also observed bringing the pups to the water possibly giving them their first 'swimming lesson'.

Once the pups officially emerged from the den around early May, Jelly's aggressiveness and protectiveness tapered off and all interactions after were as a family unit. From this point on I observed several interactions between the mother and pups as well as within the pups. Jelly and PB both engaged with the pups in a playful manner. Jelly's success in rearing the young may suggest that she has birthed litters when she was in the wild as well I attribute much of the success to the 'handsoff' tactic that Atlantis Aquarium implemented. Because they were not previously experienced with river otters they opted to allow Jelly to control the whole process. The amount of handling was kept to an extreme minimum. The first contact wasn't until April 20^{th}; the pups were weighed and were each about 4lbs.

The pups from Beardsley Zoo vocalized, however Delaney did not vocally respond to her pups. On the contrary the pups would vocalize and Delaney would leave and mate with Rizzo. When she was in the vicinity she would respond by grooming, nursing, or nesting with them. The most common calls heard from the pups were *whines*, and the *whistle*. The calls sound similar to the calls analogous in the adults, but the whistle was completely unique to only this group of pups.

Since I did not observe the Atlantis Aquarium pups until they were 2 months old, I can only speculate on the vocals produced in their early weeks of life. However, when I did observe them they exhibited many vocalizations. The vocalization most common to this group was the *chirp*, but no *whistle* was exhibited. All the calls were made during play, and grooming. The pups were highly rambunctious and Jelly was very involved with the pups. Jelly and the pups did not vocally interact, but between the pups there was a great deal of *chirping*.

Observations on individual vocal usage

Vocalizations were heard during asocial and social interactions. Rizzo would chirp intermittently while grooming or swimming. Dell used his grunt while grooming himself or massaging himself against a substrate. He would also grunt alone at night while playing with his tail. Edith grunted before she was anticipating a feed (otters in captivity become conditioned to the zoo's feeding schedule). Both PB and Rizzo grunted during and after an aggressive confrontation with the females. All their grunts occurred after the females (Jelly and Delaney, respectively) had given birth, when the females had becoming increasingly aggressive.

Delaney exhibited many calls during the 36 hours following the lost of her final pup. She would search the bedding for her pups, and would sit in the corner and release whines, and screams. However, the whines were very long and exaggerated, and could be associated with cries of pain. Oddly, all the pups passed away at different times, but her ‘cries of pain’ did not begin until the last pup was removed from the den. This period lasted for approximately 1 week, after she returned to her normal behaviors and began mating immediately with Rizzo. I never heard calls that sounded similar to any of her calls made during that period again from Delaney. No other otter produced calls that were similar.

Dell and Edith would *blow* when I would approach their area. Dell would often become aggressive if I remained in the vicinity. PB was not interactive with me, but he exhibited the *blow* during or after aggressive confrontations with Jelly. During overnight observations PB would be indoors while Jelly remained outdoors with her pups. I would observe PB exit the indoor den and could hear Jelly and PB in a confrontation, afterwards PB would return inside and pace franticly while exhibiting the *blow*.

Chapter Four

The Vocal Repertoire of North American River Otter

Introduction

Establishing a vocal repertoire is the initial step needed when studying the vocal system of a species that nothing is known for. A vocal repertoire is composed of all the acoustic sounds that a species produces. But, the most fundamental task is to delineate the repertoire. Ideally, separate vocalizations will be acoustically different without any structural overlap *(Soltis, 2004).* But this is generally not the case; often calls produce the same sound but differ in structural components, or calls could structurally overlap and produce different sounds.

Studies of otter species have used the sound produced as the distinguishing feature to place a call type in a vocal category. However, the sound produced although very useful for classification it is only one factor that characterizes the call. Both structural components (frequency, duration, pitch) and biological significance (increase reproductive success, solidify bonds, maintain group cohesiveness) influence the call and the sound that is produced. Furthermore, individual factors (gender, age,) can influence the characteristics of a vocal.

Goals

The aim of this section is to describe and analyze for the first time the vocal repertoire for North American River Otters using two classification systems: one based only on the sound produced and one a based on sound and spectral features. From the vocal repertoire I wanted to determine (1) which classification system better represents the complete vocal repertoire of river otters (2) if acoustically different calls are also structurally different (3) determine if differences in calls exist across individuals that exhibit shared call types.

Methods

Classification of Calls heard by ear

Whine: The whine is the only call type that is universal to all the otter's vocal repertoires, it is even seen in the pups. There are variations in the types of whines heard. The *whine* produces a sound comparable to a cry. The whine has been described in the European Otter *(McShane, 1995),* and the Sea Otter *(Gnoli, 1995).* Many authors have described variations of types of whines heard in otter vocalizations.

Chirp: The *chirp* can be compared to a bird chirping. The *chirp* was found in all the otters studied here except Leveau, Jelly and PB. It is likely that Leveau, PB and Jelly do have a chirp, but I may just not have observed it. Peters and Wozencraft (1989) described a chirp heard in otters in a communication studied done on carnivores.

Chatter: The chatter can be described aurally as teeth chattering. They are high-pitched and occur in rapid succession. All the adults have chatters as part of their vocal repertoires. Kassie exhibited the chatter on a single occasion, and I heard 5 chatters from the pups in Beardsley Zoo. In other otter studies the chatter has been described, but the term used is 'chittering' *(Table 1, Gnoli)*.

Creek: The *creek* sounds like an old wooden door opening, or a whine with a crack in it. The *creek* was found in 5 adult otters: Dell, Leveau, Delaney, Bert and Edith. It has not been described in other otter species.

Squeak: The *squeak* sounds like a shrieking whine. The s*queak* was heard in only 2 adult male otters, Dell and Bert. 14 *squeaks* were heard; Bert accounted for one squeak the other 13 were made by Dell. The squeak has been described in several studies, *(Table 1,Gnoli, 1995)* and in sea otters *(McShane, 1995)* although, is not clear if what these authors describe as a squeak is analogous to what I describe to be a chirp.

Scream: *Whines* and *Screams* were difficult to distinguish because they sounded very similar but the *scream* had a more piercing sound and was very loud. *Screams* were heard predominately in two adult females (Delaney and Jelly) that had given birth. The scream has been observed in sea otter mothers and pups *(McShane, 1995)*

Grunt: The *grunt* is low-pitched, short in duration and occurs intermittently. The *grunt* was heard in 4 otters: Dell, Rizzo, PB, and Edith.

Swish: The *swish* can be described as water swirling around in a container. The *swish* was heard in two otters: Leveau and PB. Leveau used it more frequently.

Hiss: The *hiss* sounds comparable to the hiss of a snake. The *hiss* was heard in 4 otters: Remus, Leveau, Bert and Edith.

Blow: The *blow* sounds like air being blown out from the nose. The *blow* was heard in 3 otters: Dell, PB, and Edith. The blow has been described in Eurasian otters *(Kruuk, 2006).*

Hiccup: The hiccup's sound is comparable to a human hiccup. It is unclear if this is a vocal or a natural internal response like a sneeze. The hiccup was heard only on 2 occasions, from Kassie and Delaney.

Whistle: The *whistle* had a unique tone to it, and is comparable to the whistle produced by dolphins during echolocation. The *whistle* was unique to the pups observed at Beardsley Zoo. I did not observe the *whistle* in the pups born to Atlantis Aquarium. (The *whistle* is not included in any of the analysis for this section since it is unique to the pups).

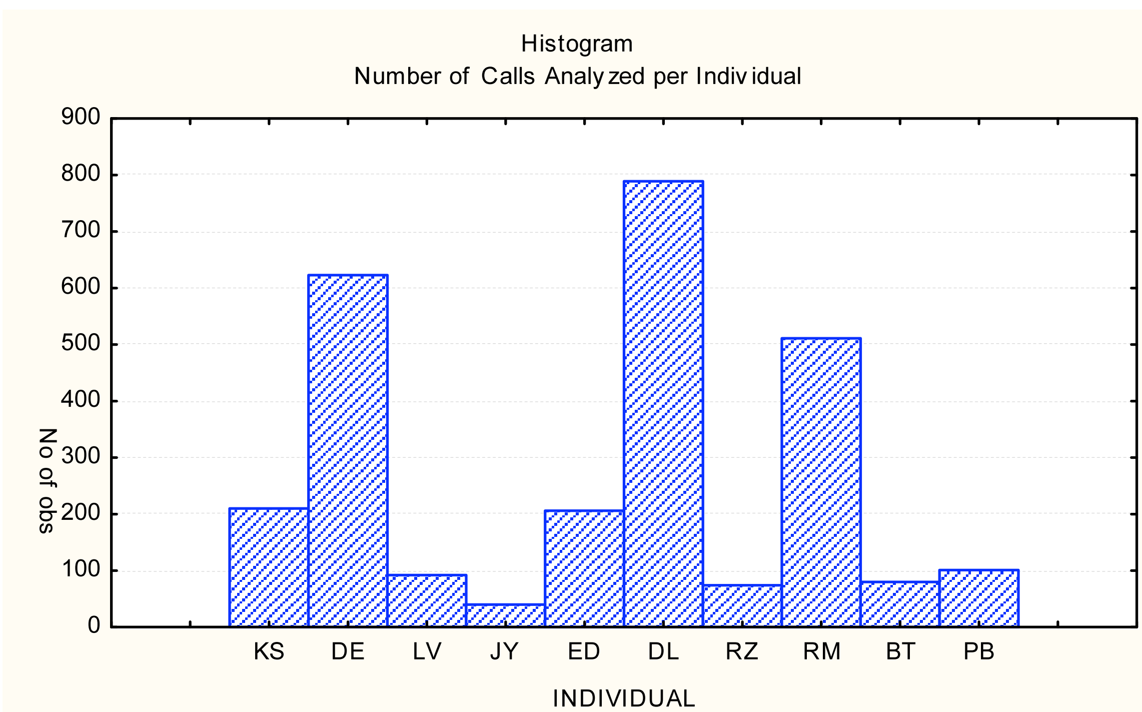
Table 4.1: Descriptive table showing age (at the beginning of the study), sex, and site (where they are housed) of each otter. The # of calls recorded and calls exhibited by each otter is also shown (pups are included).

Otter	Age (yrs)	Sex	SITE	Calls Exhibited	# of Calls
Dell	14	M	BMZ	Whine, Chirp, Chatter, Creek, Squeak, Grunt, Blow,	788
Remus	11	M	TBZ	Whine, Chirp, Chatter, Hiss	511
Rizzo	7	M	BDZ	Whine, Chirp, Chatter, Grunt	75

Table 4.1 continued: Descriptive table showing age (at the beginning of the study), sex, and site (where they are housed) of each otter. The # of calls recorded and calls exhibited by each otter is also shown (pups are included).

PB	7	M	AAQ	Whine, Chatter, Grunt, Swish, Blow	101
Bert	7	M	STF	Whine, Chirp, Chatter, Creek, Squeak, Grunt, Hiss	80
Leveau	19	F	TBZ	Whine, Chatter, Creek, Swish, Hiss	92
Jelly	5	F	AAQ	Whine, Chatter, Scream	40
Delaney	4	F	BDZ	Whine, Chirp, Chatter, Creek, Scream, Hiccup	623
Edith	4	F	STF	Whine, Chirp, Chatter, Creek, Scream, Grunt, Hiss, Blow	206
Kassie	10 mos.	F	TBZ	Whine, Chirp, Chatter, Hiccup	210
Pups 1	0	N/A	BDZ	Whine, Chirp, Chatter, Whistle	207
Pups 2	0	N/A	AAQ	Whine, Chirp	92
12 otters					**3025**

Figure 4.1a: Histogram depicting the number of calls observed/analyzed for each otter (only adults are shown).



Dell and Bert exhibited 7 of the 11 call types heard by ear. And Edith exhibited 8 of the 11 calls types. Dell had the most calls analyzed of all the otters with 788 calls. However, the large data set is due to the fact that he is solitary and all calls were isolated and free from background noise, making every call usable for analysis. In all other facilities the number of calls analyzed were limited due to identification difficulties and/or calls overlapping one another during social vocal interactions.

RAVEN spectral images

The spectral image of the whine showed two types of *whines*; static, non-harmonic, and harmonic. A harmonic call shows clear bands that are components of the frequency of the call. *(Figure 4.2a and b)*

The *chirp* occurs intermittently, and has a high frequency with a short duration. The spectrogram of the *chirp* shows that it is highly variable in the number of harmonics, with some *chirps* having as many as 11 harmonics. There were very few *chirps* that were recorded to have no harmonics (0), but this may be due to Raven's inability to create a clear picture. The harmonic bands of the *chirp* can have two appearances: they could be linear or have an inverted "v" shape to them. *(Figure 4.2c and d)*

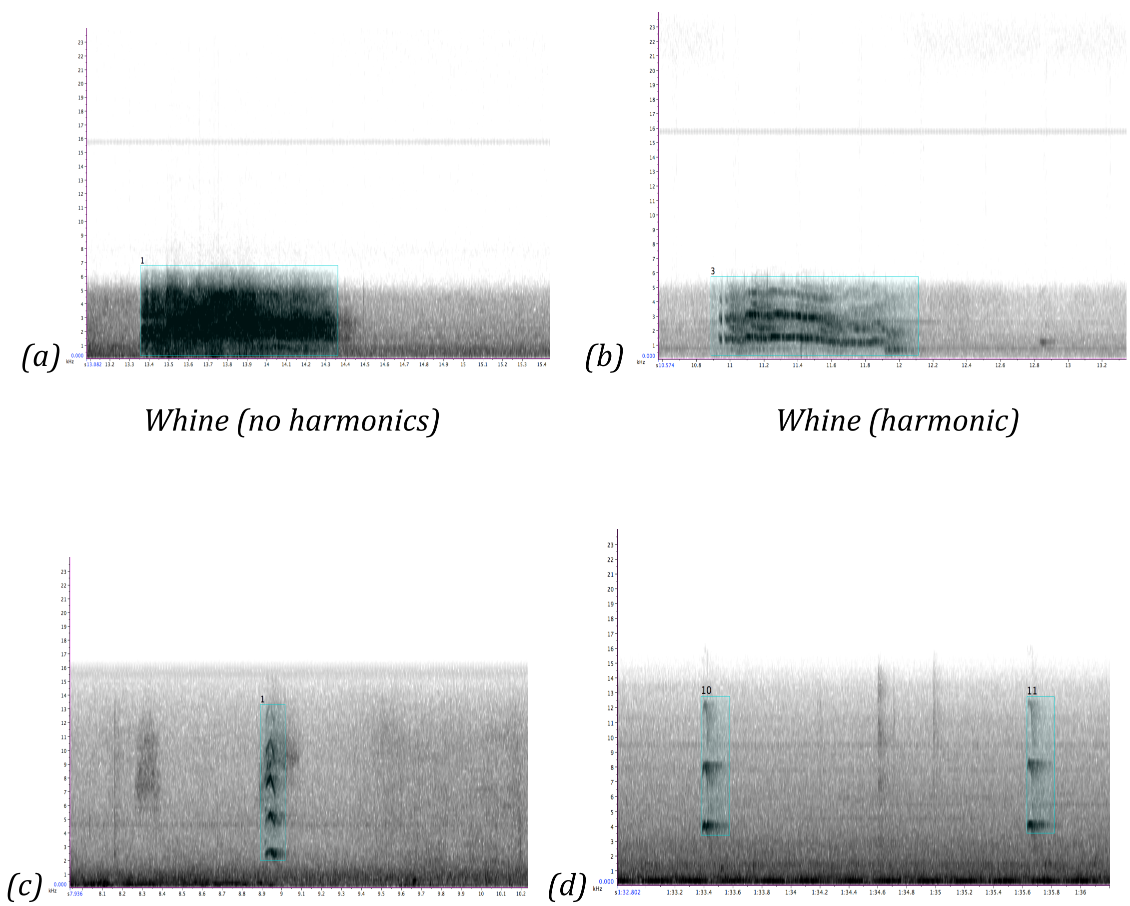
The *chatter*, *creek* and *squeak* share similarities spectrally with the *chirp* and *whines*. The *chatter* looks like a series of *chirps (Figure 4.2 e)* or *whines (Figure 4.2f)* that occur in rapid succession. The chatter-chirp is a harmonic call, and the chatter-whine is a static call. *Creeks (Figure 4.2g)* have the vertical appearance that the chirp produces but they are non-harmonic. They have a high frequency and vary in duration. The *squeak (Figure 4.2h)* spectrally appears like a *whine* with a *chirp* mixed into in. It has a high frequency and is long in duration.

The *scream (Figure 4.2i)* and the *whine* produced identical spectrograms, the only difference in the classification of this call was that it was louder and more piercing than the *whine*.

The *grunt (Figure 4.2j)* and the *blow (Figure 4.2m)* produced the most distinctive spectral images. The *grunt* was low in frequency, short in duration and occurred intermittently. There was little variation in the spectral images among the individuals that shared this call type. The *blow* is static and has a large range of frequency, but is short in duration.

The *swish (Figure 4.2k)* and *hiss (Figure 4.2l)* are spectrally identical; they have a high frequency and often appear static but some were recorded to be harmonic. The spectral appearance of the *swish* and the *hiss* are similar to the *whine*, however, they are lighter on the grayscale than the whine. The hiccup spectrally appears similar to the whine or chirp and is harmonic and short in duration.

Figure 4.2: Spectral images of the 11 call types of the North American River Otter produced by RAVEN.

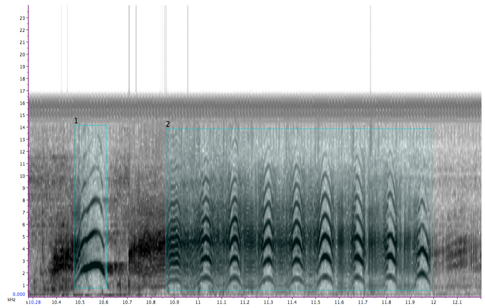


(a) *Whine (no harmonics)*

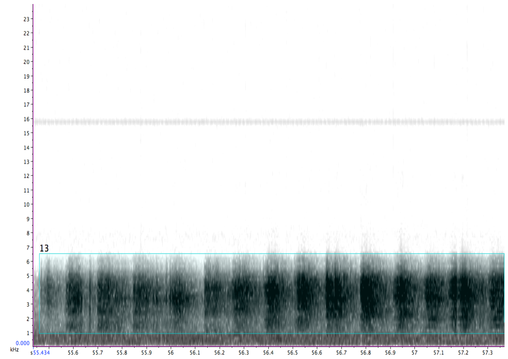
(b) *Whine (harmonic)*

(c) *Chirp ('v' shaped harmonics)*

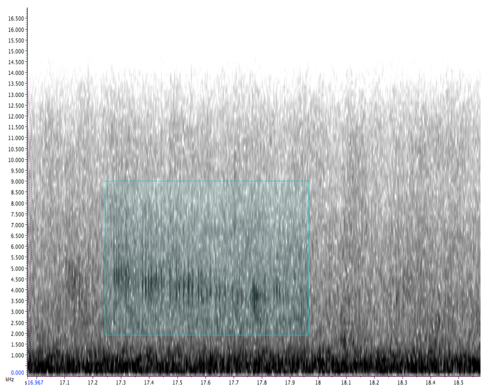
(d) *Chirp (linear harmonics)*

(e)


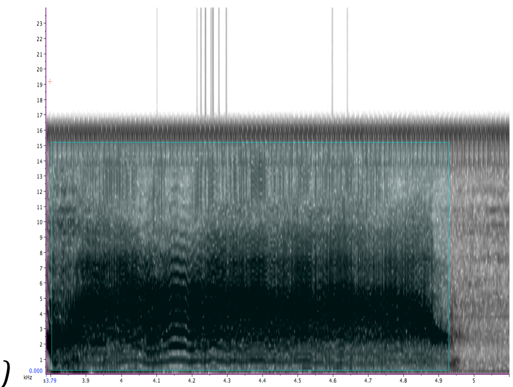
Chatter (chirp in succession)

(f)


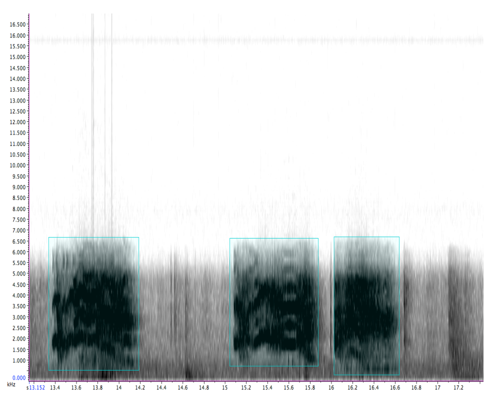
Chatter (whine in succession)

(g)


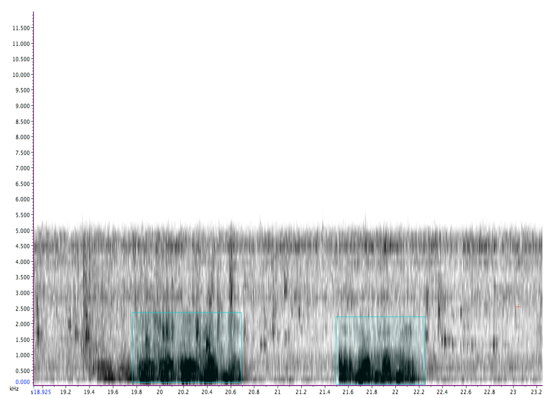
Creek

(h)


Squeak

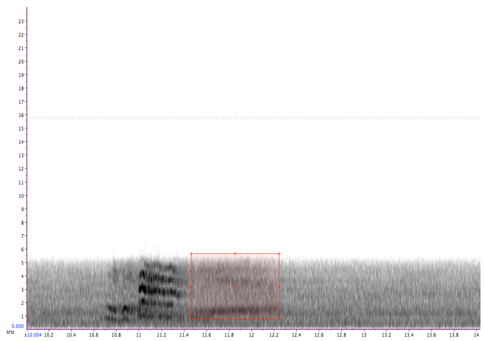
(i)


Scream

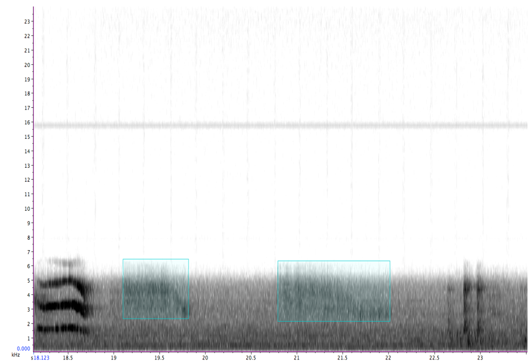
(j)


Grunt

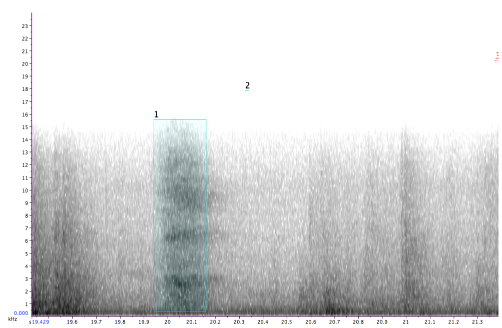
Figure 4.2 continued: Spectral images of the 11 call types of the North American River Otter produced by RAVEN.

(k) 

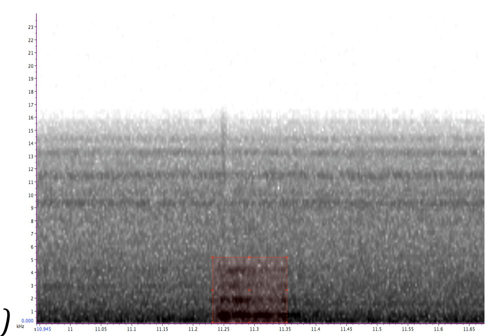
Swish

(l) 

Hiss

(m) 

Blow

(n) 

Hiccup

Modified classification using the sound and RAVEN spectral images

When reviewing the analysis of the classification heard by ear and the spectral analysis (structural view), I noticed several discrepancies. The *Whine, Chirp, Grunt,* and *Blow* were all very distinct both aurally and spectrally, suggesting that these calls are truly separate call types used in the vocal repertoire. But, the other 8 call types *(Chatter, Creek, Squeak, Scream, Hiss, Swish,* and *Hiccup*) were spectrally similar to either a whine or a chirp. (The *whistle* was not included since it was unique to the pups). Therefore I classified them with the call type it shared a similar spectral image with. The *creek, squeak, scream, swish, hiss* and *hiccup* were classified with the *whine* since they share similarities in sound and spectral images. The *chatters* that appeared spectrally similar to the *whine* were classified as a *whine* and the *chatters* that were spectrally similar to the *chirp* were classified with *chirps*. Therefore, the modified classification consisted of 4 major call types; *Whine, Chirp, Grunt, and Blow*.

Statistical Analysis

For statistical analysis I used the data set that consisted of the adults *(individuals; n=10, calls heard n=2726)*. The pups were not included in this analysis because I did not distinguish among individuals for the pup groups.

Classification of Call Types

I conducted two discriminant function analyses: one based on the raw data, and a second based on the reduced data set in which I combined call types that shared similar spectral images. If call categories are distinguishable based only on sound then they should discriminate under the 11-call type classification system. If calls categories are distinguished based on sound and spectral image they produce, then they should discriminant under the 4 major call types used in the modified classification *(Whine, Chirp, Grunt, Blow).* Using the raw data set, there was substantial overlap among calls types and indeed the classification matrix showed that in the initial analysis 114 (9.8%) calls were misclassified in the females and 201 (13%) were misclassified in the males. I reviewed the video and spectral images of all (315) calls that were misclassified. From this review I was able to correct 51 calls for the females, and 41 for the males. Corrected calls were calls that were completely misclassified based on the sound produced by me during my initial classification of calls heard by ear. Although the DFA takes into consideration the structure of the call, I only corrected calls based on the sound. The remaining 63 (5.4%) misclassified for the females, and 160 (10%) misclassified for the males were arguable, in these cases I did not agree with the classifications the DFA established.

Discriminant Function Analysis of Vocal Classifications

I used Discriminant function analysis to assess to what extent my classification by ear was supported by the quantification of the frequencies, powers, duration and harmonics *(Table 2.2)*. This was to determine if calls heard by ear that sound different are truly structurally different, and calls can be classified based on the sound they produce.

In a second discriminant function analysis I wanted to assess what extent my classification was supported when I classified using the sound produced and the spectral images to make my classification. This was to determine if classifying calls on sound and structure was sufficient enough to distinguish between call types.

Individual variation in shared call types

The video analysis suggests that individuality is an influencing factor on the way a vocal is produced. I did not collect data to determine if individuality relays specific messages to others but I wanted to determine if it was potentially present. Based on the spectral images power, duration and number of harmonics do not vary greatly, but frequencies do. I used a Kruskal-Wallis (a non-parametric test) to test the hypothesis that shared call types will show significant differences in their structural components across individuals. I then performed a multiple comparison test to get a complete pair-wise comparison of all the individuals on all the variables.

Results:

Table 4.2: Discriminant function analysis on adult data set using classification heard by ear, and classification by spectral image (% correct). Call types that showed less than 50% correct classification are highlighted in bold.

Call Type	Discriminant Function Analysis (Classification by Ear)	Discriminant Function Analysis (Classification by Spectral Images)
Whine	79.9%	90.8%
Chirp	88.3%	88%
Chatter	**23.8%**	N/A
Creek	**1.6%**	N/A
Squeak	**35.7%**	N/A
Scream	**0%**	N/A
Grunt	93%	92.2%
Swish	**30%**	N/A
Hiss	**46%**	N/A
Blow	61.5%	65.3%
Hiccup	**25%**	N/A
TOTAL	**72%**	**89.1%**

Classification by ear: Wilks' Lambda = .15206

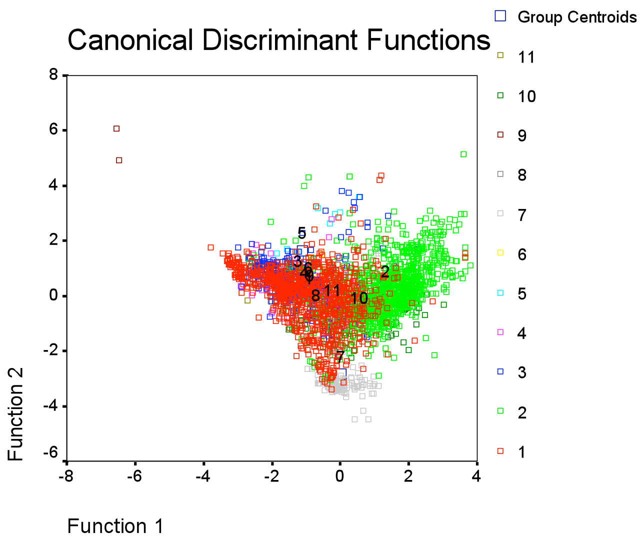
$p<0.0001$

Classification by spectral image: Wilks' Lambda = .20666

$p<0.00001$

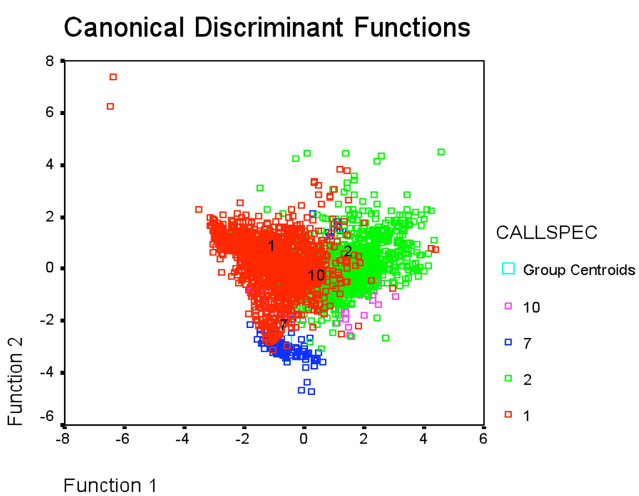
Figure 4.3: Canonical Discriminant Functions showing the classification of call types.

Classification by ear



(a)

Classification by spectral image



(b)

Classification by ear (Classification 1)

The results for the DFA *(Table 4.2-classification by ear)* using only the classification by ear shows a low % correct classification (less than 50%) for the *chatter, creek, squeak, scream, swish, hiss, and hiccup*. This suggests that these call types are structurally comparable to other call types. The *whine, chirp, grunt,* and *blow* yielded results higher than 50%, implying that these are distinct call groups. Therefore call types cannot be distinguished based solely on the sound they produce.

Classification by spectral images (Classification 2)

Using the modified 4-call type classification system *(Table 4.2-classification by spectral images)* the accuracy went from 72% correct to 89.1%. Although the overall percentage increased, the percentage increased most for the *whine*, with the *chirp*, *grunt* and *blow* staying virtually the same. This suggests that the other calls types are structurally similar to the whine, and when grouped together the classification is more accurate. The sound of a vocal can be altered based on if it is used in conjunction with other call types, in isolation, or in a series. Classification by ear is useful in determining vocal categories, but there are several call types that do not discriminate based on the sound. This suggests that both sound and spectral appearance are important in accurately classifying calls, and the DFA's confirm that.

Table 4.3a: Descriptive Statistics of Call Types: Summary and description (mean +/- SD) of the frequencies for the vocalizations produced by river otters. The number of calls analyzed and the number of individuals that exhibit the call type in () are shown*

Call Type	*Sample Size (# of ind.)**	*High Freq (kHz)*	*Low Freq (kHz)*	*Range of Freq (kHz)*	*Mean Freq (kHz)*	*Max Freq (kHz)*	*Center Freq (kHz)*
Whine	*959 (10)*	5970 +/- 1735	609 +/- 501	5471+/-4153	3289+/-922	2587 +/- 913	2573 +/- 817
Chirp	*1024 78)*	8764 +/- 3395	1407 +/- 792	7480 +/- 4951	5080 +/- 1752	2478 +/- 1077	2525 +/- 905

Table 4.3a continued: Descriptive Statistics of Call Types: Summary and description (mean +/- SD) of the frequencies for the vocalizations produced by river otters. The number of calls analyzed and the number of individuals that exhibit the call type in () are shown*

Chatter	*290 (10)*	6571 +/- 1073	661 +/- 472	5900 +/- 1233	3616 +/-577	3028 +/- 754	3076 +/- 544
Creek	*124 (5)*	6481 +/- 1216	982 +/- 582	5500 +/-1346	3669 +/- 823	2945 +/- 653	2896 +/-527
Squeak	*14 (2)*	9644 +/- 2433	447 +/- 335	9197 +/-2374	5045 +/- 1268	3295 +/- 1210	3830 +/- 689
Scream	*20 (3)*	6619 +/- 306	449 +/- 388	6170 +/- 605	3534 +/- 175	2897 +/- 575	3000 +/-304
Grunt	*154 (4)*	1996 +/- 3103	300 +/- 921	1697 +/-2266	1146 +/- 1990	583 +/- 1083	621 +/-1151
Swish	*20 (2)*	5428 +/- 901	881 +/- 300	4548 +/-1052	3155 +/- 418	2269 +/- 881	2475 +/- 862
Hiss	*39 (3)*	5502 +/- 986	1713+/- 576	3788 +/- 1072	3608 +/- 605	3034 +/- 668	3067 +/- 620
Blow	*78 (3)*	10514 +/- 5296	708 +/- 418	9807 +/- 5331	5611 +/- 2646	1897 +/- 815	2317 +/- 646
Hiccup	*4 (2)*	5698 +/- 774	543 +/- 445	5155 +/- 1092	3121 +/- 317	2344 +/- 1285	2344 +/- 1151

Table 4.3b: Descriptive Statistics of Call Types: Summary and description (mean +/- SD) of the powers, duration and harmonics for the vocalizations produced by river otters. Harmonic values are based on the number of harmonic bands present in the spectral image The number of calls analyzed and the number of individuals that exhibit the call type in () are shown.*

Call Type	*Sample Size (# of ind.)*	*Max Pwr (db)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
Whine	*959 (10)*	88+/-11	69+/-10	1.4 +/-1.1	1.1 +/-2

Table 4.3b continued: Descriptive Statistics of Call Types: Summary and description (mean +/- SD) of the powers, duration and harmonics for the vocalizations produced by river otters. Harmonic values are based on the number of harmonic bands present in the spectral image The number of calls analyzed and the number of individuals that exhibit the call type in () are shown.*

Chirp	*1024 (7)*	91 +/-8	73 +/-7	0.2 +/-0.4	3.3 +/-1.7
Chatter	*290 (10)*	94 +/-9	74 +/-8	1.8 +/-1.3	0.4 +/-1.5
Creek	*124 (5)*	86 +/-10	67 +/-10	1.1 +/-0.9	0.4 +/-1.28
Squeak	*14 (2)*	102 +/-2	83 +/- 1	2.1 +/-1.5	2.4 +/- 3.9
Scream	*20 (3)*	101 +/-2	83 +/-3	1.5 +/- 1.2	0.8 +/-1.5
Grunt	*154 (4)*	75 +/-7	62 +/- 8	0.7+/-0.4	0.01 +/-0.16
Swish	*20 (3)*	74 +/-7	58 +/-5.6	1.4 +/-1	0.9 +/-1
Hiss	*39 (3)*	73 +/-7	54 +/-11	1 +/- 0.4	0.3 +/-0.6
Blow	*78 (3)*	86 +/-8	69 +/-6	0.3 +/-0.1	0.9 +/- 0.2
Hiccup	*4 (2)*	88 +/-9	67 +/-7	0.2 +/-0.1	1.8 +/-2.1

Descriptive Statistics

The *whine*, the *chirp* and the *chatter* are the most common call used by river otters, and almost all the individuals exhibited these calls *(Table 4.3a and b)*. The *chirp*, *squeak*, and *blow* have the highest frequencies of all the call types. The *whine*, *chatter, creek squeak, scream, swish,* and *hiss* are the calls with the longest duration (>1 sec) *(Table 4.3a and b)*. The *chirp, grunt, blow* and *hiccup* are very short in duration (<1 sec), and the RAVEN images validate this. The *squeak* and the *chirp* yielded the highest value for number of harmonic bands. The RAVEN images further validate this because the chirps visually contained the most harmonic bands. The *swish*, the *hiss*, and the *grunt* showed the lowest powers/energy (dB).

Table 4.4a: Descriptive statistics on shared call types by individual: Summary and description of the frequencies (mean +/- SD) of individuals with shared call types. The individual with the highest mean value for a given variable in a call type is highlighted in bold and italicized.

Call Type	Individual	Sample Size (n)	High Freq (kHz)	Low Freq (kHz)	Range of Freq (kHz)	Mean Freq (kHz)	Max Freq (kHz)	Center Freq (kHz)
WHINE	*Dell*	*120*	***7556+/-2443***	302+/-545	***8092+/-10682***	3929+/-1431	***3498+/-518***	***3439+/-339***
	Remus	*108*	5286+/-883	984+/-626	4299+/-1106	3135+/-527	2554+/-630	2497+/-487
	Rizzo	*51*	5895+/-67	475+/-241	5420+/-561	3185+/-253	2081+/-818	2000+/-577
	PB	*62*	5311+/-1011	775+/-497	4536+/-1146	3043+/-554	2177+/-589	2640+/-626
	Bert	*65*	5554+/-896	470+/-473	5085+/-926	3012+/-547	1970+/-754	1936+/-590
	Kassie	*101*	6059+/-2860	1011+/-304	5105+/-2957	3535+/-1416	2644+/-805	2547+/-620
	Delaney	*316*	6247+/-827	556+/-358	5687+/-878	3401+/-461	2854+/-802	2824+/-720
	Leveau	*4*	6403+/-4437	**1711+/-1174**	4691+/-4300	***4057+/-2431***	2969+/-1033	3297+/-1122
	Jelly	*16*	4479+/-1632	509+/-383	3969+/-1532	2493+/-905	1992+/-780	2039+/-576
	Edith	*116*	4940+/-1493	392+/-382	*4547+/-1476*	2666+/-802	1757+/-918	1710+/-829

Table 4.4a continued: Descriptive statistics on shared call types by individual: Summary and description of the frequencies (mean +/- SD) of individuals with shared call types. The individual with the highest value mean for a given variable in a call type is highlighted in bold and italicized.

Call Type	*Individual*	*Sample Size (n)*	*High Freq (kHz)*	*Low Freq (kHz)*	*Range of Freq (kHz)*	*Mean Freq (kHz)*	*Max Freq (kHz)*	*Center Freq (kHz)*
CHIRP	*Dell*	*497*	9187+/-3940	1134+/-406	***8232+/-6303***	5149+/-1960	2291+/-817	2398+/-748
	Remus	*384*	8267+/-2396	1334+/-544	7030+/-2953	4801+/-1200	2342+/-1086	2335+/-791
	Rizzo	*7*	6079+/-898	867+/-331	5213+/-846	3473+/-528	2063+/-446	2116+/-415
	Bert	*3*	5344+/-1340	547+/-509	4797+/-1297	2945+/-779	1500+/-938	1625+/-780
	Kassie	*106*	***9605+/-3447***	***3086+/-894***	6519+/-3412	***6345+/-1852***	***3897+/-1172***	***3860+/-939***
	Delaney	*15*	6117+/-762	861+/-616	5256+/-995	3489+/-482	2638+/-391	2700+/-441
	Edith	*12*	5409+/-1931	1427+/-884	3982+/-2115	3418+/-1066	2328+/-948	2359+/-852
Call Type	*Individual*	*Sample Size (n)*	*High Freq (kHz)*	*Low Freq (kHz)*	*Range of Freq (kHz)*	*Mean Freq (kHz)*	*Max Freq (kHz)*	*Center Freq (kHz)*
CHATTER	*Dell*	*9*	***9878+/-3426***	314+/-293	***9564+/-3305***	***5096+/-1783***	***3230+/-1128***	***3625+/-487***
	Remus	*13*	6478+/-207	908+/-421	5571+/-570	3694+/-171	2899+/-827	2943+/-442
	Rizzo	*3*	5800+/-366	568+/-167	5231+/-523	3184+/-112	2188+/-659	2188+/-286
	PB	*9*	5864+/-407	667+/-407	5197+/-402	3265+/-354	2167+/-364	2068+/-643

Table 4.4a continued: Descriptive statistics on shared call types by individual: Summary and description of the frequencies (mean +/- SD) of individuals with shared call types. The individual with the highest value mean for a given variable in a call type is highlighted in bold and italicized.

	Bert	*3*	4721+/-670	217+/-27	4504+/-675	2469+/-333	1063+/-886	1188+/-758
	Kassie	*1*	14120	**1141**	**12678**	**7781**	2063	2625
	Delaney	*199*	6555+/-356	616+/-451	5923+/-712	3586+/-276	3164+/-673	3191+/-450
	Leveau	*28*	6341+/-893	**1052+/-496**	5290+/-1048	3697+/-498	3063+/-801	3036+/-534
	Jelly	*20*	6025+/-653	533+/-481	5491+/-980	3279+/-299	2578+/-482	2625+/-265
	Edith	*5*	6292+/-478	923+/-346	5409+/-709	3607+/-267	2625+/-398	2550+/-389
Call Type	*Individual*	*Sample Size (n)*	*High Freq (kHz)*	*Low Freq (kHz)*	*Range of Freq (kHz)*	*Mean Freq (kHz)*	*Max Freq (kHz)*	*Center Freq (kHz)*
CREEK	*Dell*	*6*	***8720+/-2890***	679+/-400	***8040+/-2832***	4699+/-1500	***3438+/-844***	***3531+/-401***
	Bert	*4*	6313+/-190	*1166+/-834*	5147+/-782	3740+/-462	2859+/-756	2906+/-817
	Delaney	*76*	6446+/-291	856+/-460	5590+/-542	***6550+/-645***	2970+/-571	2903+/-442
	Leveau	*18*	6500+/-2364	**1475+/-476**	5025+/-2326	3987+/-1247	2722+/-931	2688+/-710
	Edith	*20*	5961+/-400	1068+/-817	4893+/-911	3515+/-454	2916+/-539	2859+/-509

Table 4.4a continued: Descriptive statistics on shared call types by individual: Summary and description of the frequencies (mean +/- SD) of individuals with shared call types. The individual with the highest mean value for a given variable in a call type is highlighted in bold and italicized.

Call Type	*Individual*	*Sample Size (n)*	*High Freq (kHz)*	*Low Freq (kHz)*	*Range of Freq (kHz)*	*Mean Freq (kHz)*	*Max Freq (kHz)*	*Center Freq (kHz)*
SQUEAK	*Dell*	*13*	*10158+/-1550*	*471+/-336*	*9688+/-1568*	*5314+/-802*	*3418+/-1164*	*3995+/-319*
	Bert	*1*	2961	135	2826	1548	1688	1688
Call Type	*Individual*	*Sample Size (n)*	*High Freq (kHz)*	*Low Freq (kHz)*	*Range of Freq (kHz)*	*Mean Freq (kHz)*	*Max Freq (kHz)*	*Center Freq (kHz)*
SCREAM	*Delaney*	*15*	**6726+/-177**	412+/-353	**6315+/-482**	***3569+/-141***	***2975+/-621***	***3088+/-80***
	Jelly	*4*	6168+/-325	***686+/-486***	5481+/-613	3427+/-277	2625+/-405	2672+/-180
	Edith	*1*	***6808***	49	***6759***	3429	2813	3000
Call Type	*Individual*	*Sample Size (n)*	*High Freq (kHz)*	*Low Freq (kHz)*	*Range of Freq (kHz)*	*Mean Freq (kHz)*	*Max Freq (kHz)*	*Center Freq (kHz)*
GRUNT	*Dell*	*119*	1061+/-374	33+/-39	1028+/-372	544+/-196	243+/-128	258+/-109
	Rizzo	*14*	994+/-164	61+/-69	933+/-160	528+/-97	522+/-183	522+/-109
	PB	*4*	1531+/-1243	141+/-59	1390+/-1189	836+/-649	375+/-153	469+/-108
	Bert	*2*	1770+/-859	183+/-5	1588+/-864	976+/-427	1125+/-1061	750+/-530
	Edith	*15*	***10502+/-4196***	***2694+/-1564***	***7808+/-3187***	***6598+/-2736***	***3325+/-1859***	***3613+/-1901***

Table 4.4a continued: Descriptive statistics on shared call types by individual: Summary and description of the frequencies (mean +/- SD) of individuals with shared call types. The individual with the highest mean value for a given variable in a call type is highlighted in bold and italicized.

Call Type	Individual	Sample Size (n)	High Freq (kHz)	Low Freq (kHz)	Range of Freq (kHz)	Mean Freq (kHz)	Max Freq (kHz)	Center Freq (kHz)
SWISH	Leveau	12	5334+/-1144	876+/-339	4458+/-1315	3105+/-528	***2328+/-1126***	2156+/-667
	PB	8	***5569+/-335***	***888+/-253***	***4681+/-504***	***3229+/-157***	2180+/-316	***2953+/-940***
Call Type	Individual	Sample Size (n)	High Freq (kHz)	Low Freq (kHz)	Range of Freq (kHz)	Mean Freq (kHz)	Max Freq (kHz)	Center Freq (kHz)
HISS	Remus	6	4945+/-1198	1537+/-340	3407+/-1389	3241+/-541	2719+/-719	2594+/-434
	Bert	2	**6217+/-144**	**2191+/-0**	***4025+/-144***	**4204+/-72**	***3563+/-0***	***3656+/-133***
	Leveau	30	5554+/-959	1700+/-620	3854+/-1064	3627+/-607	3063+/-674	3125+/-629
	Edith	1	5838	***2205***	3632	4022	3000	3000
Call Type	Individual	Sample Size (n)	High Freq (kHz)	Low Freq (kHz)	Range of Freq (kHz)	Mean Freq (kHz)	Max Freq (kHz)	Center Freq (kHz)
BLOW	Dell	24	7346+/-3358	833+/-503	6515+/-3494	4089+/-1648	***2438+/-967***	***2648+/-667***
	PB	18	4468+/-1092	523+/-381	3945+/-1868	2496+/-449	1198+/-451	1979+/-829
	Edith	36	***15650+/-946***	***717+/-346***	***14932+/-1218***	***8183+/-369***	1885+/-793	2267+/-394

Table 4.4a continued: Descriptive statistics on shared call types by individual: Summary and description of the frequencies (mean +/- SD) of individuals with shared call types. The individual with the highest mean value for a given variable in a call type is highlighted in bold and italicized.

Call Type	*Individual*	*Sample Size (n)*	*High Freq (kHz)*	*Low Freq (kHz)*	*Range of Freq (kHz)*	*Mean Freq (kHz)*	*Max Freq (kHz)*	*Center Freq (kHz)*
HICCUP	*Kassie*	*2*	5203+/-689	***721+/-611***	4483+/-1300	2962+/-39	***2531+/-928***	***2531+/-928***
	Delaney	*2*	***6192+/-587***	366+/-308	***5827+/-279***	***3279+/-447***	2156+/-1989	2156+/-1724

Table 4.4b: Descriptive Statistics of Call Types: Summary and description (mean +/- SD) of the powers, duration and harmonics for the shared vocalizations exhibited by individuals. The individual with the highest mean value for a given variable in a call type is highlighted in bold and italicized.

Call Type	*Individual*	*Sample Size*	*Max Pwr (db)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
WHINE	*Dell*	*120*	***95+/-5***	74+/-6	***2.7+/-1.3***	0.3+/1.4
	Remus	*108*	77+/-8	61+/-6	1+/-0.7	**1.8+/-2.3**
	Rizzo	*51*	83+/11	***82+/-9***	1.3+/1	2.7+/1.8
	PB	*62*	90+/-8	72+/-7	2.2+/-1.1	0.2+/-0.6
	Bert	*65*	82+/-10	64+/-8	0.9+/-0.08	0.4+/-1.1
	Kassie	*101*	88+/-9	70+/-7	0.7+/-0.5	*2.8+/-1.8*
	Delaney	*316*	94+/-8	75+/-8	1.4+/-1	0.8+/-1.8
	Leveau	*4*	86+/-8	71+/-9	0.8+/-0.5	0.8+/-1
	Jelly	*16*	86+/-10	69+/-7	0.9+/-0.7	1.6+/-1.5
	Edith	*116*	78+/-12	61+/-9	0.9+/-0.8	1.2+/-1.7

Table 4.4b continued: Descriptive Statistics of Call Types: Summary and description (mean +/- SD) of the powers, duration and harmonics for the shared vocalizations exhibited by individuals. The individual with the highest mean value for a given variable in a call type is highlighted in bold and italicized.

Call Type	*Individual*	*Sample Size*	*Max Pwr (db)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
CHIRP	*Dell*	*497*	**93+/-9**	**74+/-8**	**0.2+/-0.4**	***3.5+/-2***
	Remus	*384*	88+/-4	71+/-4	0.1+/-0.1	3.3+/-1.6
	Rizzo	*7*	91+/-12	70+/-11	0.7+/-0.3	2.6+/-1.8
	Bert	*3*	81+/-8	65+/-4	0.7+/-0.3	2+/-1.7
	Kassie	*106*	*96+/-8*	*77+/-6*	**0.2+/-0.1**	2.4+/-0.8
	Delaney	*15*	91+/-11	67+/-13	*1.7+/-1*	1.6+/-1.4
	Edith	*12*	70+/-13	53+/-11	**0.2+/-0.1**	2.2+/-1
Call Type	*Individual*	*Sample Size*	*Max Pwr (db)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
CHATTER	*Dell*	*9*	***98+/-7***	***78+/-8***	1.5+/-0.7	**4.2+/-4.7**
	Remus	*13*	88+/-10	68+/-8	1.4+/-1	1.8+/-2
	Rizzo	*3*	86+/-13	63+/-10	***1.7+/-1.2***	2.7+/-2.5
	PB	*9*	88+/-5	70+/-4	0.7+/-0.2	0+/-0
	Bert	*3*	72+/-6	54+/-3	0.5+/-0.2	2+/-2
	Kassie	*1*	98	71	0.8	0
	Delaney	*199*	***98+/-6***	77+/-6	2+/-1.4	0.2+/-0.9
	Leveau	*28*	80+/-8	61+/-6	1+/-1	0.1+/-0.4
	Jelly	*20*	93+/-6	73+/-5	1.5+/-1.5	0.3+/-0.6
	Edith	*5*	84+/-8	64+/-7	1.2+/-0.4	0+/0

Table 4.4b continued: Descriptive Statistics of Call Types: Summary and description (mean +/- SD) of the powers, duration and harmonics for the shared vocalizations exhibited by individuals. The individual with the highest mean value for a given variable in a call type is highlighted in bold and italicized.

Call Type	Individual	Sample Size	Max Pwr (db)	Avg Pwr (db)	Duration (s)	Harmonics (#)
CREEK	*Dell*	*6*	***97+/-8***	***77+/-7***	***1.7+/-1.1***	***2.3+/-2.9***
	Bert	*4*	80+/-9	61+/-8	1.1+/-0.4	0+/-0
	Delaney	*76*	92+/-6	72+/-6	1.1+/-0.8	0.02+/-0.2
	Leveau	*18*	76+/-8	57+/-6	1.2+/-1.4	0.9+/-1
	Edith	*20*	74+/-8	56+/-6	0.9+/-0.5	1.1+/-2
Call Type	*Individual*	*Sample Size*	*Max Pwr (db)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
SQUEAK	*Dell*	*13*	***102+/-2***	83+/-1	***2.2+/-1.4***	***2.5+/-4***
	Bert	*1*	98	***84***	0.103	0
Call Type	*Individual*	*Sample Size*	*Max Pwr (db)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
SCREAM	*Delaney*	*15*	***102+/-2***	83+/-3	***1.7+/-1.3***	***1.1+/-1.7***
	Jelly	*4*	98+/-4	80+/-3	0.6+/-0.3	0+/-0
	Edith	*1*	*102*	***86***	1.6	0
Call Type	*Individual*	*Sample Size*	*Max Pwr (db)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
GRUNT	*Dell*	*119*	77+/-6	64+/-7	0.7+/-0.4	*0.01+/-0.2*
	Rizzo	*14*	72+/-7	61+/-6	***0.5+/-0.4***	0+/-0
	PB	*4*	71+/-3	60+/-2	0.9+/-0.5	0+/-0
	Bert	*2*	***81+/-14***	**69+/-15**	**0.5+/-0.2**	0+/-0
	Edith	*15*	67+/-7	50+/-6	0.6+/-0.3	0+/-0

Table 4.4b continued: Descriptive Statistics of Call Types: Summary and description (mean +/- SD) of the powers, duration and harmonics for the shared vocalizations exhibited by individuals. The individual with the highest mean value for a given variable in a call type is highlighted in bold and italicized.

Call Type	*Individual*	*Sample Size*	*Max Pwr (db)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
SWISH	*Leveau*	*12*	70+/-5	55+/-4	0.9+/-0.5	***1.4+/-1***
	PB	*8*	***80+/-4***	***63+/-3***	***2.2+/-1***	0+/-0
Call Type	*Individual*	*Sample Size*	*Max Pwr (db)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
HISS	*Remus*	*6*	72+/-3	**57+/-2**	***1.1+/-0.5***	0+/-0
	Bert	*2*	69+/-8	55+/-5	1+/-0.2	0+/-0
	Leveau	*30*	**73+/-8**	53+/-13	1+/-0.4	*0.3+/-0.7*
	Edith	*1*	*74*	*59*	***1.1***	0
Call Type	*Individual*	*Sample Size*	*Max Pwr (db)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
BLOW	*Dell*	*24*	85+/-5	69+/-3	0.6+/-0.03	0+/0
	PB	*18*	75+/-4	60+/-4	0.2+/-0.05	0+/-0
	Edith	*36*	***91+/-4***	***73+/-3***	***0.4+/-0.07***	***1.9+/-1.7***
Call Type	*Individual*	*Sample Size*	*Max Pwr (db)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
HICCUP	*Kassie*	*2*	***92+/-4***	***71+/-8***	***0.3+/-0.2***	***3.5+/-0.7***
	Delaney	*2*	79+/-7	63+/-1	0.16+/-0	0+/0

Table 4.5: Kruskal-Wallis testing the differences among individuals with shared call types. Call Types with significant differences are highlighted in bold and marked with and asterisk (*).

Whine	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*9*	575318661.2249	63924295.69166	26.28837	**<0.001***
	Within Groups	*949*	2307642699.00206	2431657.21707		
Chirp	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*6*	584028236.16952	97338039.36159	8.83566	**<0.001***
	Within Groups	*1017*	1.12038	11016496.44091		
Chatter	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*9*	179975041.23887	19997226.80432	36.70185	**<0.001***
	Within Groups	*280*	152559700.21496	544856.0722		
Creek	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*4*	35676165.76923	8919041.44231	7.25704	**<0.001***
	Within Groups	*119*	146253265.72754	1229019.03973		

Table 4.5 continued: Kruskal-Wallis testing the differences among individuals with shared call types. Call Types with significant differences are highlighted in bold and marked with and asterisk (*).

Squeak	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*1*	48104234.1978	48104234.1978	20.01708	>0.05
	Within Groups	*12*	28831914.91077	2403159.5759		
Scream	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*2*	1024152.56617	512076.28308	11.52863	>0.05
	Within Groups	*17*	755102.58333	44417.79902		
Grunt	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*4*	1204316994.28191	301079248.57048	166.95141	**<0.01***
	Within Groups	*149*	268705774.35167	1803394.45874		
Swish	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*12*	263906.30208	263906.30208	0.31311	**<0.01***
	Within Groups	*8*	15171295.89542	842.849.77197		

Table 4.5 continued: Kruskal-Wallis testing the differences among individuals with shared call types. Call Types with significant differences are highlighted in bold and marked with and asterisk (*).

Hiss	*Source of Variation*	*d.f*	SS	MS	F	p-level significance
	Between Groups	*3*	3080790.78031	1026930.2601	1.06097	>0.05
	Within Groups	*35*	33877067.332	967916.20949		
Blow	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*2*	1848184480.94388	924092240.47194	222.92068	**<0.001***
	Within Groups	*75*	310903936.78958	4145385.82386		
Hiccup	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*1*	978318.81	978318.81	2.38946	>0.05
	Within Groups	*2*	818860.25	409430.125		

Table 4.6a: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

Call Type	*Comparison*	*High Frequency (kHz)*	*Low Frequency (kHz)*	*Range of Frequency (kHz)*
WHINE	*KS vs DE*	**<0.000000001***	**<0.000000001***	**<0.000000001***
	KS vs LV	>0.05	>0.05	>0.05
	KS vs JY	>0.05	**<0.002***	>0.05
	KS vs ED	>0.05	**<0.000000001***	>0.05
	KS vs DL	**<0.000000001***	**<0.000000001***	**<0.000000001***
	KS vs RZ	>0.05	**<0.000000001***	**<0.01***
	KS vs RM	>0.05	>0.05	>0.05
	KS vs BT	>0.05	**<0.000000001***	>0.05
	KS vs PB	>0.05	**<0.01***	>0.05
	DE vs LV	>0.05	>0.05	>0.05
	DE vs JY	**<0.000001***	>0.05	**<0.0001***
	DE vs ED	**<0.000000001***	**<0.0004***	**<0.000000001***
	DE vs DL	**<0.0003***	**<0.000000001***	**<0.000000001***
	DE vs RZ	**<0.0002***	>0.05	>0.05
	DE vs RM	**<0.000000001***	**<0.000000001***	**<0.000000001***
	DE vs BT	**<0.000000001***	>0.05	**<0.0003***
	DE vs PB	**<0.000000001***	>0.05	**<0.000000001***
	LV vs JY	>0.05	>0.05	>0.05
	LV vs ED	>0.05	>0.05	>0.05
	LV vs DL	>0.05	**<0.001***	**<0.003***
	LV vs RZ	>0.05	>0.05	>0.05
	LV vs RM	>0.05	>0.05	>0.05
	LV vs BT	>0.05	>0.05	>0.05
	LV vs PB	>0.05	>0.05	>0.05

Table 4.6a continued: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

	JY vs ED	>0.05	>0.05	>0.05
	JY vs DL	>0.05	>0.05	>0.05
	JY vs RZ	>0.05	>0.05	>0.05
	JY vs RM	>0.05	>0.05	>0.05
	JY vs BT	>0.05	>0.05	>0.05
	JY vs PB	>0.05	>0.05	>0.05
	ED vs DL	**<0.000000001***	**<0.08***	**<0.000000001***
	ED vs RZ	>0.05	>0.05	>0.05
	ED vs RM	>0.05	**<0.000000001***	>0.05
	ED vs BT	>0.05	>0.05	>0.05
	ED vs PB	>0.05	**<0.000004***	>0.05
	DL vs RZ	**<0.000000007***	**<0.000000001***	**<0.000000001***
	DL vs RM	**<0.000000007***	**<0.005***	**<0.000000001***
	DL vs BT	**<0.000000007***	**<0.000000001***	**<0.000000001***
	DL vs PB	**<0.000000007***	**<0.000000001***	**<0.000000001***
	RZ vs RM	>0.05	**<0.0001***	**<0.0001***
	RZ vs BT	>0.05	>0.05	<0.05
	RZ vs PB	>0.05	>0.05	**<0.04***
	RM vs BT	>0.05	**<0.000000002***	**>0.02***
	RM vs PB	>0.05	>0.05	>0.05
	BT vs PB	>0.05	**<0.001***	>0.05

Table 4.6a continued: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

Call Type	*Comparison*	*Mean Frequency (kHz)*	*Max Frequency (kHz)*	*Center Frequency (kHz)*
WHINE	*KS vs DE*	**<0.00001***	>0.05	**<0.002***
	KS vs LV	>0.05	>0.05	>0.05
	KS vs JY	>0.05	>0.05	>0.05
	KS vs ED	**<0.00003***	**<0.000000001***	**<0.00000006***
	KS vs DL	**<0.01***	**<0.000000001***	**<0.000000001***
	KS vs RZ	>0.05	**<0.002***	**<0.002***
	KS vs RM	>0.05	>0.05	>0.05
	KS vs BT	>0.05	**<0.00002***	**<0.00006***
	KS vs PB	>0.05	**<0.002***	>0.05
	DE vs LV	>0.05	>0.05	>0.05
	DE vs JY	**<0.000008***	**<0.002***	**<0.0005***
	DE vs ED	**<0.000000001***	**<0.000000001***	**<0.000000001***
	DE vs DL	>0.05	**<0.0000000001***	**<0.0000000001***
	DE vs RZ	**<0.00005**	**<0.000000001***	**<0.000000001***
	DE vs RM	**<0.000000003***	**<0.01***	**<0.000005***
	DE vs BT	**<0.000000001***	**<0.000000001***	**<0.000000001***
	DE vs PB	**<0.000000001***	**<0.000000001***	>0.05
	LV vs JY	>0.05	>0.05	>0.05
	LV vs ED	>0.05	>0.05	>0.05
	LV vs DL	>0.05	>0.05	>0.05
	LV vs RZ	>0.05	>0.05	>0.05
	LV vs RM	>0.05	>0.05	>0.05
	LV vs BT	>0.05	>0.05	>0.05
	LV vs PB	>0.05	>0.05	>0.05
	JY vs ED	>0.05	>0.05	>0.05
	JY vs DL	**<0.001***	**<0.0000000003***	**<0.000000001***

Table 4.6a continued: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

	JY vs RZ	>0.05	>0.05	>0.05
	JY vs RM	>0.05	>0.05	>0.05
	JY vs BT	>0.05	>0.05	>0.05
	JY vs PB	>0.05	>0.05	>0.05
	ED vs DL	**<0.000000001***	**<0.000000001***	**<0.000000001***
	ED vs RZ	>0.05	>0.05	>0.05
	ED vs RM	**<0.003***	**<0.0000004***	**<0.00001***
	ED vs BT	>0.05	>0.05	>0.05
	ED vs PB	>0.05	>0.05	**<0.0000001***
	DL vs RZ	**<0.004***	**<0.000000001***	**<0.000000001***
	DL vs RM	**<0.00007***	**<0.000000001***	**<0.000000001***
	DL vs BT	**<0.000005***	**<0.000000001***	**<0.000000001***
	DL vs PB	**<0.001***	**<0.000000001***	**<0.000000001***
	RZ vs RM	>0.05	>0.05	**<0.03***
	RZ vs BT	>0.05	>0.05	>0.05
	RZ vs PB	>0.05	>0.05	**<0.0006***
	RM vs BT	>0.05	**<0.001***	**<0.002***
	RM vs PB	>0.05	**<0.04***	>0.05
	BT vs PB	>0.05	>0.05	**<0.00003***

Call Type	*Comparison*	*High Frequency (kHz)*	*Low Frequency (kHz)*	*Range of Frequency (kHz)*
CHIRP	*KS vs DE*	**<0.006***	**<0.000002***	>0.05
	KS vs ED	**<0.001***	**<0.00001***	>0.05
	KS vs DL	>0.05	**<0.000002***	>0.05
	KS vs RZ	>0.05	**<0.000002***	>0.05

Table 4.6a continued: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

	KS vs RM	>0.05	**<0.000002***	>0.05
	KS vs BT	**<0.03***	**<0.000002***	>0.05
	DE vs ED	>0.05	>0.05	>0.05
	DE vs DL	**<0.01***	>0.05	>0.05
	DE vs RZ	>0.05	>0.05	>0.05
	DE vs RM	>0.05	>0.05	>0.05
	DE vs BT	>0.05	>0.05	>0.05
	ED vs DL	**<0.02***	>0.05	**<0.004***
	ED vs RZ	>0.05	>0.05	<0.05
	ED vs RM	**<0.03***	>0.05	**<0.04***
	ED vs BT	>0.05	>0.05	<0.05
	DL vs RZ	>0.05	>0.05	>0.05
	DL vs RM	>0.05	>0.05	>0.05
	DL vs BT	>0.05	>0.05	>0.05
	RZ vs RM	>0.05	>0.05	>0.05
	RZ vs BT	>0.05	>0.05	>0.05
	RM vs BT	>0.05	>0.05	>0.05
Call Type	*Comparison*	*Mean Frequency (kHz)*	*Max Frequency (kHz)*	*Center Frequency (kHz)*
CHIRP	*KS vs DE*	**<0.000001***	>0.05	**<0.002***
	KS vs ED	**<0.0000002***	**<0.008***	**<0.00000006***
	KS vs DL	**<0.00000002***	**<0.000000001***	**<0.000000001***
	KS vs RZ	**<0.005***	**<0.002***	>0.05
	KS vs RM	**<0.0000002***	>0.05	**<0.000000001***
	KS vs BT	**<0.0003***	**<0.00002***	**<0.002***

Table 4.6a continued: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

	DE vs ED	>0.05	**<0.000000001***	>0.05
	DE vs DL	**<0.004***	**<0.0000000001***	>0.05
	DE vs RZ	>0.05	**<0.000000001***	>0.05
	DE vs RM	**<0.04***	**<0.01***	**<0.0006***
	DE vs BT	>0.05	**<0.000000001***	**<0.04***
	ED vs DL	**<0.02***	**<0.000000001***	>0.05
	ED vs RZ	>0.05	>0.05	>0.05
	ED vs RM	>0.05	**<0.0000004***	>0.05
	ED vs BT	>0.05	>0.05	>0.05
	DL vs RZ	>0.05	**<0.000000001***	>0.05
	DL vs RM	>0.05	**<0.000000001***	**<0.000000008***
	DL vs BT	**<0.04***	**<0.000000001***	>0.05
	RZ vs RM	>0.05	>0.05	>0.05
	RZ vs BT	>0.05	>0.05	>0.05
	RM vs BT	>0.05	**<0.001***	>0.05

Call Type	*Comparison*	*High Frequency (kHz)*	*Low Frequency (kHz)*	*Range of Frequency (kHz)*
CHATTER	*DE vs LV*	**<0.0001***	**<0.003***	**<0.0001**
	DE vs JY	**<0.00006***	>0.05	.0.05
	DE vs ED	>0.05	>0.05	>0.05
	DE vs DL	>0.05	>0.05	**<0.007***
	DE vs RZ	>0.05	>0.05	>0.05
	DE vs RM	>0.05	>0.05	>0.05
	DE vs BT	**<0.004***	>0.05	>0.05
	DE vs PB	**<0.0003***	>0.05	**<0.01***

Table 4.6a continued: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

	LV vs JY	>0.05	**<0.04***	>0.05
	LV vs ED	>0.05	>0.05	>0.05
	LV vs DL	**<0.0003***	**<0.003***	**<0.00000003***
	LV vs RZ	>0.05	>0.05	>0.05
	LV vs RM	>0.05	>0.05	>0.05
	LV vs BT	>0.05	>0.05	>0.05
	LV vs PB	>0.05	>0.05	>0.05
	JY vs ED	>0.05	>0.05	>0.05
	JY vs DL	**<0.00008***	>0.05	**<0.0006***
	JY vs RZ	>0.05	>0.05	>0.05
	JY vs RM	>0.05	>0.05	>0.05
	JY vs BT	>0.05	>0.05	>0.05
	JY vs PB	>0.05	>0.05	>0.05
	ED vs DL	>0.05	>0.05	**<0.007***
	ED vs RZ	>0.05	>0.05	>0.05
	ED vs RM	>0.05	>0.05	>0.05
	ED vs BT	>0.05	>0.05	>0.05
	ED vs PB	>0.05	>0.05	>0.05
	DL vs RZ	**<0.01***	>0.05	**<0.01***
	DL vs RM	>0.05	>0.05	**<0.0006***
	DL vs BT	**<0.002***	>0.05	**<0.0004***
	DL vs PB	**<0.0004***	>0.05	**<0.000005***
	RZ vs RM	>0.05	>0.05	>0.05
	RZ vs BT	>0.05	>0.05	>0.05
	RZ vs PB	>0.05	>0.05	>0.05

Table 4.6a continued: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

	RM vs BT	>0.05	>0.05	>0.05
	RM vs PB	>0.05	>0.05	>0.05
	BT vs PB	>0.05	>0.05	<0.05
Call Type	*Comparison*	*Mean Frequency (kHz)*	*Max Frequency (kHz)*	*Center Frequency (kHz)*
CHATTER	*DE vs LV*	>0.05	>0.05	>0.05
	DE vs JY	**<0.002***	**<0.006***	**<0.000001***
	DE vs ED	>0.05	>0.05	>0.05
	DE vs DL	>0.05	>0.05	>0.05
	DE vs RZ	>0.05	>0.05	>0.05
	DE vs RM	>0.05	>0.05	>0.05
	DE vs BT	>0.05	>0.05	>0.05
	DE vs PB	>0.05	**<0.009***	>0.05
	LV vs JY	**<0.009***	>0.05	>0.05
	LV vs ED	>0.05	>0.05	>0.05
	LV vs DL	>0.05	>0.05	>0.05
	LV vs RZ	>0.05	>0.05	>0.05
	LV vs RM	>0.05	>0.05	>0.05
	LV vs BT	>0.05	>0.05	>0.05
	LV vs PB	>0.05	**<0.02***	>0.05
	JY vs ED	>0.05	>0.05	>0.05
	JY vs DL	**<0.003***	>0.05	**<0.00001***
	JY vs RZ	>0.05	>0.05	>0.05
	JY vs RM	**<0.01**	>0.05	>0.05
	JY vs BT	>0.05	>0.05	>0.05
	JY vs PB	>0.05	>0.05	>0.05

Table 4.6a continued: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

	ED vs DL	>0.05	>0.05	**<0.009***
	ED vs RZ	>0.05	>0.05	>0.05
	ED vs RM	>0.05	>0.05	>0.05
	ED vs BT	>0.05	>0.05	>0.05
	ED vs PB	>0.05	>0.05	>0.05
	DL vs RZ	>0.05	>0.05	**<0.01***
	DL vs RM	>0.05	>0.05	>0.05
	DL vs BT	**<0.01***	>0.05	**<0.004***
	DL vs PB	>0.05	>0.05	**<0.006***
	RZ vs RM	>0.05	>0.05	>0.05
	RZ vs BT	>0.05	>0.05	>0.05
	RZ vs PB	>0.05	>0.05	>0.05
	RM vs BT	**<0.04***	>0.05	>0.05
	RM vs PB	>0.05	>0.05	>0.05
	BT vs PB	>0.05	>0.05	>0.05

Call Type	*Comparison*	*High Frequency (kHz)*	*Low Frequency (kHz)*	*Range of Frequency (kHz)*
CREEK	*DE vs LV*	>0.05	**<0.0005***	**<0.0003***
	DE vs ED	**<0.003***	>0.05	**<0.03***
	DE vs DL	>0.05	>0.05	>0.05
	DE vs BT	>0.05	>0.05	>0.05
	LV vs ED	>0.05	>0.05	>0.05
	LV vs DL	**<0.03***	**<0.002***	**<0.0006***
	LV vs BT	>0.05	>0.05	>0.05

Table 4.6a continued: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

	ED vs DL	**<0.01***	>0.05	**<0.03***
	ED vs BT	>0.05	>0.05	<0.05
	DL vs BT	>0.05	>0.05	>0.05
Call Type	*Comparison*	*Mean Frequency (kHz)*	*Max Frequency (kHz)*	*Center Frequency (kHz)*
CREEK	*DE vs LV*	>0.05	>0.05	>0.05
	DE vs JY	>0.05	>0.05	>0.05
	DE vs ED	>0.05	>0.05	>0.05
	DE vs DL	>0.05	>0.05	>0.05
	DE vs BT	>0.05	>0.05	>0.05
	LV vs ED	>0.05	>0.05	>0.05
	LV vs DL	>0.05	>0.05	>0.05
	LV vs BT	>0.05	>0.05	>0.05
	ED vs DL	>0.05	>0.05	>0.05
	ED vs BT	>0.05	>0.05	>0.05
	DL vs BT	>0.05	>0.05	>0.05

Call Type	*Comparison*	*High Frequency (kHz)*	*Low Frequency (kHz)*	*Range of Frequency (kHz)*
SWISH	*PB vs LV*	>0.05	>0.05	>0.05
Call Type	*Comparison*	*Mean Frequency (kHz)*	*Max Frequency (kHz)*	*Center Frequency (kHz)*
SWISH	*PB vs LV*	>0.05	>0.05	>0.05

Table 4.6a continued: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

Call Type	*Comparison*	*High Frequency (kHz)*	*Low Frequency (kHz)*	*Range of Frequency (kHz)*
GRUNT	*ED vs DL*	**<0.00000002***	**<0.00000002***	**<0.00000004***
	ED vs PB	**<0.04***	>0.05	**<0.01***
	ED vs BT	>0.05	>0.05	>0.05
	ED vs RZ	**<0.000008**	**<0.0003***	**<0.00005***
	DL vs PB	>0.05	>0.05	>0.05
	DL vs BT	>0.05	>0.05	>0.05
	DL vs RZ	>0.05	>0.05	>0.05
	PB vs BT	>0.05	>0.05	>0.05
	PB vs RZ	>0.05	>0.05	>0.05
	RZ vs BT	>0.05	>0.05	>0.05

Call Type	*Comparison*	*Mean Frequency (kHz)*	*Max Frequency (kHz)*	*Center Frequency (kHz)*
GRUNT	*ED vs DL*	**<0.000000001***	**<0.000000003***	**<0.00000001***
	ED vs PB	>0.05	>0.05	>0.05
	ED vs BT	>0.05	>0.05	>0.05
	ED vs RZ	**<0.00001***	**<0.00009***	>0.05
	DL vs PB	>0.05	>0.05	>0.05
	DL vs BT	>0.05	>0.05	>0.05
	DL vs RZ	>0.05	>0.05	**<0.00006***
	PB vs BT	>0.05	>0.05	>0.05
	PB vs RZ	>0.05	>0.05	>0.05
	RZ vs BT	>0.05	>0.05	>0.05

Table 4.6a continued: Kruskal-Wallis multiple comparison tests for differences in individuals across frequencies. Significant differences are highlighted in bold and marked with an asterisk (*).

Call Type	*Comparison*	*High Frequency (kHz)*	*Low Frequency (kHz)*	*Range of Frequency (kHz)*
BLOW	*ED vs DL*	**<0.0000001***	>0.05	**<0.00000001***
	ED vs PB	**<0.00000000002***	>0.05	**0.000000***
	DL vs PB	>0.05	>0.05	>0.05
Call Type	*Comparison*	*Mean Frequency (kHz)*	*Max Frequency (kHz)*	*Center Frequency (kHz)*
BLOW	*ED vs DL*	**<0.00000004***	**<0.00001***	>0.05
	ED vs PB	**0.00000001***	**<0.003***	>0.05
	DL vs PB	>0.05	>0.05	>0.05

Table 4.6b: Kruskal-Wallis multiple comparison tests for differences in individuals for powers, duration, and harmonics. Significant differences are highlighted in bold and marked with an asterisk (*).

Call Type	*Comparison*	*MAX PWR (dB)*	*AVG PWR (dB)*	*Duration*	*Harmonics*
WHINE	*KS vs DE*	**<0.00008***	**<0.000003***	**<0.0000006***	**<0.000000001***
	KS vs LV	>0.05	>0.05	>0.05	>0.05
	KS vs JY	>0.05	>0.05	>0.05	>0.05
	KS vs ED	**0.000001***	**<0.00000007***	>0.05	**<0.00000003***
	KS vs DL	**<0.00002***	**<0.003***	**<0.0000000001***	**<0.000000001***
	KS vs RZ	>0.05	**<0.003***	**<0.001***	>0.05
	KS vs RM	**0.0000000003***	**<0.007***	>0.05	**<0.0002***
	KS vs BT	**<0.03***	**<0.00000001**	>0.05	**<0.000000001***
	KS vs PB	>0.05	**<0.006***	**<0.0000000001***	**<0.000000001***
	DE vs LV	>0.05	>0.05	>0.05	>0.05
	DE vs JY	>0.05	>0.05	>0.05	>0.05
	DE vs ED	**<0.0000001***	**<0.00000001***	**<0.0000001***	>0.05
	DE vs DL	>0.05	>0.05	**<0.0000001***	>0.05

Table 4.6b continued: Kruskal-Wallis multiple comparison tests for differences in individuals for powers, duration, and harmonics. Significant differences are highlighted in bold and marked with an asterisk (*).

	DE vs RZ	**<0.0000000001***	**<0.00000001***	>0.05	**0.00000006***
	DE vs RM	**<0.000000001***	**<0.00000001***	**<0.009***	**<0.001***
	DE vs BT	**<0.000000001***	**<0.00000001***	**<0.009***	>0.05
	DE vs PB	**<0.03***	>0.05	**<0.00002***	>0.05
	LV vs JY	>0.05	>0.05	>0.05	>0.05
	LV vs ED	>0.05	>0.05	>0.05	>0.05
	LV vs DL	>0.05	>0.05	**<0.03***	>0.05
	LV vs RZ	>0.05	>0.05	>0.05	>0.05
	LV vs RM	>0.05	>0.05	>0.05	>0.05
	LV vs BT	>0.05	>0.05	>0.05	>0.05
	LV vs PB	>0.05	>0.05	>0.05	>0.05
	JY vs ED	>0.05	>0.05	>0.05	>0.05
	JY vs DL	**<0.02***	>0.05	**<0.000001***	**<0.002***
	JY vs RZ	>0.05	>0.05	>0.05	>0.05
	JY vs RM	>0.05	>0.05	>0.05	>0.05
	JY vs BT	>0.05	>0.05	>0.05	>0.05
	JY vs PB	>0.05	>0.05	**<0.0004***	>0.05
	ED vs DL	**<0.000000001***	**<0.00000001***	**<0.00000001***	**<0.001***
	ED vs RZ	>0.05	>0.05	>0.05	**<0.002***
	ED vs RM	>0.05	>0.05	>0.05	>0.05
	ED vs BT	>0.05	>0.05	>0.05	>0.05
	ED vs PB	**<0.000001***	**<0.00000001***	**<0.00000001***	>0.05
	DL vs RZ	**<0.0000000006***	**<0.00000001**	**<0.00000001**	**<0.000000001***
	DL vs RM	**<0.000000001***	**<0.00000001**	**<0.00000001**	**<0.0000005***
	DL vs BT	**<0.000000001***	**<0.00000001**	**<0.00000001**	>0.05
	DL vs PB	**<0.001***	>0.05	>0.05	>0.05

Table 4.6b continued: Kruskal-Wallis multiple comparison tests for differences in individuals for powers, duration, and harmonics. Significant differences are highlighted in bold and marked with an asterisk (*).

	RZ vs RM	>0.05	>0.05	>0.05	>0.05
	RZ vs BT	>0.05	>0.05	>0.05	**<0.000001***
	RZ vs PB	>0.05	**<0.00004***	**<0.0008***	**<0.0000001***
	RM vs BT	>0.05	>0.05	>0.05	**<0.009***
	RM vs PB	**<0.0000000009***	**<0.00000001***	**<0.00000001***	**<0.001***
	BT vs PB	**<0.001***	**<0.00003***	**<0.00000003***	>0.05
Call Type	*Comparison*	*MAX PWR (dB)*	*AVG PWR (dB)*	*Duration*	*Harmonics*
CHIRP	*KS vs DE*	>0.05	**<0.002***	**<0.04***	>0.05
	KS vs ED	**<0.000000003***	**<0.00000002***	>0.05	>0.05
	KS vs DL	**<0.0007***	**<0.00000002***	**<0.00000003***	**<0.00000003***
	KS vs RZ	>0.05	>0.05	>0.05	>0.05
	KS vs RM	**<0.00000001***	**<0.000000001***	**<0.000000001***	**<0.00000008***
	KS vs BT	>0.05	>0.05	>0.05	>0.05
	DE vs ED	**<0.001***	>0.05	**<0.03***	>0.05
	DE vs DL	>0.05	>0.05	**<0.0000001***	**<0.002***
	DE vs RZ	>0.05	>0.05	>0.05	>0.05
	DE vs RM	>0.05	>0.05	**<0.00000001***	**<0.001***
	DE vs BT	>0.05	>0.05	>0.05	>0.05
	ED vs DL	**<0.000001***	**<0.000005***	>0.05	>0.05
	ED vs RZ	**<0.003***	>0.05	>0.05	>0.05
	ED vs RM	**<0.01***	**<0.0001***	>0.05	>0.05
	ED vs BT	>0.05	>0.05	>0.05	>0.05
	DL vs RZ	>0.05	>0.05	**<0.001***	>0.05
	DL vs RM	**<0.000000001***	>0.05	**<0.000000002***	>0.05

Table 4.6b continued: Kruskal-Wallis multiple comparison tests for differences in individuals for powers, duration, and harmonics. Significant differences are highlighted in bold and marked with an asterisk (*).

	DL vs BT	>0.05	>0.05	>0.05	>0.05
	RZ vs RM	>0.05	>0.05	**<0.000006***	>0.05
	RZ vs BT	>0.05	>0.05	>0.05	>0.05
	RM vs BT	>0.05	>0.05	**<0.04***	>0.05
Call Type	*Comparison*	*MAX PWR (dB)*	*AVG PWR (dB)*	*Duration*	*Harmonics*
CHATTER	*DE vs LV*	**<0.00000001***	**<0.00000001***	**<0.0004***	>0.05
	DE vs JY	>0.05	>0.05	>0.05	>0.05
	DE vs ED	**<0.04***	**<0.0004***	>0.05	>0.05
	DE vs DL	>0.05	>0.05	>0.05	>0.05
	DE vs RZ	>0.05	>0.05	>0.05	>0.05
	DE vs RM	**<0.01***	**<0.001***	>0.05	>0.05
	DE vs BT	**<0.03***	**<0.03***	>0.05	>0.05
	DE vs PB	**<0.02***	>0.05	**<0.007***	>0.05
	LV vs JY	**<0.02***	**<0.007***	>0.05	>0.05
	LV vs ED	>0.05	>0.05	>0.05	>0.05
	LV vs DL	**<0.005***	**<0.00005***	>0.05	>0.05
	LV vs RZ	>0.05	>0.05	>0.05	>0.05
	LV vs RM	**<0.01***	>0.05	>0.05	>0.05
	LV vs BT	>0.05	>0.05	>0.05	>0.05
	LV vs PB	>0.05	>0.05	>0.05	>0.05
	JY vs ED	>0.05	>0.05	>0.05	>0.05
	JY vs DL	>0.05	>0.05	>0.05	>0.05
	JY vs RZ	>0.05	>0.05	>0.05	>0.05
	JY vs RM	>0.05	>0.05	>0.05	**<0.01***
	JY vs BT	>0.05	>0.05	>0.05	>0.05
	JY vs PB	>0.05	>0.05	>0.05	>0.05

Table 4.6b continued: Kruskal-Wallis multiple comparison tests for differences in individuals for powers, duration, and harmonics. Significant differences are highlighted in bold and marked with an asterisk (*).

	ED vs DL	**<0.007***	>0.05	>0.05	>0.05
	ED vs RZ	>0.05	>0.05	>0.05	>0.05
	ED vs RM	>0.05	>0.05	>0.05	>0.05
	ED vs BT	>0.05	>0.05	>0.05	>0.05
	ED vs PB	>0.05	>0.05	>0.05	>0.05
	DL vs RZ	>0.05	>0.05	>0.05	>0.05
	DL vs RM	>0.05	>0.05	>0.05	>0.05
	DL vs BT	>0.05	>0.05	>0.05	>0.05
	DL vs PB	>0.05	>0.05	>0.05	>0.05
	RZ vs RM	>0.05	>0.05	>0.05	>0.05
	RZ vs BT	>0.05	>0.05	>0.05	>0.05
	RZ vs PB	>0.05	>0.05	>0.05	>0.05
	RM vs BT	>0.05	>0.05	>0.05	>0.05
	RM vs PB	>0.05	>0.05	>0.05	>0.05
	BT vs PB	>0.05	0.05	>0.05	>0.05
Call Type	*Comparison*	*MAX PWR (dB)*	*AVG PWR (dB)*	*Duration*	*Harmonics*
CREEK	*DE vs LV*	**<0.0000004***	**<0.0000001***	>0.05	>0.05
	DE vs ED	**<0.000000002***	**<0.00000003***	>0.05	>0.05
	DE vs DL	>0.05	>0.05	>0.05	>0.05
	DE vs BT	>0.05	>0.05	>0.05	>0.05
	LV vs ED	>0.05	>0.05	>0.05	>0.05
	LV vs DL	**0.001***	**0.00007***	>0.05	>0.05
	LV vs BT	>0.05	>0.05	>0.05	>0.05

Table 4.6b continued: Kruskal-Wallis multiple comparison tests for differences in individuals for powers, duration, and harmonics. Significant differences are highlighted in bold and marked with an asterisk (*).

	ED vs DL	**<0.00002***	**<0.00002***	>0.05	>0.05
	ED vs BT	>0.05	>0.05	>0.05	>0.05
	DL vs BT	>0.05	**<0.001***	>0.05	<0.01*
Call Type	*Comparison*	*MAX PWR (dB)*	*AVG PWR (dB)*	*Duration*	*Harmonics*
SWISH	*PB vs LV*	**<0.002***	**<0.0009***	**<0.005***	**<0.005***
Call Type	*Comparison*	*MAX PWR (dB)*	*AVG PWR (dB)*	*Duration*	*Harmonics*
GRUNT	*ED vs DL*	**<0.0001***	**<0.00000003***	>0.05	>0.05
	ED vs PB	>0.05	>0.05	>0.05	>0.05
	ED vs BT	>0.05	>0.05	>0.05	>0.05
	ED vs RZ	>0.05	>0.05	>0.05	>0.05
	DL vs PB	>0.05	>0.05	>0.05	>0.05
	DL vs BT	>0.05	>0.05	>0.05	>0.05
	DL vs RZ	**<0.009***	>0.05	>0.05	>0.05
	PB vs BT	>0.05	>0.05	>0.05	>0.05
	PB vs RZ	>0.05	>0.05	>0.05	>0.05
	RZ vs BT	>0.05	>0.05	>0.05	>0.05
Call Type	*Comparison*	*MAX PWR (dB)*	*AVG PWR (dB)*	*Duration*	*Harmonics*
BLOW	*ED vs DL*	**<0.001***	**<0.01***	**<0.00000001***	**<0.0004***
	ED vs PB	**<0.00000001***	**<0.00000000002***	**<0.0001***	**<0.001***
	DL vs PB	**<0.001***	**<0.0002***	**<0.003***	>0.05

Shared Call Types by Individuality

The summary of the descriptive statistics *(Table 4.4a and b)* shows that there are individual differences across the calls. Specifically, the Kruskal-Wallis test *(Table 4.5)* shows significant differences across individuals for the *whine, chirp, chatter, creek, swish, grunt* and *blow*. The *squeak, scream, hiss,* and *hiccup* show no significant differences. The bonferroni comparison was conducted on the call types that showed a significant difference. The *squeak* was not compared because of the 14 calls heard 13 were produced by Dell and 1 was produced by Bert, and Kassie was not included in the comparison of the *chatter* because she produced it only once.

The *whine* is a universal call that is highly variable. The results of the Kruskal-Wallis multiple comparison suggest that the call characteristics are variable among individuals, but several comparisons showed no significant differences. Dell showed significant differences with all the individuals (except Leveau) for the high frequency, range of frequency, mean frequency, max frequency, center frequency. He also showed significant differences for the powers across individuals except for Leveau and Delaney. The similarities in call characteristic between Leveau and Dell may be age related since they are the eldest otters in the study.

The results of the Kruskal-Wallis multiple comparison for the *chirp* show that Kassie showed significant differences with all the individuals for the low frequency, mean frequency, max frequency, center frequency and average power. The differences seen in Kassie's call characteristics are likely due to age differences because Kassie was the youngest of all the otters in the study (excluding the pups). Both Delaney and Dell showed significant differences with all other otters for the max frequency. Dell and Remus showed similar behaviors when they exhibited their *chirp*, they would both station themselves on a substrate and exhibit the chirp with no apparent purpose or function. However, the results of the multiple comparison test showed significant differences in the max frequency, center frequency, max power and duration.

The chatter showed few differences across individuals and across the variables. However, the max frequency and the range of frequency showed significant differences across several individuals. Dell showed the most significant differences across the variables with other individuals.

The *creek* showed significant differences across individuals for the high frequency, low frequency, range of frequency, and the powers. The mean frequency, max frequency, center frequency, duration and harmonics of the *creek* showed no significant differences.

The results for the *swish* indicate that there is no significant difference in the frequencies between Leveau and PB (the only otters to exhibit this call type). However, there were significant differences for the powers, duration and the harmonics.

Edith's *grunt* showed the greatest significance in comparison to the other otters that exhibited the call in particular she showed significant differences with Dell and Rizzo across the frequencies. Dell, PB, Rizzo and Bert showed no significant differences across all the call characteristics (with the exception of the center frequency and max power) suggesting that the *grunt* is used different among sexes but not within sex.

For the *blow,* Edith showed significant differences with the other otters for the high frequency, range of frequency, mean frequency, max frequency, max power, average power, and duration, and harmonics. The low frequency and center frequency showed no significant differences across individuals. The results suggest that the differences are gender based since Edith was the only female to exhibit this call type.

Kassie and Delaney were an interesting comparison because they were a mother and daughter pair that were housed at separate locations during the study. They shared 3 call types in their repertoire (the *whine, chirp,* and *hiccup*). They were the only otters to exhibit the *hiccup* and it showed no significant difference between mother and offspring. The *whine* showed significant differences across all the. On

The *chirp* showed significant differences in the high frequency, low frequency, mean frequency, mean frequency, center frequency, average power, and duration, but their were no significant differences in the mean frequency and the max power, and the harmonics.

The *whine* is a universal call and is the foundation of the vocal repertoire, however Dell showed the greatest acoustical differences when compared with other individuals. The differences may exist because Dell has lived a completely solitary lifestyle and has only been in the presence of humans. This may have affected the vocal repertoire he developed because he does not have outside influences from other otters.

The results show strong evidence for individuality that is primarily due to differences in frequencies. The high frequency, low frequency, mean frequency, max frequency, and center frequency showed differences across individuals with shared call types. The max power and average power, duration and harmonics do not vary as much among individuals. This supports the hypothesis that frequencies differ across individuals with shared call types, with other components of the calls showing no such differences. The individuality that is present may have created some of the ambiguity found in the classification results of the discriminant function analysis.

Discussion

The vocal repertoire of river otters is a complex system. They use 4 major calls types *(Whine, Chirp, Grunt,* and *Blow)* as the foundation of the repertoire, but there are variations within the *whine* and *chirp* that create several sub-call types. The sub-call types produce calls that sound distinctively different to the ear but structurally overlap. The results suggest that if vocalizations are used in conjunction with other call types, in isolation, or in a series it can alter the sound produced. Other factors such as: individuality, sex, and age, influence the development of the repertoire and the vocals that are exhibited.

The *whine* and the *chirp* are the most common call types made and they make up the foundation for the vocal repertoire. These calls are universal and can even be observed in newborn pups. It is therefore, likely that they are present from birth and are not learned or acquired. Of all the call types the *grunt* and the *blow* were the most distinct in both the sound and spectral images they produce. Across individuals and sex the *grunt* showed little variation. The *blow* sounded similar across individuals, but spectrally differences existed between the sexes.

Call Types-Sub-Call Type

The *chatter, creek, squeak, scream, swish*, and *hiss* are all sub types of the *whine* or chirp. The *chatter* is a rapid *chirp* or rapid *whine*, and because they occur so rapidly they produce a sound that is different from an isolated *whine* or *chirp*. The *creek* had a minor difference in the sound when compared to the *whine*, and the *squeak* is spectrally a combination of the *whine* and *chirp*. The *scream* is a loud whine, and the *swish* and *hiss* are low *whines*.

Individuality

The results of the Kruskal-Wallis show evidence for the individual differences. This individuality likely contributed to the ambiguity in the discriminant function analysis. The individuality is present most in the frequency characteristics, with powers, duration and harmonics not varying much across individuals with shared call types. Furthermore, Dell and Kassie showed the greatest individuality of all the otters. Dell showed differences with all individuals for the *whine, chatter* and *creek*, with Kassie showing the greatest differences in the *chirp*. Kassie's differences are likely age related, but Dell's differences are likely due to his solitary lifestyle.

Chapter Five

Data Analysis I-Vocal Variations Among Genders

Introduction

Sexual differences are commonly seen in social species where male-competition is present. In several species males have evolved different communicative techniques to relays messages to the females, such as: sexual status, social status, or fitness to increase their reproductive success when competing for females. Sexual differences in vocalizations have been observed in birds, ungulates, and marine mammals *(Vicario, 2001; Yorzinski, 2006; Feighny, 2006, Khan, 2006)* and several hypotheses have explained the reasons for these differences. In zebra finches *(Taenopygia guttata)* the long calls of males are learned but the long calls of females are not which leads to variation in the males calls but not in the females. American Crows *(Corvus brachyrhynchos)* showed sex differences in the structures in the alarm caw call type that potentially are used to identify the sex and the individual making the call. North American Elks *(Cervus elaphus)* give bugle calls that vary among sexes and the male vocals follow the motivational-structure rule. The motivational-structural rule predicts that males have calls that are a low frequency to give the appearance of large body size to competitors. In harbor seal pups gender variations exist with females mean frequencies increasing and the males decreasing with age.

Sociality between males and females in the North American River Otter

Female river otters reach sexual maturity at 2 years old and often produce a litter annually. Kruuk (*2006)* notes the river otter has a reproductive advantage over the closely related Eurasian otter due to delayed implantation allowing an embryo to remain dormant for up to 10 months. This permits the river otter to mate quickly after weaning a litter, or losing a litter, so she can always produce pups each spring. Since they reach sexual maturity early and can produce annual litters, they spend most of their life in some stage of reproduction: either mating, being pregnant, or weaning pups. When weaning pups the females must be very cautious with males since infanticide is common in river otters. This leads to variability in the social dynamic between males and females in the wild, because females will seek out males during her receptive periods, but will avoid them during all other periods. Female-female social units are commonly observed in the wild, and consist of related females that are weaning pups, or assisting in the rearing. Males are not seen in these groups unless they are pups. Female pups will stay with the group for up to two years, and sometimes longer.

Male river otters reach maturity at about 10-12 months old. They leave their mothers and siblings at maturity or sometimes sooner. Males live a generally solitary lifestyle, but join short-lived male social units. Unlike the females the males form groups that are temporary cohesions that benefit the individual. Two ideas have been proposed to explain this phenomenon: it may be an anti-predation strategy or a foraging strategy *(Blundell, 2001)*. Blundell *(2001)* suggests that the latter is the more likely of the two, since the river otter is not highly threatened by predation. In Prince William Sound otters form groups for cooperative foraging. Their two main sources of food is schooling pelagic fish available seasonally which gives a high energy density, or intertidal organisms that are easier to catch but yield low energy (*Blundell, 2001)*. Otters band together in groups up to 18 to forage in order to increase their success of capturing the schooling pelagic fish. The groups usually consist of males, but females not rearing young have been known to join groups to increase the quality of their food source. Tom Serfass *(1995)* observed 2 otters dive simultaneously and perform a zigzag motion to the center of the pool and when they converged white suckerfish were leaping out for the 2 other otters to feed, then the process was reversed. This type of cooperative behavior requires extensive cognitive abilities. Both individual (understanding the situation) and social competence (who cooperates with who?) is needed to solve these cooperative tasks *(Chalmeau, 1996).*

Goals

In the wild North American River Otters *(Gorman, 2006)* Southern River Otters *(Sepulveda, 2007)* and Sea Otters *(Finnerty, 2009)*, home ranges of the males and females overlap, but social contact is rare. The contact is most frequent during mating season *(Kruuk, 2006)*. During these social contacts otters have been observed exchanging vocalizations. Little is known about how males and females differ in their vocals and why differences would exist. I set out to develop a better understanding of the sexual vocal differences of river otters to determine how the males and females differ in their (1) repertoires, and (2) structure of the calls. If differences exist it is likely because vocals can relay important information about the signaler.

Methods

The data set was divided into males and females; with sub-datasets further dividing the groups based on the 11 call types heard by ear. Collectively 2726 *(Figure 5.1)* calls were analyzed, the males contributed 1555 calls (57%) and the females contributed 1171 calls (43%). The pups were excluded from all the analyses in this section because gender and individuality of the pups were unknown at the time of the study. Figure 5.2 shows a visual comparison of the spectrograms for the shared calls types between males and females.

Figure 5.1: Histogram showing the number of calls observed for each call type in males and females.

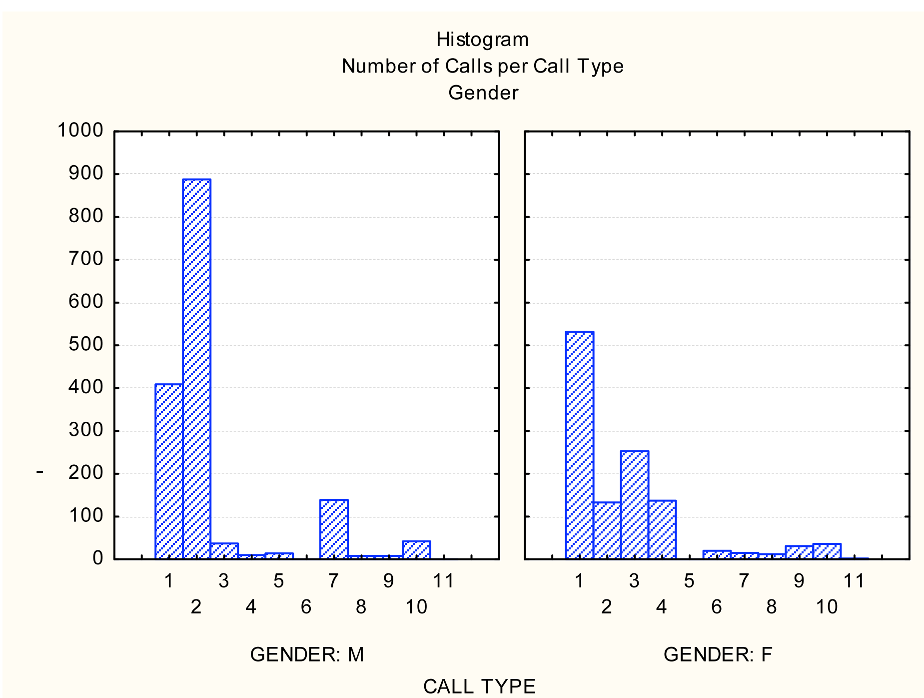


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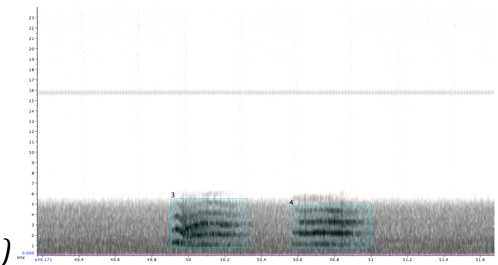
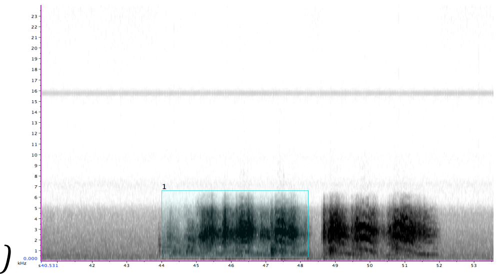
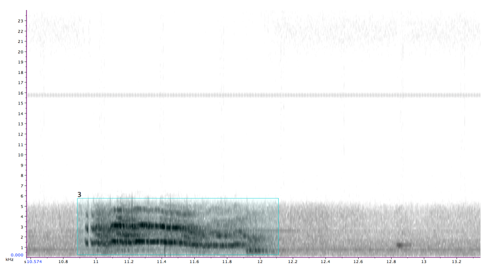
Figure 5.2: Spectrograms of males and females with shared call types.

(a) 

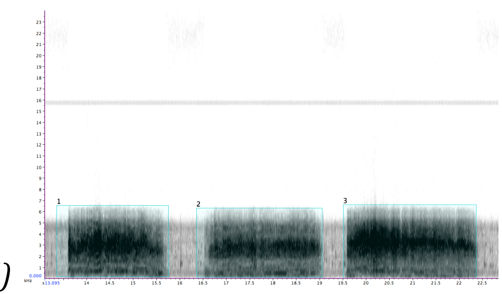
Female-Whine (harmonic)

(b) 

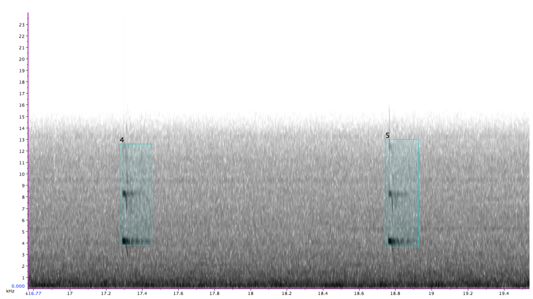
Female-Whine-(Static)

(c) 

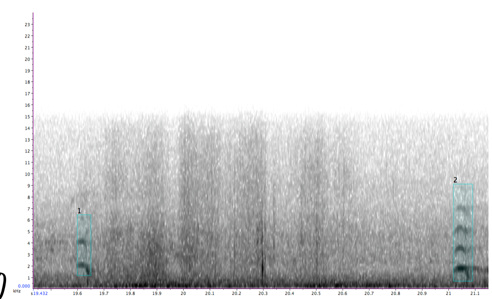
Male-Whine (harmonic)

(d) 

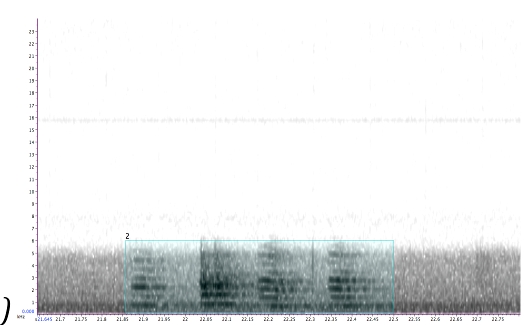
Male-Whine-(Static)

(e) 

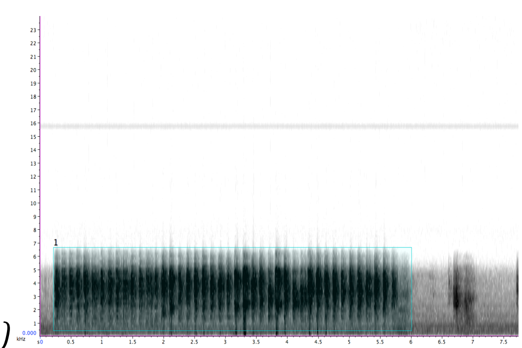
Female-Chirp (linear harmonics)

(f) 

Male-Chirp ('v' shaped harmonics)

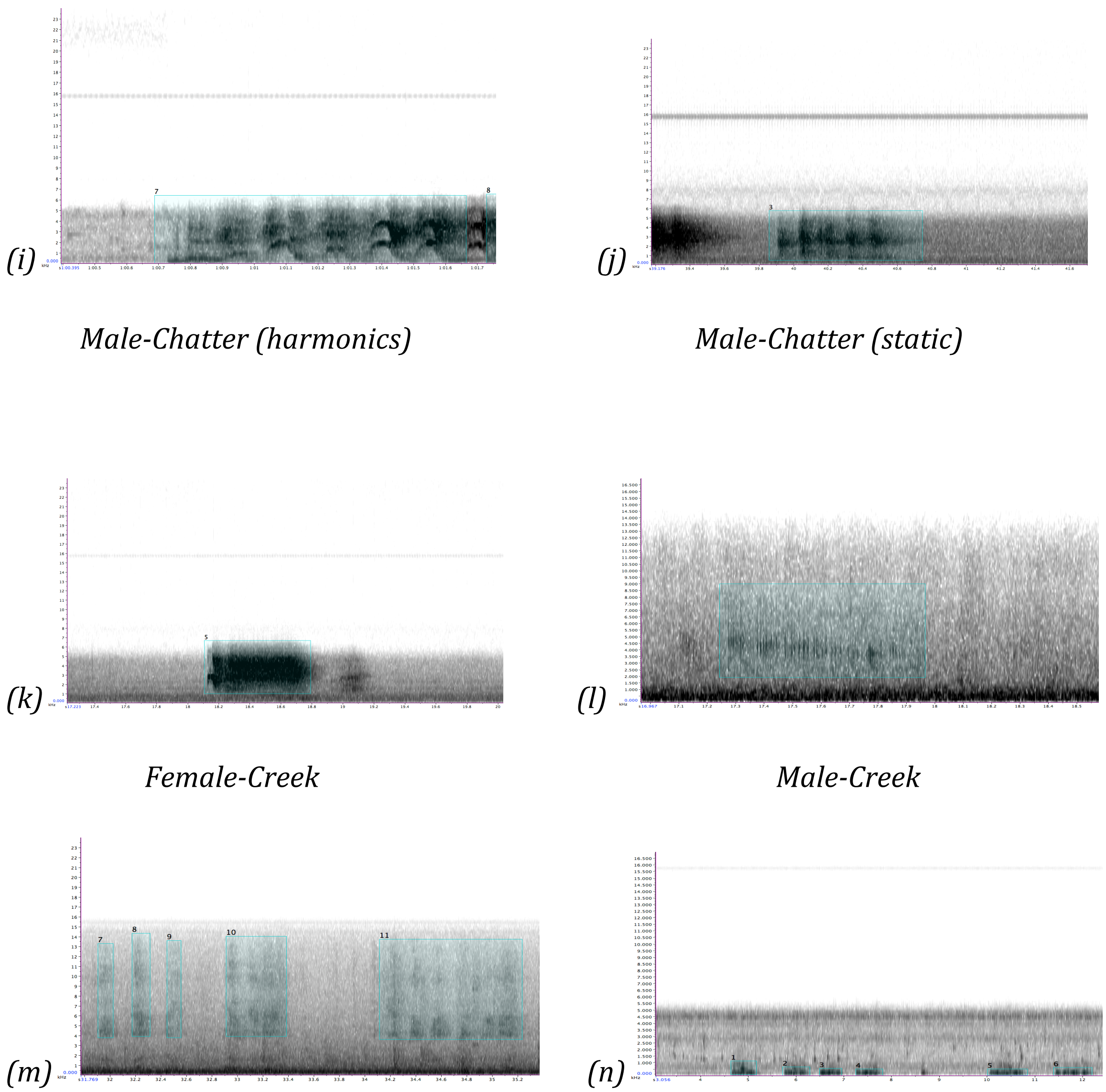
(g) 

Female-Chatter (harmonic)

(h) 

Female-Chatter (static)

Figure 5.2 continued: Spectrograms of males and females with shared call types.



(i) Male-Chatter (harmonics)

(j) Male-Chatter (static)

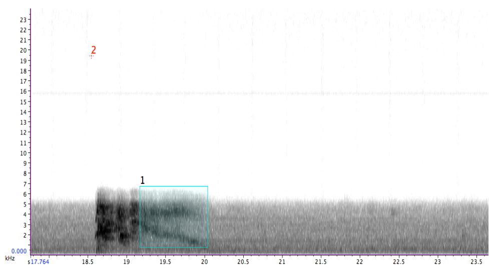
(k) Female-Creek

(l) Male-Creek

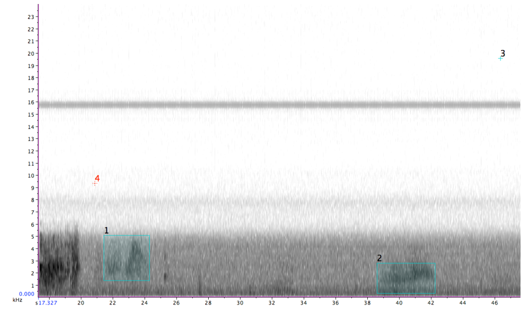
(m) Female-Grunt

(n) Male-Grunt

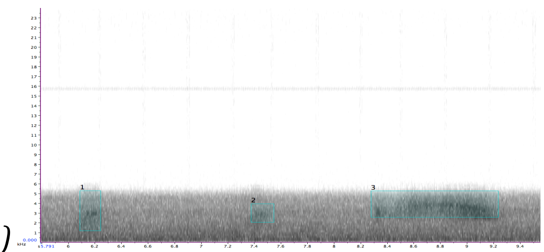
Figure 5.2 continued: Spectrograms of males and females with shared call types.

(o)


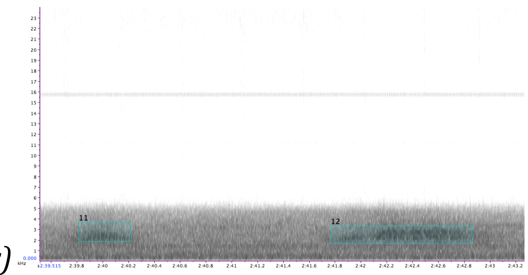
Female-Swish

(p)


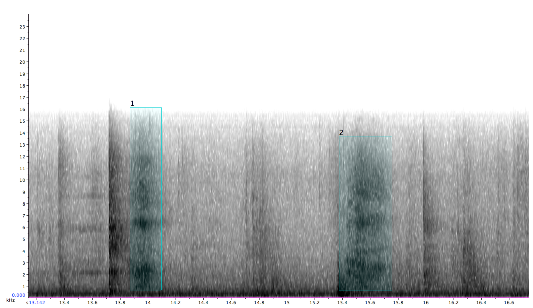
Male-Swish

(q)


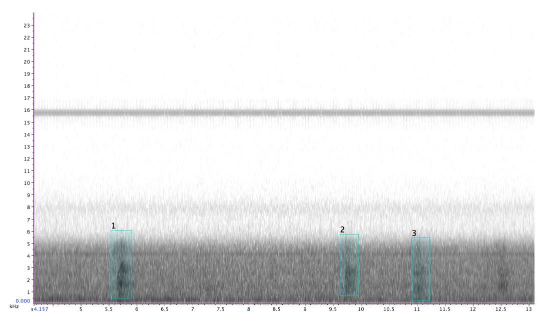
Female-Hiss

(r)


Male-Hiss

(s)


Female-Blow

(t)


Male-Blow

Statistical Analysis

Comparison of frequencies, harmonics, power and duration between males and females on shared call types

Sexual dimorphism exist in the river otter, based on this idea there should be significant differences in the repertoires based on gender. Using my observations and the spectral analysis I proposed several hypotheses *(Table 5.3)*. To test the hypothesis that shared call types have significant differences in frequencies, harmonics, powers and duration among genders I used a Mann-Whitney Test. I used the Mann-Whitney Test because it's a non-parametric test that does not assume a normal distribution. Due to the large number of comparisons I included a bonferroni correction to determine the accurate level of significance ($p<0.006$). I did not include a comparison for the *squeak, scream*, or *hiccup* because they were not observed in both sexes. I conducted a comparison on all the variables, but the high frequency, low frequency, max frequency, max power, duration and harmonics are the variables that give the best description of the calls visually.

Results

Table 5.1a:Descriptive Statistics of frequencies of call types based on sex. (Means +/- SD) The sex with the highest mean is highlighted in bold.

Call Type	*Sex*	*Sample Size (# of individuals)*	*High Freq (kHz)*	*Low Freq (KHz)*	*Range of Freq (KHz)*	*Mean Freq (KHz)*	*Max Freq (KHz)*	*Center Freq (KHz)*
Whine	*M*	*406 (5)*	**6080+/-1795**	604 +/- 588	**5723+/-6060**	**3342+/-961**	**2622 +/-879**	**2645 +/-760**
	F	*553 (5)*	5888+/-1686	**612 +/-426**	5286 +/-1705	3250 +/-891	2561 +/-938	2520 +/-853

Table 5.1a continued: Descriptive Statistics of frequencies of call types based on sex. (Means +/-SD) The s ex with the highest mean is highlighted in bold.

Call Type	*Sex*	*Sample Size (# of individuals)*	*High Freq (kHz)*	*Low Freq (KHz)*	*Range of Freq (KHz)*	*Mean Freq (KHz)*	*Max Freq (KHz)*	*Center Freq (KHz)*
Chirp	*M*	*891 (4)*	8753+/-3381	1216+/-483	**7679+/-5131**	4978+/-1681	2307+/-942	2366+/-766
	F	*133 (3)*	**8833+/-3494**	**2685+/-1180**	6148+/-3220	**5759+/-2051**	**3613+/-1228**	**3594+/-1034**
Call Type	*Sex*	*Sample Size (# of individuals)*	*High Freq (kHz)*	*Low Freq (KHz)*	*Range of Freq (KHz)*	*Mean Freq (KHz)*	*Max Freq (KHz)*	*Center Freq (KHz)*
Chatter	*M*	*37 (5)*	**6958+/-2395**	621+/-429	**6337+/-2477**	**3790+/-1194**	2595+/-999	2812+/-828
	F	*252 (5)*	6484+/-496	**664+/-477**	5808+/-807	3574+/-322	**3095+/-690**	**3116+/-479**

Call Type	*Sex*	*Sample Size (# of individuals)*	*High Freq (kHz)*	*Low Freq (KHz)*	*Range of Freq (KHz)*	*Mean Freq (KHz)*	*Max Freq (KHz)*	*Center Freq (KHz)*
Creek	*M*	*10 (2)*	**7757+/-2489**	874+/-620	**6883+/-2626**	3420+/-1252	**3206+/-822**	**3281+/-645**
	F	*114 (3)*	6370 +/-980	**991+/-580**	5378+/-1113	**3612+/-756**	2922+/-635	2862+/-505

Table 5.1a continued: Descriptive Statistics of frequencies of call types based on sex. (Means +/-SD) The sex with the highest mean is highlighted in bold.

Call Type	*Gender*	*Sample Size (# of individuals)*	*High Freq (kHz)*	*Low Freq (KHz)*	*Range of Freq (KHz)*	*Mean Freq (KHz)*	*Max Freq (KHz)*	*Center Freq (KHz)*
Squeak	*M*	*14 (2)*	9644+/-2433	447+/-335	9197+/-2374	5045+/-1268	3295+/-1210	3830+/-689
	F	*N/A*						
Call Type	*Gender*	*Sample Size (# of individuals)*	*High Freq (kHz)*	*Low Freq (KHz)*	*Range of Freq (KHz)*	*Mean Freq (KHz)*	*Max Freq (KHz)*	*Center Freq (KHz)*
Scream	*M*	*N/A*						
	F	*20 (3)*	6619+/-306	449+/-388	6170+/-605	3534+/-175	2867+/-575	3000+/-304
Call Type	*Gender*	*Sample Size (# of individuals)*	*High Freq (kHz)*	*Low Freq (KHz)*	*Range of Freq (KHz)*	*Mean Freq (KHz)*	*Max Freq (KHz)*	*Center Freq (KHz)*
Grunt	*M*	*139 (3)*	1079+/-418	42+/-50	1037+/-407	557+/-222	287+/-208	298+/-154
	F	*15 (1)*	**10502+/-4196**	**2694+/-1564**	**7808+/-3187**	**6598+/-2736**	**3325+/-1859**	**3613+/-1901**

Table 5.1a continued: Descriptive Statistics of frequencies of call types based on sex. (Means +/-SD) The sex with the highest mean is highlighted in bold.

Call Type	*Gender*	*Sample Size (# of individuals)*	*High Freq (kHz)*	*Low Freq (KHz)*	*Range of Freq (KHz)*	*Mean Freq (KHz)*	*Max Freq (KHz)*	*Center Freq (KHz)*
Swish	*M*	*8 (1)*	**5569+/-335**	**888+/-253**	**4681+/-504**	**3229+/-157**	2180+/-316	**2953+/-939**
	F	*12 (1)*	5335+/-1144	876+/-339	4459+/-1315	3105+/-528	**2328+/-1126**	2156+/-667
Call Type	*Gender*	*Sample Size (# of individuals)*	*High Freq (kHz)*	*Low Freq (KHz)*	*Range of Freq (KHz)*	*Mean Freq (KHz)*	*Max Freq (KHz)*	*Center Freq (KHz)*
Hiss	*M*	*8 (2)*	5263+/-1173	1701+/-417	3562+/-1210	3482+/-639	2930+/-722	2859+/-616
	F	*31 (2)*	**5563+/-944**	**1716+/-616**	**3847+/-1047**	**3640+/-601**	**3060+/-663**	**3121+/-619**
Call Type	*Gender*	*Sample Size (# of individuals)*	*High Freq (kHz)*	*Low Freq (KHz)*	*Range of Freq (KHz)*	*Mean Freq (KHz)*	*Max Freq (KHz)*	*Center Freq (KHz)*
Blow	*M*	*42 (2)*	6113+/-2983	700+/-475	5414+/-3046	3406+/-1498	**1906+/-997**	**2362+/-804**
	F	*36 (1)*	**15650+/-946**	**717+/-346**	**14932+/-1218**	**8183+/-369**	1885+/-793	2266+/-394

Table 5.1a continued: Descriptive Statistics of frequencies of call types based on sex. (Means +/-SD) The sex with the highest mean is highlighted in bold.

Call Type	Gender	Sample Size (# of individuals)	High Freq (kHz)	Low Freq (KHz)	Range of Freq (KHz)	Mean Freq (KHz)	Max Freq (KHz)	Center Freq (KHz)
Hiccup	M	N/A						
	F	4 (2)	5698+/-774	543+/-445	5155+/-1092	3121+/-317	2344+/-1285	2344+/-1151

Table 5.1b continued: Descriptive Statistics of powers, duration and harmonics of call types based on sex. (Mean +/-SD). The sex with the higher mean is highlighted in bold.

Call Type	Sex	Sample Size (# of individuals)	Max Pwr (dB)	Avg Pwr (db)	Duration (s)	Harmonics (#)
Whine	M	406 (5)	86 +/-11	66 +/- 9	1.6 +/- 1.2	1 +/-1.9
	F	553 (5)	**89 +/-11**	**71 +/-10**	**1.7 +/-1**	**1.3+/-2**
Call Type	Sex	Sample Size (# of individuals)	Max Pwr (dB)	Avg Pwr (db)	Duration (s)	Harmonics (#)
Chirp	M	891 (4)	91+/-8	73+/-7	**0.1+/-0.3**	**3.5+/-1.8**
	F	133 (3)	**93+/-11**	**74+/-10**	0.3+/-0.6	2.3+/-1
Call Type	Sex	Sample Size (# of individuals)	Max Pwr (dB)	Avg Pwr (db)	Duration (s)	Harmonics (#)
Chatter	M	37 (5)	89+/-10	69+/-9	1.2+/-0.8	**2+/-3**
	F	252 (5)	**95+/-8**	**75+/-8**	**1.9+/-1.4**	0.2+/-0.8

Table 5.1b continued: Descriptive Statistics of powers, duration and harmonics of call types based on sex. (Mean +/-SD). The sex with the higher mean is highlighted in bold.

Call Type	*Sex*	*Sample Size (# of individuals)*	*Max Pwr (dB)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
Creek	*M*	*10 (2)*	81+/-12	**71+/-10**	**1.5+/-0.9**	**1.4+/-2.4**
	F	*114 (3)*	**86+/-10**	67+/-7	1.1+/-0.9	0.4+/-1
Call Type	*Sex*	*Sample Size (# of individuals)*	*Max Pwr (dB)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
Squeak	*M*	*14 (2)*	102+/-2	83+/-1	2+/-1.5	2+/-4
	F	*N/A*				
Call Type	*Sex*	*Sample Size (# of individuals)*	*Max Pwr (dB)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
Scream	*M*	*N/A*				
	F	*20 (3)*	101+/-3	83+/-3	1.5+/-1.2	0.8+/-1.5
Call Type	*Sex*	*Sample Size (# of individuals)*	*Max Pwr (dB)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
Grunt	*M*	*139 (3)*	***76+/-7***	**64+/-7**	0.7+/-0.4	0.01+/-0.2
	F	*15 (1)*	*67+/-7*	50+/-6	**0.6+/-0.3**	0+/-0

Table 5.1b continued: Descriptive Statistics of powers, duration and harmonics of call types based on sex. (Mean +/-SD). The sex with the higher mean is highlighted in bold.

Call Type	*Sex*	*Sample Size (# of individuals)*	*Max Pwr (dB)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
Swish	*M*	*8 (1)*	***80+/-4***	**63+/-3**	**2.2+/-1**	0+/-0
	F	*12 (1)*	*70+/-5*	55+/-4	0.9+/-0.5	**1.4+/-1**
Call Type	*Sex*	*Sample Size (# of individuals)*	*Max Pwr (dB)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
Hiss	*M*	*8 (2)*	*71+/-4*	**57+/-3**	**1.1+/-0.5**	0+/-0
	F	*31 (2)*	***73+/-8***	54+/-12	1+/-0.4	**0.3+/-0.7**
Call Type	*Sex*	*Sample Size (# of individuals)*	*Max Pwr (dB)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
Blow	*M*	*42 (2)*	*81+/-7*	65+/-6	**0.2+/-0.2**	0+/-0
	F	*36 (1)*	***91+/-4***	**73+/-3**	0.4+/-0.2	**1.9+/-1.7**
Call Type	*Sex*	*Sample Size (# of individuals)*	*Max Pwr (dB)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
Hiccup	*M*	*N/A*				
	F	*4 (2)*	86+/-9	67+/-7	0.2+/-0.1	1.8+/-2

Table 5.2: Table of hypotheses proposed on the variations of males and females with shared call types. (HF=high frequency; LF=low frequency; RGF=range of frequency; MNF=mean frequency; MXF=maximum frequency; CTF=center frequency MXPWR=maximum power; AVGPWR=average power; DRT=duration and HRM=harmonics). The results of the Mann-Whitney and interpretation of results are shown. Bonferonni correction sets the significant p-value at <0.006, significant p-values are highlighted in bold and marked with an asterisk (*). p-values <0.05 were marked with an asterisk (*).

Call Type	H_a	H_o	*Mann-Whitney p-value*
Whine	$HF_M \neq HF_F$	$HF_M = HF_F$	>0.05
	$LF_M \neq LF_F$	$LF_M = LF_F$	<0.002*
	$RGF_M \neq RGF_F$	$RGF_M = RGF_F$	>0.05
	$MNF_M \neq MNF_F$	$MNF_M = MNF_F$	<0.009*
	$MXF_M \neq MXF_F$	$MXF_M = MXF_F$	>0.05
	$CTF_M \neq CTF_M$	$CTF_M = CTF_M$	>0.05
	$MXPWR_M \neq MXPWR_F$	$MXPWR_M = MXPWR_F$	**<0.0000000000001***
	$AVGPWR_M \neq AVGPWR_F$	$AVGPWR_M = AVGPWR_F$	**<0.00000009***
	$DRT_M \neq DRT_F$	$DRT_M = DRT_F$	**<0.0000000003***
	$HRM_M \neq HRM_F$	$HRM_M = HRM_F$	**<0.0002***
Chirp	$HF_M \neq HF_F$	$HF_M = HF_F$	>0.05
	$LF_M \neq LF_F$	$LF_M = LF_F$	**<0.00000001***
	$RGF_M \neq RGF_F$	$RGF_M = RGF_F$	**<0.00004***
	$MNF_M \neq MNF_F$	$MNF_M = MNF_F$	**<0.00001***
	$MXF_M \neq MXF_F$	$MXF_M = MXF_F$	**<0.00000000004***
	$CTF_M \neq CTF_M$	$CTF_M = CTF_M$	**0.000000***
	$MXPWR_M \neq MXPWR_F$	$MXPWR_M = MXPWR_F$	**<0.000002***
	$AVGPWR_M \neq AVGPWR_F$	$AVGPWR_M = AVGPWR_F$	**<0.00000001***
	$DRT_M \neq DRT_F$	$DRT_M = DRT_F$	**0.000000***
	$HRM_M \neq HRM_F$	$HRM_M = HRM_F$	**<0.000000000006***

Table 5.2 continued: Table of hypotheses proposed on the variations of males and females with shared call types. (HF=high frequency; LF=low frequency; RGF=range of frequency; MNF=mean frequency; MXF=maximum frequency; CTF=center frequency MXPWR=maximum power; AVGPWR=average power; DRT=duration and HRM=harmonics). The results of the Mann-Whitney and interpretation of results are shown. Bonferonni correction sets the significant p-value at <0.006, significant p-values are highlighted in bold and marked with an asterisk (*). p-values <0.05 were marked with an asterisk (*).

Chatter	$HF_M \neq HF_F$	$HF_M = HF_F$	<0.002*
	$LF_M \neq LF_F$	$LF_M = LF_F$	>0.05
	$RGF_M \neq RGF_F$	$RGF_M = RGF_F$	>0.05
	$MNF_M \neq MNF_F$	$MNF_M = MNF_F$	>0.05
	$MXF_M \neq MXF_F$	$MXF_M = MXF_F$	**<0.00009***
	$CTF_M \neq CTF_M$	$CTF_M = CTF_M$	<0.01*
	$MXPWR_M \neq MXPWR_F$	$MXPWR_M = MXPWR_F$	**<0.0003***
	$AVGPWR_M \neq AVGPWR_F$	$AVGPWR_M = AVGPWR_F$	**<0.0006***
	$DRT_M \neq DRT_F$	$DRT_M = DRT_F$	**<0.002***
	$HRM_M \neq HRM_F$	$HRM_M = HRM_F$	**<0.00000000007***
Creek	$HF_M \neq HF_F$	$HF_M = HF_F$	>0.05
	$LF_M \neq LF_F$	$LF_M = LF_F$	>0.05
	$RGF_M \neq RGF_F$	$RGF_M = RGF_F$	>0.05
	$MNF_M \neq MNF_F$	$MNF_M = MNF_F$	>0.05
	$MXF_M \neq MXF_F$	$MXF_M = MXF_F$	>0.05
	$CTF_M \neq CTF_M$	$CTF_M = CTF_M$	<0.02*
	$MXPWR_M \neq MXPWR_F$	$MXPWR_M = MXPWR_F$	>0.05
	$AVGPWR_M \neq AVGPWR_F$	$AVGPWR_M = AVGPWR_F$	>0.05
	$DRT_M \neq DRT_F$	$DRT_M = DRT_F$	>0.05
	$HRM_M \neq HRM_F$	$HRM_M = HRM_F$	>0.05

Table 5.2 continued: Table of hypotheses proposed on the variations of males and females with shared call types. (HF=high frequency; LF=low frequency; RGF=range of frequency; MNF=mean frequency; MXF=maximum frequency; CTF=center frequency MXPWR=maximum power; AVGPWR=average power; DRT=duration and HRM=harmonics). The results of the Mann-Whitney and interpretation of results are shown. Bonferonni correction sets the significant p-value at <0.006, significant p-values are highlighted in bold and marked with an asterisk (*). p-values <0.05 were marked with an asterisk (*).

Grunt	$HF_M \neq HF_F$	$HF_M = HF_F$	**<0.00000002***
	$LF_M \neq LF_F$	$LF_M = LF_F$	**<0.00000002***
	$RGF_M \neq RGF_F$	$RGF_M = RGF_F$	**<0.00000002***
	$MNF_M \neq MNF_F$	$MNF_M = MNF_F$	**<0.00000002***
	$MXF_M \neq MXF_F$	$MXF_M = MXF_F$	**<0.00000001***
	$CTF_M \neq CTF_M$	$CTF_M = CTF_M$	**<0.00000001***
	$MXPWR_M \neq MXPWR_F$	$MXPWR_M = MXPWR_F$	**<0.00006***
	$AVGPWR_M \neq AVGPWR_F$	$AVGPWR_M = AVGPWR_F$	**<0.00000001***
	$DRT_M \neq DRT_F$	$DRT_M = DRT_F$	>0.05
	$HRM_M \neq HRM_F$	$HRM_M = HRM_F$	>0.05
Swish	$HF_M \neq HF_F$	$HF_M = HF_F$	>0.05
	$LF_M \neq LF_F$	$LF_M = LF_F$	>0.05
	$RGF_M \neq RGF_F$	$RGF_M = RGF_F$	>0.05
	$MNF_M \neq MNF_F$	$MNF_M = MNF_F$	>0.05
	$MXF_M \neq MXF_F$	$MXF_M = MXF_F$	>0.05
	$CTF_M \neq CTF_M$	$CTF_M = CTF_M$	>0.05
	$MXPWR_M \neq MXPWR_F$	$MXPWR_M = MXPWR_F$	>0.05
	$AVGPWR_M \neq AVGPWR_F$	$AVGPWR_M = AVGPWR_F$	>0.05
	$DRT_M \neq DRT_F$	$DRT_M = DRT_F$	>0.05
	$HRM_M \neq HRM_F$	$HRM_M = HRM_F$	>0.05
Hiss	$HF_M \neq HF_F$	$HF_M = HF_F$	>0.05
	$LF_M \neq LF_F$	$LF_M = LF_F$	>0.05
	$RGF_M \neq RGF_F$	$RGF_M = RGF_F$	>0.05
	$MNF_M \neq MNF_F$	$MNF_M = MNF_F$	>0.05

Table 5.2 continued: Table of hypotheses proposed on the variations of males and females with shared call types. (HF=high frequency; LF=low frequency; RGF=range of frequency; MNF=mean frequency; MXF=maximum frequency; CTF=center frequency MXPWR=maximum power; AVGPWR=average power; DRT=duration and HRM=harmonics). The results of the Mann-Whitney and interpretation of results are shown. Bonferonni correction sets the significant p-value at <0.006, significant p-values are highlighted in bold and marked with an asterisk (*). p-values <0.05 were marked with an asterisk (*).

	$MXF_M \neq MXF_F$	$MXF_M = MXF_F$	>0.05
	$CTF_M \neq CTF_M$	$CTF_M = CTF_M$	>0.05
	$MXPWR_M \neq MXPWR_F$	$MXPWR_M = MXPWR_F$	>0.05
	$AVGPWR_M \neq AVGPWR_F$	$AVGPWR_M = AVGPWR_F$	>0.05
	$DRT_M \neq DRT_F$	$DRT_M = DRT_F$	>0.05
	$HRM_M \neq HRM_F$	$HRM_M = HRM_F$	>0.05
Blow	$HF_M \neq HF_F$	$HF_M = HF_F$	**<0.0000000003***
	$LF_M \neq LF_F$	$LF_M = LF_F$	>0.05
	$RGF_M \neq RGF_F$	$RGF_M = RGF_F$	**<0.0000000004***
	$MNF_M \neq MNF_F$	$MNF_M = MNF_F$	**<0.0000000003***
	$MXF_M \neq MXF_F$	$MXF_M = MXF_F$	>0.05
	$CTF_M \neq CTF_M$	$CTF_M = CTF_M$	>0.05
	$MXPWR_M \neq MXPWR_F$	$MXPWR_M = MXPWR_F$	**<0.0000000005***
	$AVGPWR_M \neq AVGPWR_F$	$AVGPWR_M = AVGPWR_F$	**<0.00000002***
	$DRT_M \neq DRT_F$	$DRT_M = DRT_F$	**<0.000000000006***
	$HRM_M \neq HRM_F$	$HRM_M = HRM_F$	**<0.00000001***

Sex Comparison based on spectral images and Mann-Whitney Results

The *whine* has two spectral appearances, the static and harmonic. Both sexes exhibited both versions and when compared they show no visual difference *(Figure 5.2a and b)*. The Mann-Whitney *(Table 5.2)* results show significant differences only in the powers, duration and harmonics. Confirming the similarities in structural factors across sexes.

The spectral images of the *chirp (Figure 5.2c and d)* show that the females have higher frequencies, but the males have a greater number of harmonics, therefore they also have a larger range of frequency The females have a linear harmonic band and the males have the inverted 'v' shaped harmonics. The results of the Mann-Whitney further confirm the spectral differences *(Table 5.2)*. The *chirp* showed a significant difference in the low, mean, max and center frequencies, powers, duration, and number of harmonics. The low frequency and max frequency were higher in the females, and although the high frequency showed no significant difference the average high frequency was larger than the males. The male's *chirps* also had higher range of frequency as shown in the spectral images.

In both sexes the *chatter (Figure 5.2e-h)* could appear like a series of *whines*, or a series of *chirps*. Spectrally, the most distinct sexual difference is in the harmonic chatter; the harmonics appear linear in the females and the males have the inverted 'v' shaped harmonic, this is expected since the same visual difference exist in the chirp. The Mann-Whitney results *(Table 5.2)* showed the females were significantly higher in the max frequency, powers and durations, but males had a significantly greater number of harmonics.

Edith was the only female that exhibited the *grunt (Figure 5.2m)*, and her spectral images were distinctively different in the high, low, and range of frequency, but the length of the calls were the same and almost all her *grunts* contained no harmonics like the males. The Mann-Whitney further proves the differences that are apparent in the spectral images *(Table 5.2)*. The *grunt* showed significant differences in the frequencies and the powers, with the female having higher frequencies across all the frequency variables, and the males having higher powers. The duration and number of harmonics were not significantly different.

Edith was the only female to exhibit the *blow* and her spectral image *(Figure 5.2s)* showed a difference in the high frequency, low frequency, and the range of frequency but the duration, and harmonics were spectrally identical. The Mann-Whitney results *(Table 5.2)* are reflected in the spectral images with the high frequency and range of frequency being higher in Edith. The Mann-Whitney also showed differences in the power, duration, and harmonics with Edith have a significantly higher power and number of harmonics, with the male's *blow* being longer.

The spectral images of the *swish, hiss* and *creek (Figure 5.2i-l and o-r)* are almost identical and there appears to be no sexual differences. The results of the Mann-Whitney *(Table 5.2)* confirm that there is no significant difference in sex for the *swish*, *hiss* or the *creek*, all comparisons yield p-values <0.05. Although the squeak and scream were not compared in this analysis because they are unique the spectral analysis suggests that they are analogous to each other.

Sexual dimorphism is present in river otters so morphological differences likely affect the vocal repertoires. However, there is likely a biological significance to the differences. Unlike female river otters, adult male otters are highly territorially and defend their home ranges *(Chanin, 1985).* They use spraints to establish their territories and travel to the borders of their home ranges often to maintain their territory. Male's reproductive success relies heavily on their ability to establish and maintain a large home range with exclusive access to females. Defense of a territory is often achieved without physical confrontations and mutual avoidance is a common behavior in otters. But when more than one male's home range overlaps with a female's home range male competition becomes more prevalent. Wild male otters have been observed fighting attempting to bite the penis of the rival *(Chanin, 1985)*. In these instances female's choice is important, and vocalizations may be useful to relay male dominance. There is little understanding on how females select their mate or to what extent female choice is present. But, based on the amount of energy a female invest in rearing her young it is likely to have some influence on selection of a mate.

Discussion

The results of the descriptive analysis, spectral image comparison, and the Mann-Whitney two group comparison all confirm that there are sexual differences in some call types that make up the river otter's vocal repertoire. There are calls types that are unique to sexes: *squeak* for the males and the *scream* for the females. The *whine* is very variable across sexes therefore sex does not appear to be an influence on the whines that are produced. The *chatter* shows significant differences in the max frequency, and the average power. But, the greatest sexual differences are in the *chirp, grunt,* and *blow*. The *swish, hiss,* and *creek* are identical and sex does not affect the call. The analysis confirms that there are sexual differences in vocalizations, but it does not explain why the differences exist.

Based on my observations and knowledge of river otter behaviors I suggest that the differences exist because of the morphological differences that result from sexual dimorphism, and to relay information about sex, and dominance. I speculate that females are not highly selective, and mate selection relies most on males overlapping their territories with receptive females. But, if presented with several mate choices females will be selective in their choice, and vocalizations may contribute to increasing a male's reproductive success.

Chapter Six

VI-Data Analysis II-Vocal Variation between Adults and Pups

Introduction

The literature on mother-pup interactions of river otters is extremely limited, and since they give birth inside dens evidence of imprinting is also limited. Evolution theory predicts that species that give birth to precocial young will use various imprinting techniques to form a mutual recognition of mother and pup *(Knornschild, 2008).* The mutual recognition is driven by coloniality, offspring motility, and time span of parental separation *(Knornschild, 2008).* On the contrary, altricial young do not require this same imprinting and mother-pup recognition is not vital until the pup is no longer dependent *(Val-Laillet, 2007).* Inside the den there are few threats to pups (i.e. predation, infanticide), but once the pup is independent they are mobile which can lead to separations and are more vulnerable to predation.

Studies performed on seals, sea lions, and rodents *(Opzeeland, 2004; Charrier, 2009; Kober, 2007*) suggest that since these species birth precocial young there is a need to individually identify young. Vocal imprinting is the dominant form and this occurs immediately after the birth. The vocal imprinting assists mothers in correctly identifying their young when reunited after a separation and there are several individuals in a group so visual or scent factors are not useful. Knornschild *(2008)* studied the greater sac-winged bat *(Saccopteryz bilineata)* and showed that the mother can correctly identify her young based on a unique isolation call, but the pups indiscriminately vocalize in response to females. This is an example of uni-directional recognition and occurs when the young will benefit from nursing indiscriminately. On the other hand, some birds, marsupials, and some species of mammals give birth to altricial young, and in these species the weaning period often occurs in a nest, den, or holt. Most altricial young spend the first several weeks of their lives inside and do not leave until they are no longer completely dependant on the mother. For example, ground squirrels *(Val-Laillet, 2007)* do not form mother recognition until 3 weeks of age, which is also when they emerge from the den.

Mother-Pup Interactions In Otters

Despite the level of sociality, all otters form strong mother-pup bonds. They give birth to 1-5 pups per litter and some species reproduce annually. All otters expend a great deal of time and energy in the rearing of the young, and females are the predominate caretakers. They give birth to altricial young that can remain reliant on the mother for up to two months.

Sea otters have different reproductive social constraints in comparison to other otter species since all the rearing occurs in the ocean. The sea otter gives birth to one pup, and they form strong mother-pup bonds that are common to marine mammals like the pinnipeds and cetaceans. The pups are highly susceptible to predation therefore separation is very limited and occurs only during hunting. During these periods screams are usually exchanged. Mother and pups have been observed showing affection by clasping paws, and hugging. This type of affection is also seen in the highly cognitive primate *(Kruuk, 2006).*

The giant otter gives birth to an average of 2 pups per litter, and can reproduce annually. Unlike, other otter species where males are not involved in rearing, the male giant otters contribute in the rearing of the young, and have been observed transferring pups between dens *(Evangelista, 2011)*. The family units consist of a breeding pair, sub-adults, and pups. The adults and sub-adults both contribute to the teaching of the pups, and engage in swimming and fishing lessons.

Reproductive behavior in female river otters is not well understood, but there natal denning behavior suggest that females use various forms of landscape for dens, but they are always located an average of 316m from a body of water *(Goran, 2005)*. The study implies that females are very meticulous in building their nest and choosing the location, because it is crucial to the survival of the pups. As well, females have been observed moving their pups to a secondary den when they are developed enough to enter the water.

Goals

The aim of this chapter is to quantify the vocal patterns of mother and pups and conduct a comparison of the two to determine the extent of vocal differences. Based on the extreme size differences between the adults and pups I suggest that variations exist in the vocal repertories, and these variations may help to solidify the mother-pup bond.

Methods

I divided the data set into adults and pups; with sub-datasets dividing the pups and adults based on the 3 shared call types heard by ear. Collectively 3025 calls were analyzed for the adults and pups. The adults contributed 2726 calls (90%) and the pups contributed 299 calls (9.9%) to the complete data set *(Figure 6.1)*. The pups from Beardsley Zoo are one group and the pups from Atlantis Aquarium are another group, each group is counted as one individual. The groups of pups did not have an individual identity at the time of the study, so it was not possible to make individual identifications. Figure 3.2 shows a spectral image comparison of the shared calls types between adult and pups

Figure 6.1: Histograms of the number of calls analyzed by call types, by age groups.

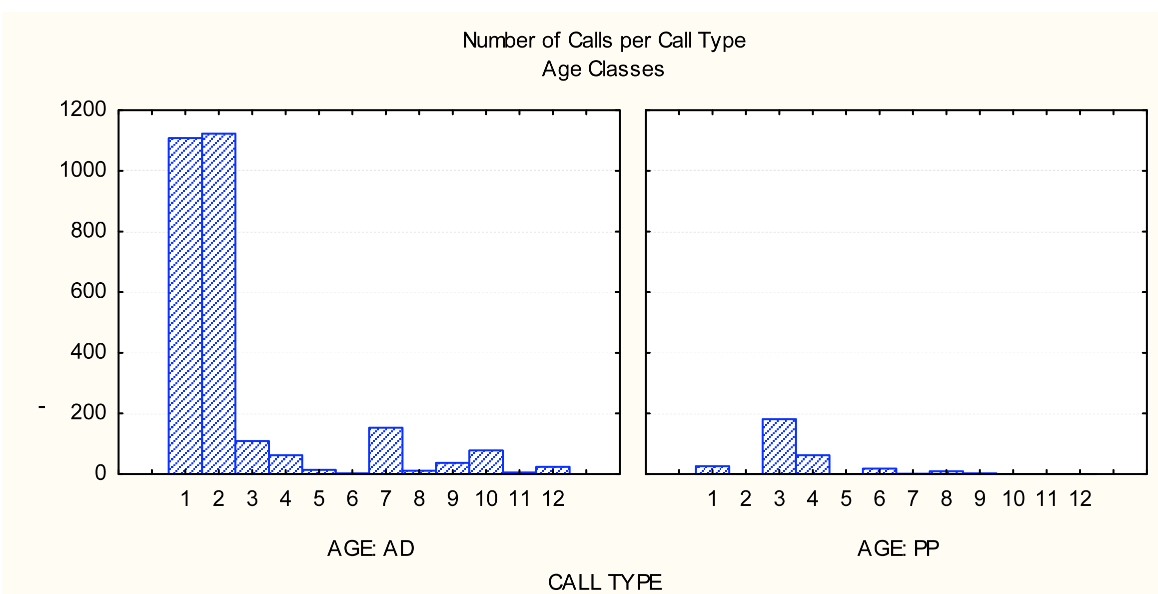
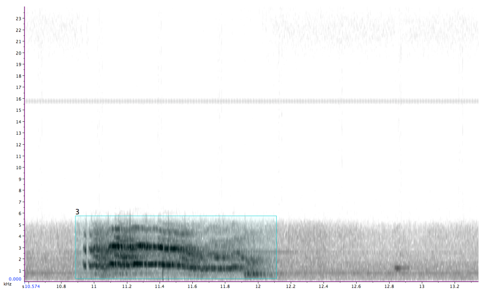


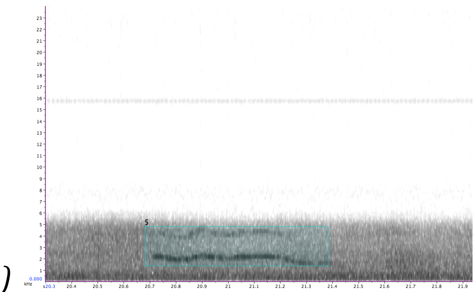
Figure 6.2: Spectral comparison of adult and pups based on shared call types. Whistle is unique to the pups

(a)



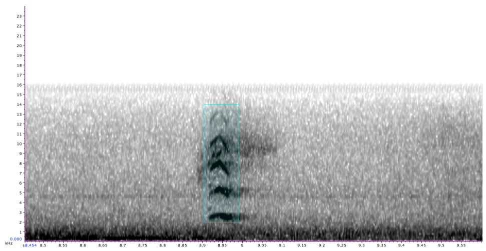
Adult-Whine (harmonic)

(b)



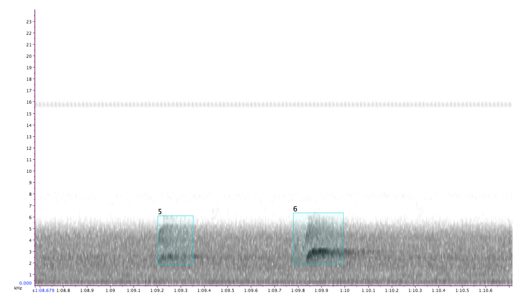
Pup-Whine (harmonic)

(c)



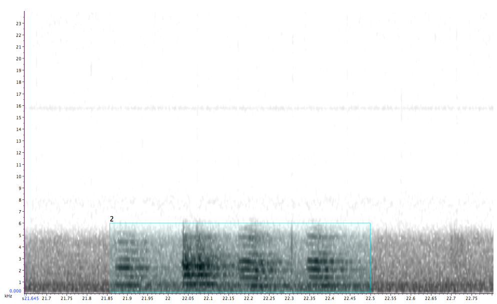
Adult-Chirp

(d)



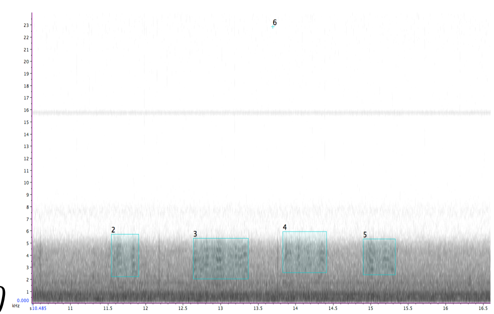
Pup-Chirp

(e)



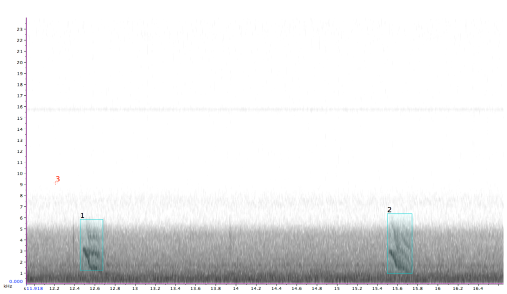
Adult-Chatter (harmonic)

(f)



Pup-Chatter (harmonic)

(g)



Pup-Whistle

Statistical Analysis

Comparison of frequencies, harmonics, power and duration between adults and pups shared call types

Morphological variations exist between adults and pups therefore variations will exist in the vocal repertoires. Based on my observations I propose several hypotheses *(Table 6.2)*. To test the hypotheses that in shared call types there are significant differences in frequencies, harmonics, powers and duration among age classes I employed a Mann-Whitney Test to determine the variation among variables. I used the Mann-Whitney Test because it's a non-parametric test that does not assume a normal distribution. The *whine*, *chirp* and *chatter* are compared because they are the only shared calls across age classes.

Results

Table 6.1a: Descriptive Statistics of frequencies of call types based on age. (Means +/- SD). The age class with the higher mean is highlighted in bold.

Call Type	*Age*	*Sample Size (# of individuals)*	*High Freq (kHz)*	*Low Freq (kHz)*	*Range of Freq (kHz)*	*Mean Freq (kHz)*	*Max Freq (kHz)*	*Center Freq (kHz)*
Whine	*AD*	*959 (10)*	**5970+/-1735**	609+/-501	**5471+/-4153**	**3289+/-922**	**2587+/-913**	**2573+/-817**
	PP	*170 (2)*	4852+/-754	**1165+/-450**	3695+/-923	3009+/-478	1993+/-667	1980+/-539
Chirp	*AD*	*1024 (7)*	**8764+/-3395**	1407+/-792	**7480+/-4951**	**5080+/-1752**	**2478+/-1077**	2525+/-905
	PP	*100 (2)*	4209+/-1120	**1890+/-684**	2706+/-4354	3049+/-530	2700 +/-572	**2681+/-484**
Chatter	*AD*	*290 (10)*	**6571+/-1073**	661+/-472	**5900+/-1233**	3616+/-577	3028+/-754	3076+/-544
	PP	*5 (1)*	5453+/-122	**2342+/-136**	2982+/-103	**3897+/-119**	3188+/-265	3263+/-168
Whistle	*PP*	*24 (1)*	4947+/-868	998+/-274	3949+/-924	2973+/-448	1898+/-545	1789+/-354

Table 6.1b: Descriptive Statistics of powers, duration and harmonics of call types based on gender. (Means +/- SD). The age class with the higher mean is highlighted in bold.

Call Type	*Age*	*Sample Size (# of individuals)*	*Max Pwr (dB)*	*Avg Pwr (db)*	*Duration (s)*	*Harmonics (#)*
Whine	*AD*	*959 (10)*	**88+/-11**	**69+/-10**	**1.4+/-1.1**	1.1+/-1.9
	PP	*170(2)*	70+/-4	54+/-3	0.5+/-0.2	**1.9+/-0.8**
Chirp	*AD*	*1024 (7)*	91+/-8	73+/-7	0.2+/-0.4	**3.3+/-1.7**
	PP	*100 (2)*	81+/-6	66+/-5	**0.2+/-0.1**	1.6+/-0.8
Chatter	*AD*	*290 (10)*	**94+/-9**	**74+/-8**	**1.8+/-1.3**	0.4+/-1.5
	PP	*5 (1)*	58+/-1.5	45+/-1.5	0.6+/-0.1	**2.4+/-2.2**
Whistle	*PP*	*24 (1)*	71+/-3	55+/-3	0.4+/-0.1	2+/-1

Table 6.2: Table of hypotheses proposed on the variations of adults and pups (HF=high frequency; LF=low frequency, MXF=maximum frequency; MXPWR=maximum power DRT=duration and HRM=harmonics). Hypotheses, the results of the Mann-Whitney and interpretation of results are shown. Significant p-values are highlighted in bold and marked with an asterisk (*).

Call Type	H_a	H_o	*Mann-Whitney p-value*
Whine	$HF_{AD} \neq HF_{PP}$	$HF_{AD} = HF_{PP}$	**<0.000000005***
	$LF_{AD} \neq LF_{PP}$	$LF_{AD} = LF_{PP}$	**<0.000000005***
	$RGF_{AD} \neq RGF_{PP}$	$RGF_{AD} = RGF_{PP}$	**<0.000000005***
	$MNF_{AD} \neq MNF_{PP}$	$MNF_{AD} = MNF_{PP}$	**<0.000000005***
	$MXF_{AD} \neq MXF_{PP}$	$MXF_{AD} = MXF_{PP}$	**<0.000000003***
	$CTF_{AD} \neq CTF_{PP}$	$CTF_{AD} = CTF_{PP}$	**<0.000000002***
	$MXPWR_{AD} \neq MXPWR_{PP}$	$MXPWR_{AD} = MXPWR_{PP}$	**<0.000000005***
	$AVGPWR_{AD} \neq AVGPWR_{PP}$	$AVGPWR_{AD} = AVGPWR_{PP}$	**<0.000000005***
	$DRT_{AD} \neq DRT_{PP}$	$DRT_{AD} = DRT_{PP}$	**<0.000000005***
	$HRM_{AD} \neq HRM_{PP}$	$HRM_{AD} = HRM_{PP}$	**<0.0000001***

Table 6.2 continued: Table of hypotheses proposed on the variations of adults and pups (HF=high frequency; LF=low frequency, MXF=maximum frequency; MXPWR=maximum power DRT=duration and HRM=harmonics). Hypotheses, the results of the Mann-Whitney and interpretation of results are shown. Significant p-values are highlighted in bold and marked with an asterisk (*).

Chirp	$HF_{AD} \neq HF_{PP}$	$HF_{AD} = HF_{PP}$	**<0.000000000004***
	$LF_{AD} \neq LF_{PP}$	$LF_{AD} = LF_{PP}$	**<0.000000000004***
	$RGF_{AD} \neq RGF_{PP}$	$RGF_{AD} = RGF_{PP}$	**<0.000000000004***
	$MNF_{AD} \neq MNF_{PP}$	$MNF_{AD} = MNF_{PP}$	**<0.000000000004***
	$MXF_{AD} \neq MXF_{PP}$	$MXF_{AD} = MXF_{PP}$	**<0.0000000004***
	$CTF_{AD} \neq CTF_{PP}$	$CTF_{AD} = CTF_{PP}$	**<0.0000000004***
	$MXPWR_{AD} \neq MXPWR_{PP}$	$MXPWR_{AD} = MXPWR_{PP}$	**<0.0000000008***
	$AVGPWR_{AD} \neq AVGPWR_{PP}$	$AVGPWR_{AD} = AVGPWR_{PP}$	**<0.0000000004***
	$DRT_{AD} \neq DRT_{PP}$	$DRT_{AD} = DRT_{PP}$	**<0.0000000004***
	$HRM_{AD} \neq HRM_{PP}$	$HRM_{AD} = HRM_{PP}$	**<0.0000000005***
Chatter	$HF_{AD} \neq HF_{PP}$	$HF_{AD} = HF_{PP}$	**<0.0005***
	$LF_{AD} \neq LF_{PP}$	$LF_{AD} = LF_{PP}$	**<0.0001***
	$RGF_{AD} \neq RGF_{PP}$	$RGF_{AD} = RGF_{PP}$	**<0.0001***
	$MNF_{AD} \neq MNF_{PP}$	$MNF_{AD} = MNF_{PP}$	**<0.007***
	$MXF_{AD} \neq MXF_{PP}$	$MXF_{AD} = MXF_{PP}$	>0.05
	$CTF_{AD} \neq CTF_{PP}$	$CTF_{AD} = CTF_{PP}$	>0.05
	$MXPWR_{AD} \neq MXPWR_{PP}$	$MXPWR_{AD} = MXPWR_{PP}$	**<0.0001***
	$AVGPWR_{AD} \neq AVGPWR_{PP}$	$AVGPWR_{AD} = AVGPWR_{PP}$	**<0.0001***
	$DRT_{AD} \neq DRT_{PP}$	$DRT_{AD} = DRT_{PP}$	**<0.07***
	$HRM_{AD} \neq HRM_{PP}$	$HRM_{AD} = HRM_{PP}$	**<0.0002***

Age Class Comparison based on spectral images and Mann-Whitney Results

The spectral images of the *whines (Figure 6.2a and b)* show no distinct differences, except in the harmonics, the pups have less harmonics bands in comparison to the adults giving them a lower range of frequency, but it should be noted that there are some adult whines that could have low number of harmonics. The Mann-Whitney results *(Table 6.2)* show a significant difference in all the variables. The adults are significantly higher across variables except in the low frequency and the duration. The pups have a higher low frequency but a lower high frequency therefore they have an overall lower range of frequency.

The *chirp's* spectral images *(Figure 6.2c and d)* show that the range of frequency is different in pups and adults. The adults have more harmonic bands, but the pup's harmonics are linear which is comparable to the adult females. The Mann-Whitney shows *(Table 6.2)* that there were significant differences across all the variables. The pups have higher frequencies, and the adults have higher powers and are longer in duration. The results further confirm that adults did have a significantly higher range of frequency.

The *chatter* has a similar appearance *(Figure 6.2e and f)* to the *chatter* of adults and looks like a series of chirps in succession. There are no distinct differences except the harmonics are linear which is comparable to the harmonics in the chatter of adult females. The results of the Mann-Whitney *(Table 6.2)* suggest that the *chatter* is significantly different in all variables except the max frequency and the center frequency. But, it should be noted that the sample size for the pups was very small (*n=6)* which could affect the results.

The *whistle (Figure 6.2g)* is unique to the pups born at Beardsley Zoo, it is harmonic and appears similar to the chirp, but has a down sweep of the harmonic bands in the beginning. Based on my observations, I suggest that the whistle is apparent in the early stages of life as a form of echolocation to locate their mother. The pups have three limiting factors in the first two months of their life (1) they are inside a dark den or holt (2) they are completely blind (3) their mother has very minimal vocal interactions with them. I speculate that the *whistle* is used to make-up for the limitations and give the pups the ability to locate their mother and food source. Furthermore, as the dependency on the mother reduces the whistle reduces and eventually is eliminated from the repertoire. Jelly's pups gave insight to the vocals at an age where the pups are less dependent, and I did not observe any whistles in this group. However, because I did not observe them in the early weeks of their lives, I can only speculate if the whistle existed in their repertoires during their dependent phase and eventually was reduced.

Discussion

There were significant variations in the frequencies, powers, duration and harmonics. However, the results do not suggest whether the variation exist because it is used in identifying or locating purposes. Based on my observations of mother-pup interactions I suggest that the vocal variation exist due to two reasons: (1) size and morphological differences create vocal age differences (2) it assists the pup in locating its mother.

The spectral comparison suggests that the pups have under-developed versions of the adult's calls. The pups unlike the adults have little variation in their whines and chirps. I speculate that at the early stages of life the repertoire is simplistic and as they get older and develop the repertoire becomes more complex. It's appropriate that the whine or the chirp would be so prevalent since they are the most dominant call types in the repertoire.

River otters do not have the same limitations on identifying or locating their pups as more social species do. Females rear the young inside private dens, and often remain solitary until the young are no longer dependent. Therefore, there is no need for a female to have to use vocalization to accurately identify or even locate her young. It is likely that olfactory recognition would the influencing factor for this. But, the pups have limitations on locating their mother, and they are likely using their vocal system to assist them.

Chapter Seven

Data Analysis III-Vocal Repertoire and its uses

Introduction

Communication can be defined in various ways, but I've defined communication as a "behavior involving signals", with a signal being something that has evolved by natural selection to transmit information *(Bolhuis, 2005).* The signal requires a signaler and receiver, but the receiver does not necessarily need to be aware of the intention. I used this definition of communication because it takes into consideration a signal, signaler and receiver, without implying any intentionality. Communication is fundamental to many aspects of life, in reproduction it assist in achieving mating success, in parental care it is often the factor that solidifies the mother-pup bond, and in survival it assist in avoiding predators or increasing prey capture *(Bolhuis 2005).*

Visual signals (e.g. fiddler crab dance), chemical signals (e.g. scent marking) and acoustic signals (e.g. vocals, songs) are the most common form of communication. Often these forms of communication are used in conjunction to relay a message(s). Wild chimpanzees *(Herbinger, 2009)* use vocal, gestural, and locomotive responses when in contact with unfamiliar members of their communities. Acoustic communication is particularly prevalent in aquatic mammals. The literature on the vocal communicative systems of highly social species propose several hypotheses to explain the systems found in sea lions, harbor seals, harps seals, killer whales, and sperm whales *(Charrier, 2008; Khan, 2006; Opzeeland, 2003; Reisch 2011; and Rendell, 2003)*. Sea lion, harbor seals, and harp seal mother and pups use vocal imprinting to solidify their bond. Killer whales and sperm whales develop unique dialects within pods or clans that help maintain cohesiveness of groups. Chemical signaling has several purposes; prairie voles scent mark to relay individual identity *(Thomas, 2002)*, and tree shrews regulate their marking based on the marking behaviors of con-specifics, and their social status *(Holst, 1997).*

Communication and Otters

Otters avoid interactions with unfamiliar individuals, because these confrontations can be highly violent and lead to serious consequences. But, despite their ability to avoid one another, physical interactions occur. When home ranges overlap and males come in direct contact, physical bouts often ensue. Aggressive interactions have been observed when males come too close to females with pups. Vocalizations are commonly heard during these intra-specific interactions.

During aggressive interactions Eurasian otters release high-pitched screams, and 'wickering' sounds, and if mother and pup are separated they 'whistle' to one another *(Kruuk, 2006).* Giant otters travel in troops along rivers and release screams, wails, barks, and snorts to avoid strangers in their path. Physical confrontations do occur, but this is often seen in areas where individuals are in high-density *(Kruuk, 2006).* Giant otters also use a HAH as an alarm call to warn other members of the groups of a potential danger, and they vocalize underwater. Other otter species like the Smooth and spotted otter *(Kruuk, 2006),* and Asian small-clawed otters show acoustic communicative system, but Sea otters *(McShane, 1995)* and Giant otters appear to have the most elaborate systems of all otters. There are no studies that focus on the vocal system of river otters. But, based on my observations, river otters are like other otters in their communicative systems. They use both scent and vocal communication to relay messages. And in close contact ('friendly' or aggressive) vocalization is the dominant form of communication.

Goal

The presence of a vocal system is apparent in river otters, but to get a better understanding of the vocal repertoire it is crucial to evaluate when calls are used. The goal of this section is to use the behavioral observations of captive otters along with the vocal repertoires to determine if (1) quantified measurements of structural components (duration, max frequency, and max power) of a vocalization can be used as an indicator of the arousal state of the otter (2) the type of interaction is associated with the call type heard (3) the arousal state of the otter is associated with the call type heard.

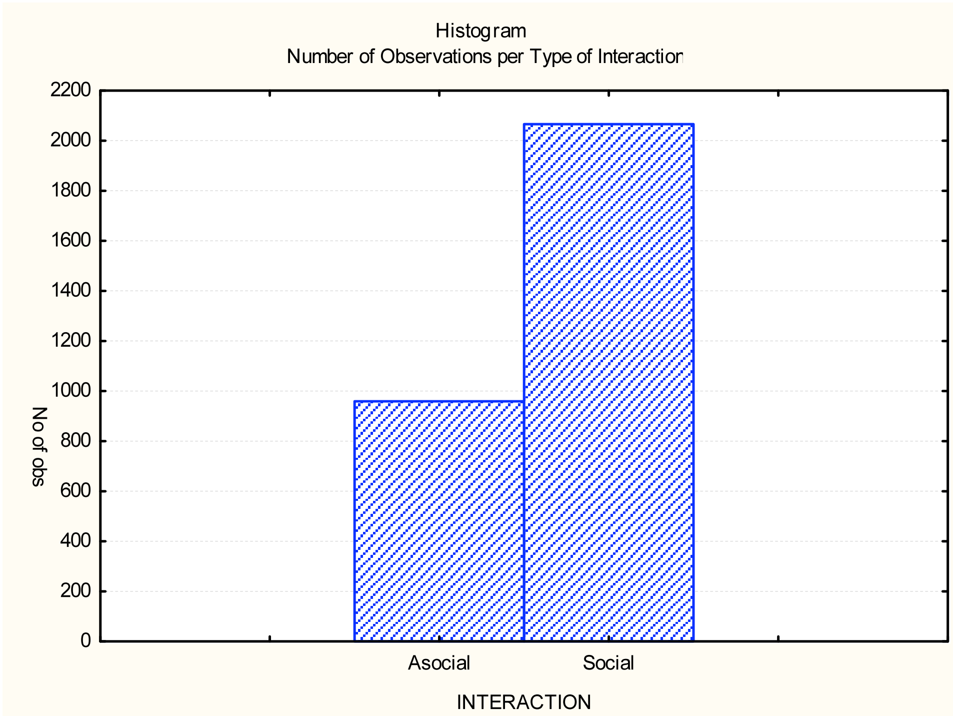
Methods

Each call type was categorized into two separate categories: the type of interaction *(Table 7.1a)* it was heard in, and the arousal state *(Table 7.1b)* of the individual at the time of the call. An interaction is defined to be any individual act that includes the involvement of another individual or object. The interactions had two sub-categories: asocial or social.

Table 7.1: Definitions of Types of Interactions.

Interaction	Interactive With	Definition
Asocial	Environment	One individual involved in a behavior that includes something from the environment, can be an inanimate object. Behaviors: Swimming, massaging self using a substrate, climbing, interact with rock, or twig
	Self	One individual involved in a behavior that includes something from the individuals body Behaviors: grooming, chewing or biting on body parts
Social	Otter	(1) Two or more individuals, at least an otters distance apart, are involved in reciprocal exchange of signals. (2) Two or more individuals simultaneously involved in the same behavior, an otters distance apart.
	Human	One or more otter(s) involved in a reciprocal exchange of message(s) with a human(s). Otter and human are at least an otter distance apart. Behaviors: training, feeding, visitors approaching exhibits

Figure 7.1: Histogram depicting the number of calls observed per type of interaction

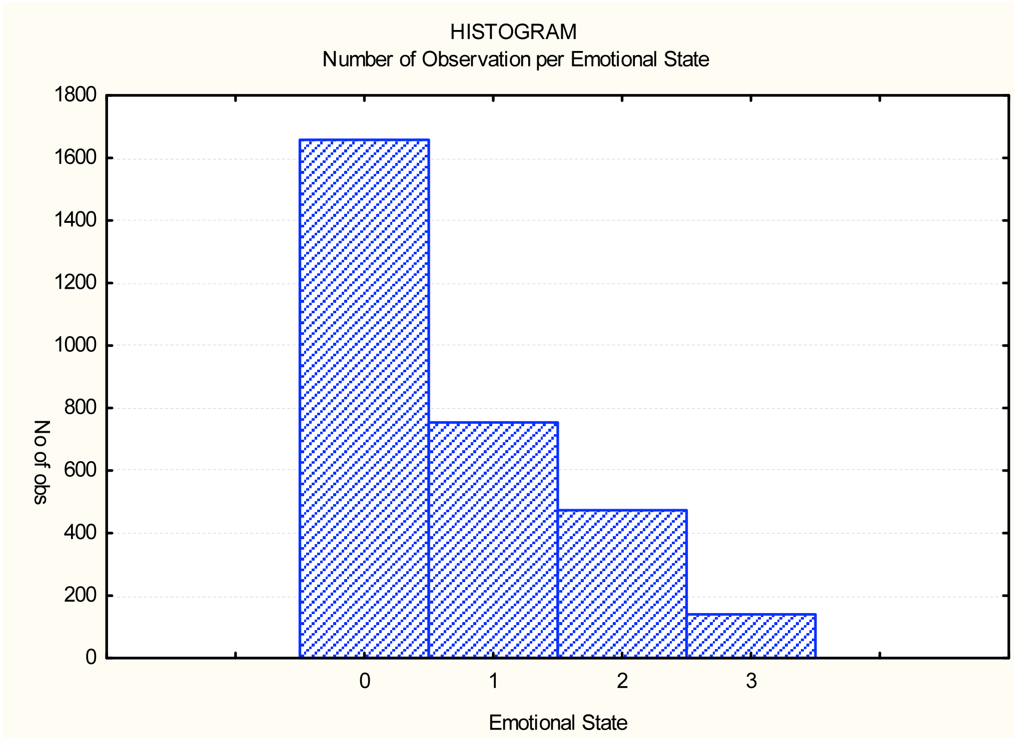


I defined an arousal state as a particular state of mind that is in regards to the individual's level of agitation. To determine an individual's arousal state I used factors that are outwardly expressed through behaviors. I categorized the behaviors that I observed into 4 levels of arousal state. Specific definitions are listed in the Table 7.2a.

Table 7.2: Definitions of Arousal States

Arousal State	Code	Definition
Non-agitated	0	Otter exhibits 'friendly' or timid behaviors. Behaviors: play (wrestling, chasing, inanimate object, body parts) grooming
Mildly agitated	1	Otter exhibits behaviors of frustration. Behaviors: biting or chewing on self, another, or object; pacing
Moderately agitated	2	Otter exhibits aggressive behaviors. Aggressive behaviors were defined based on the otter's body language. Behaviors: crouching head down, tail is positioned down, hunching of the back.
Highly agitated	3	Otter exhibits physical aggressive behaviors. Aggressive behaviors were defined based on the otter's body language, and the involvement of a physical confrontation. Behaviors: physically attacks (biting, violent wrestling)

Figure 7.2: Histogram depicting the number of calls observed per arousal state



Statistical Analysis

For all statistical analyses I used the complete data set consisting of all the vocalizations observed in adults and pups *(n=3025)*.

Duration, Max Frequency, and Max Power and Arousal State

To test the predication that call characteristics (a) duration, (b) max frequency, and (c) max power are significantly different across the levels of arousal state, I used a Kruskal-Wallis test with a multiple comparison test to determine where the underlying differences exist.

The Kruskal-Wallis can determine the differences, but I also wanted to determine if there was a correlation between the value of the call characteristic (duration, max frequency, max power) and the arousal state of the individual producing the call. To test the hypothesis that the value of the call characteristic increases as the level of emotional state increases, I used a non-parametric Spearman Rank Correlation test to obtain the correlation coefficient for each comparison.

Call types and the association with interactions and arousal state

I hypothesize that the vocals produced in river otters are associated with the type of interaction they are engaged in and the emotional state they are in. To test these hypotheses I created 2 separate contingency tables testing for the association of (a) call type and type of interaction and (b) call type and the state of arousal. I then conducted a chi-square test to the significance of the associations.

Results:

Table 7.3: Kruskal-Wallis testing the differences across the arousal state of the otter listed by acoustical structures (duration, max frequency, and max power)

Duration	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*3*	587.22353	195.74118	224.50972	**<0.0000000001***
	Within Groups	*3021*	2633.89078	0.87186		
Max Frequency	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*3*	199513132.37637	66504377.45879	62.68955	**<0.0000000001***
	Within Groups	*3021*	3204835990.72831	1060852.69471		
Max Power	*Source of Variation*	*d.f*	*SS*	*MS*	*F*	*p-level significance*
	Between Groups	*3*	36979.49784	12326.49928	107.85549	**<0.0000000001***
	Within Groups	*3021*	345261.55116	114.28717		

Table 7.4: Kruskal-Wallis multiple comparison of arousal state for duration, max frequency, and max power.

	Comparison	*Bonferroni p-value*	*Higher Mean (Level)*
DURATION			
	3 vs 0	**<0.0000000001***	3
H_a:	*3 vs 1*	**<0.0000000001***	3
Level 0≠ Level 1 ≠Level 2≠Level 3	*3 vs 2*	**<0.0006***	3
H_0:	*2 vs 0*	**<0.0000000001***	2
Level 0= Level 1= Level 2=Level 3	*2 vs 1*	**<0.0000000001***	2
	1 vs 0	**<0.0000000001***	1
MAX FREQUENCY			
	3 vs 0	**<0.000000002***	3
H_a:	*3 vs 1*	**<0.003***	3
Level 0≠ Level 1 ≠Level 2≠Level 3	*3 vs 2*	>0.05	=
H_0:	*2 vs 0*	**<0.000000002***	2
Level 0= Level 1= Level 2=Level 3	*2 vs 1*	**<0.00008***	2
	1 vs 0	**<0.000000001***	1
MAX POWER			
	3 vs 0	**<0.00000001***	3
H_a:	*3 vs 1*	**0.0001***	3
Level 0≠ Level 1 ≠Level 2≠Level 3	*3 vs 2*	>0.05	=
H_0:	*2 vs 0*	**<0.0000001***	2
Level 0= Level 1= Level 2=Level 3	*2 vs 1*	**0.00006***	2
	1 vs 0	**<0.0000001***	1

Difference in duration/power/max frequency variables based on arousal state (Kruskal-Wallis)

The Kruskal-Wallis shows that there are significant differences in the means of the structural components based on the arousal state the otter is in. The results of the multiple comparisons show that the differences are present for all comparisons, across the structural variables. The exception is in the max power and max frequency they show no significant difference in the means for the moderately agitated (level 2) and highly agitated (level 3) arousal state.

Correlation between arousal state and duration/power/max frequency

Table 7.5: Relationship between duration of a call and arousal state of the otter.

Spearman R	*0.54803*
Rank Difference Squares Sum	*1,905,283,004.5*
t-test value for hypothesis r = 0	*36.02334*
p-level	***0.000000****
Gamma	*0.54643*
Pearson Correlation Coefficient	*0.42461*

Figure 7.5: Correlation between duration and arousal state.

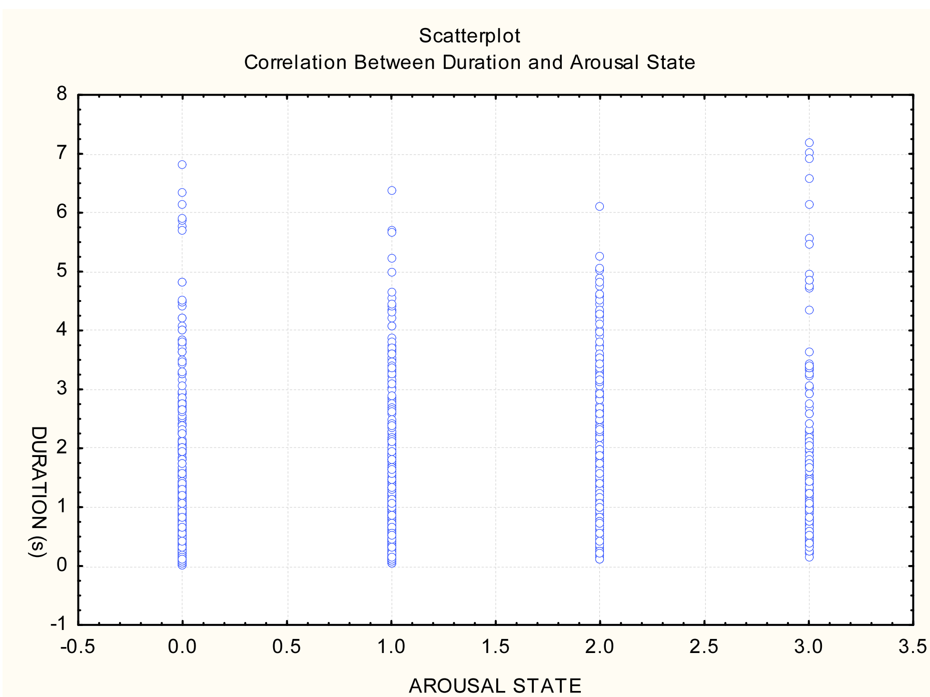


Table 7.6: Relationship between max frequency and arousal state of the otter.

Spearman R	*0.32802*
Rank Difference Squares Sum	*2,815,332,956.*
t-test value for hypothesis r = 0	*19.09148*
p-level	***0.000000****
Gamma	*0.34227*
Pearson Correlation Coefficient	*0.23655*

Figure 7.6: Correlation between max power and arousal state.

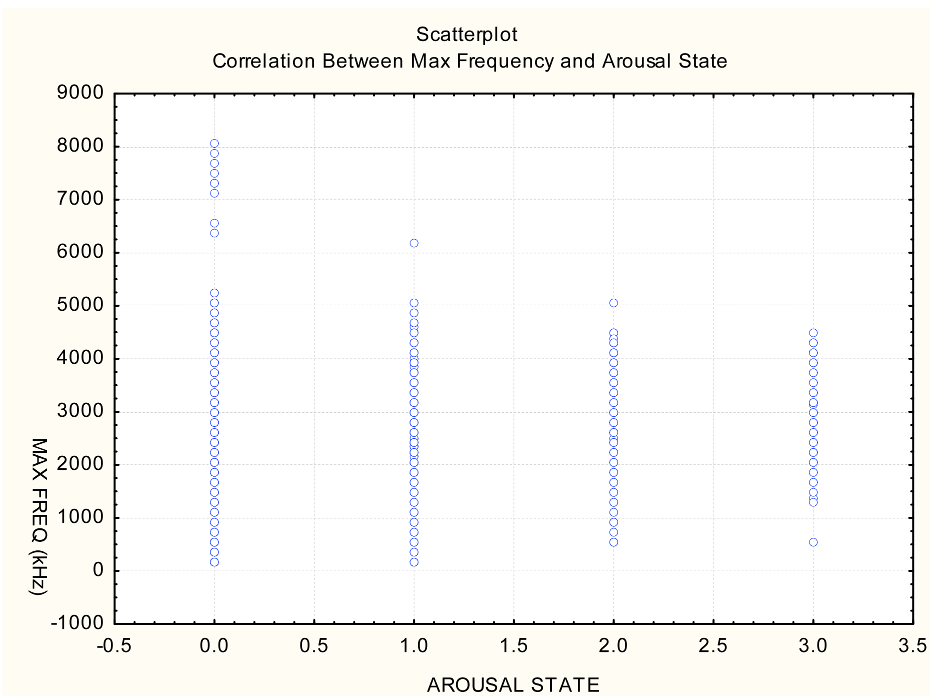
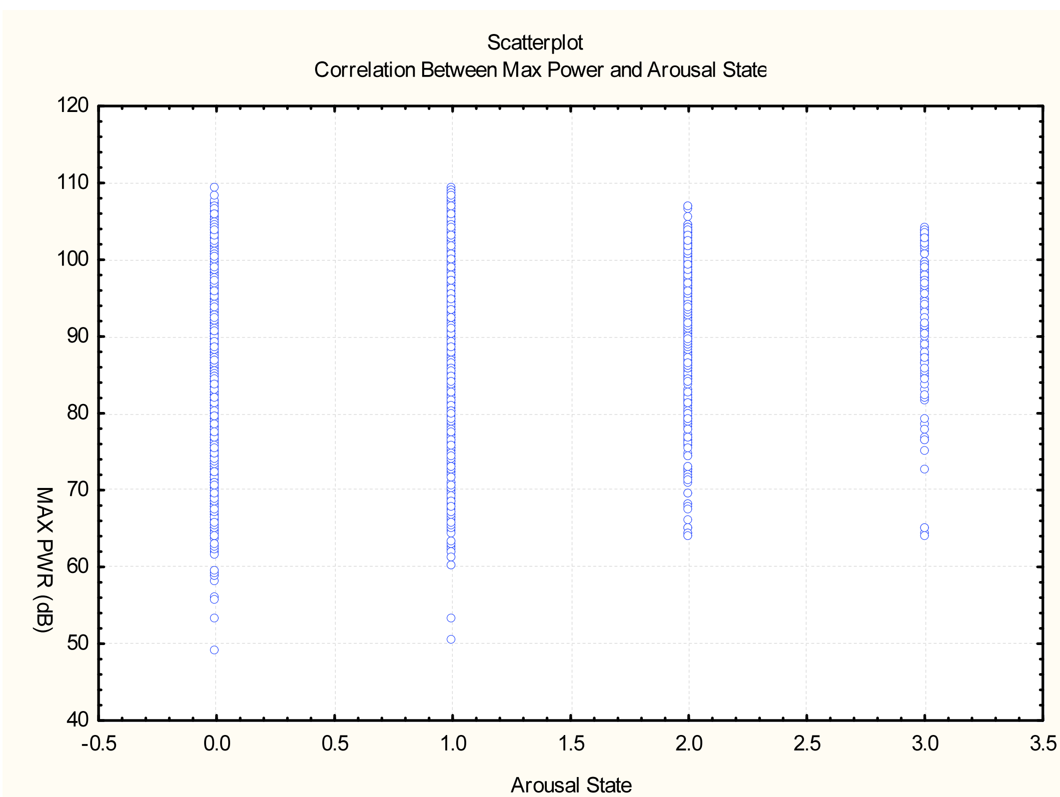


Table 7.7: Relationship between max power of a call and arousal state of the otter.

Spearman R	*0.33129*
Rank Difference Squares Sum	*2,808,644,995.5*
t-test value for hypothesis r = 0	*19.30533*
p-level	***0.000000****
Gamma	*0.32145*
Pearson Correlation Coefficient	*0.30444*

Figure 7.7: Correlation between max power and arousal state.



The Spearman Correlation tests produced positive Pearson Correlation Coefficients indicating that there is a positive correlation between the level of arousal state and (a) duration (b) max frequency and (c) max power. Scatter plots with are also shown to give a graphical view of the correlation.

Specificity of Call Types (Interactions and Arousal State)

Figure 7.8: Histograms showing the number of calls (n) observed for each type of interaction based on call types.

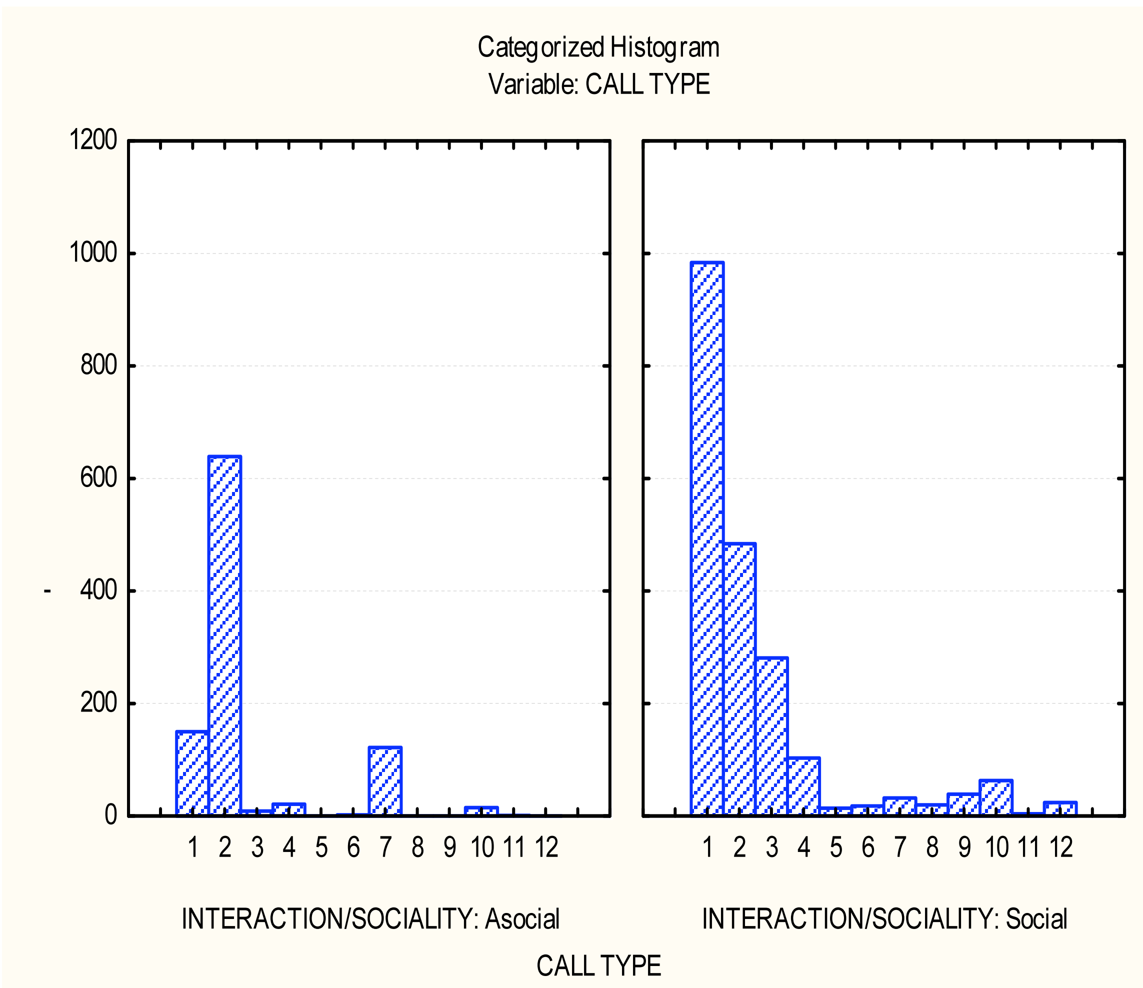


Figure 7.8: Contingency table reflecting the number of calls (n) observed and the expected values for each level based on call types and the results of the chi-square test and critical value is shown

	Asocial	***Social***	***Total***
Whine	151 *(357.17)*	978 *(771.08)*	**1129**
Chirp	639 *(355.60)*	485 *(766.76)*	**1124**
Chatter	9 *(93.33)*	286 *(201.48)*	**295**
Creek	21 *(39.23)*	103 *(84.69)*	**124**
Squeak	0 *(4.43)*	14 *(9.56)*	**14**
Scream	2 *(6.33)*	18 *(13.66)*	**20**
Grunt	122 *(48.72)*	32 *(105.18)*	**154**
Swish	0 *(6.33)*	20 *(13.66)*	**20**
Hiss	0 *(12.33)*	39 *(26.66)*	**39**
Blow	15 *(24.68)*	63 *(53.28)*	**78**
Hiccup	1 *(1.27)*	3 *(2.73)*	**4**
Whistle	0 *(7.59)*	24 *(16.39)*	**24**
Total	**959**	**2066**	**3025**

Figure 7.8 continued: Contingency table reflecting the number of calls (n) observed and the expected values for each level based on call types and the results of the chi-square test and critical value is shown

Chi Square	*d.f.*	*Chi-square (CV)*	*p-level*
877.38	22	33.924	**0.000000***
Results **The call type heard is not independent of the type of interaction**			

The results indicate that the call type and the type of interaction are not independent of each other. Call types are highly associated *(p=0.0000000)* with the type of interaction they are observed in, implying that the absence or presence of a con-specifics can directly affect the frequency of call type.

The contingency table depicts the number of observed values compared to the expected values for call type and type of interaction. The central tendency is for call types to be heard in social interactions. The table indicates that the *chirp* and the *grunt* were more frequently heard during asocial interactions. All other call types (*whine, chatter, creek, squeak, scream, swish, hiss, blow* and *hiccup*) were heard most frequently during social interactions.

Figure 7.9: Histograms showing the number of calls (n) observed for each level of arousal state based on call types

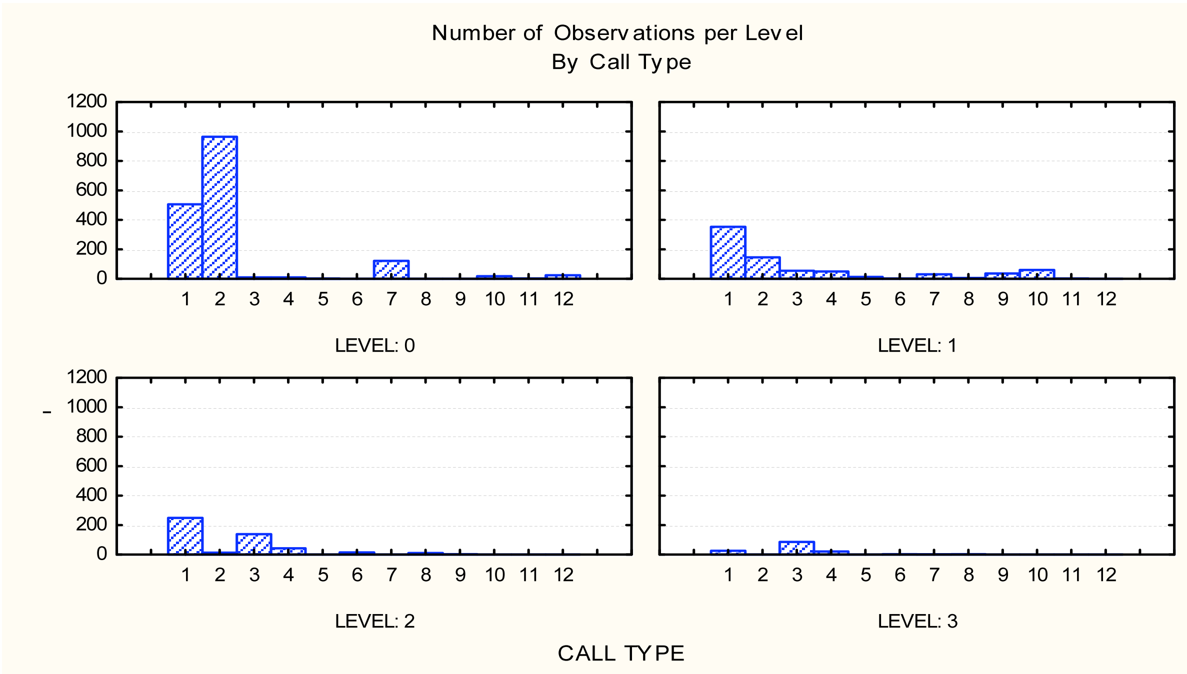


Figure 7.9: Contingency table reflecting the number of calls (n) observed and expected values for each level of arousal state based on call types, the results of the chi-square and critical value are shown.

Call Type	***None***	***Mild***	***Moderate***	***High***	***Total***
Whine	501 *(618.804)*	353 *(281.410)*	249 *(176.535)*	26 *(52.251)*	**1129**
Chirp	965 *(616.063)*	146 *(280.164)*	13 *(175.753)*	0 *(52.0198)*	**1124**
Chatter	15 *(161.689)*	55 *(73.531)*	139 *(36.127)*	86 *(13.653)*	**295**
Creek	10 *(67.964)*	50 *(30.908)*	43 *(19.389)*	21 *(5.739)*	**124**
Squeak	1 *(7.673)*	13 *(3.490)*	0 *(2.189)*	0 *(0.678)*	**14**
Scream	0 *(10.962)*	2 *(4.985)*	15 *(3.127)*	3 *(0.927)*	**20**
Grunt	122 *(84.407)*	31 *(38.385)*	0 *(24.08)*	1 *(7.127)*	**154**
Swish	0 *(10.962)*	6 *(4.985)*	11 *(3.127)*	3 *(0.927)*	**20**
Hiss	0 *(21.376)*	36 *(9.720)*	3 *(6.098)*	0 *(1.804)*	**39**
Blow	18 *(42.751)*	60 *(19.442)*	0 *(12.196)*	0 *(3.610)*	**78**
Hiccup	2 *(2.192)*	2 *(0.997)*	0 *(0.625)*	0 *(0.185)*	**4**
Whistle	24 *(13.154)*	0 *(5.982)*	0 *(3.752)*	0 *(1.110)*	**24**
Total	**1658**	**754**	**473**	**140**	**3025**

Figure 7.9 continued: Contingency table reflecting the number of calls (n) observed and expected values for each level based on call types, the results of the chi-square and critical value are shown.

Chi Square	***d.f.***	***Chi-square (CV)***	***p-level***
1818.48	33	47.400	**0.000000***
Results			
The call type heard is not independent of the level of agitation			

The chi-square results indicate that the call type heard is not independent of the level of arousal. Vocal call types are highly associated *(p=0.000000)* with the state of agitation the otter is in.

The contingency table depicts the number of observed values compared to the expected values for call type and levels of arousal. It indicates that the central tendency was for calls to be exhibited during non-agitated states. The *whine, chirp*, *grunt*, were most frequently heard when the otter was in a non-agitated state. The *creek, squeak, hiss,* and *blow* were most frequently heard when the otter was in a mildly agitated state, and the *chatter, scream*, and *swish* were most frequently heard in moderately agitated states.

Discussion

My results indicate that structural components of a vocal are good indicators of the arousal state of the otter. Particularly the duration, max frequency, and max power show a positive correlation with the emotional state of the individual producing it. Furthermore, the vocal types that are exhibited by an individual are associated with the type of interaction the otter is engaged in, and the arousal state the otter.

The results of the chi-square show strong evidence of contextual purpose of calls, furthermore structural components of the call can relay information. This further confirms that the vocal repertoire of river otters is complex.

Contextual purpose for calls is likely present because river otters avoid confrontation at all cost. Although, scent communication is important for this, it is only useful in long distance communication. Therefore, when individuals come in closer contact they need another form of communication to relay information and vocalizations are the dominant form. Relaying arousal state can be very useful information to others, because it allows others to know the type of interaction they may be engaging in, and it can prevent physical confrontations.

Summary/Conclusions

This study has established several new ideas and insights about the behaviors and the communication system of North American River Otters. The vocal repertoire is a complex system that consists of 4 major vocal types *(Whine, Chirp, Grunt, Blow)*. These four call types are the foundation for all the other calls that are heard by ear. All the other call types are variations or hybrids of the *whine,* and *chirp.* Therefore, river otters use their calls in conjunction with other calls, in isolation or in a rapid series to produce vocals that sound different to the human ear.

When vocal repertoires are compared there are significant differences across acoustical structures. Individuality is present in several of the call types (*whine, chirp, chatter, creek, swish, grunt, and blow)*, which likely caused some ambiguity in the ability to classify calls. The presence of individual differences may exist for the purpose of identification (but further analysis must be conducted to confirm this). However, there are specific differences in the sexes and in the age groups. In both sexes there are unique calls present *(squeak, scream).* Based on the spectral images they are likely analogous to each other, but sound different because of the morphological differences in males and females. The pups exhibit a unique call-the *whistle*, which is likely present in the early dependent weeks of life and reduced as they develop and become independent. The shared call types between sexes, and age groups showed significant differences across acoustical structures that are likely due to morphological differences, but I speculate that these differences may also help in identification.

The repertoire has contextual purposes. The results showed that the quantifications of acoustical structures in particular the duration, max frequency, and max power positively correlate to the arousal state of the otter. River otters show tendencies to exhibit specific call types during specific interactions (asocial or social). And they also have tendencies to exhibit specific call types when in a particular arousal state. This implies that call types exhibited relay specific information about the individual producing the vocalization.

Bibliography

Books

Bolhuis, J.J. and Giraldeau, L. 2005. The Behavior of Animals: Mechanisms, Function, and Evolution. *Blackwell Publishing.*

Campbell, R.C. 1989. Statistics for Biologists: Third Edition. *Cambridge University Press.*

Chanin, P. 1985. The Natural History of Otters*. Facts on File Publishing.*

Kruuk, H. 2006. Otters: Ecology, behaviour, and conservation*. Oxford University Press.*

Hauser, M.D. 2000. Wild Minds: What Animals Really Think. *Henry Holt and Company, LLC.*

Martin, P. and Bateson, P. 2009. Measuring Animal Behavior: An Introductory Guide (Third Edition). *Cambridge University Press.*

Shettleworth, S.J. 1998. Cognition, Evolution, and Behavior *Oxford University Press: pp-523-565.*

Senter, R.J. 1969. Analysis of Data: Introductory Statisitics for the Behavioral Sciences. *Scott, Foresman and Company.*

Zar, J.H. 1999. Biostatistical Analysis: Fourth Edition. *Prentice Hall.*

Articles

Anderson, P.K., and Barclay, R.M.R. 1995. Acoustic signals of solitary Dugongs: Physical characteristics and behavioral correlates. *Journal of Mammalogy:* 76(4): 1226-1237.

Ben-David, M., Bowyer, R.T., Duffy, L.K., Roby, D.D., and Schell, D.M. 1998. Social Behavior and Ecosystem processes: River otter latrines and nutrient dynamics of terrestrial vegetation. *The Ecological Society of America:* 79(7): 2567-2571.

Ben-David, M., Blundell, G.M., Kern, J.W., Maier, J.A.K., Brown, E.D. and Jewitt, S.C. 2005. Communication in River Otters: Creation of variable resource sheds for terrestrial communities.

Bezzera, B.M.,Souto, A.S., and Schiel,N. 2010. Notes on vocalizations of giant otters in the flooded Igapo forests of Jau National Park, Amazonas, Brazil. *Journal of Ethology:* 29:169-175.

Blundell, G.M., Ben-David, M., and Bowyer, R.T. 2001. Sociality in river otters: cooperative foraging or reproductive strategies? *Behavioral Ecology:* 13 (1): 234-141.

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? *Behavioural Ecology;* 15 (5): 705-714.

Chalmeau, R. and Gallo, A. 1995. Cooperation in primates: Critical analysis of behavioural criteria. *Behavioural Processes:* 35:101-111.

Charrier, I., Mathevon, N., and Jouventin, P. 2002. How does a fur seal mother recognize the voice of her pup? An experimental study of *Artocephalus tropicalis. The Journal of Experimental Biology:* 205: 603-612.

Charrier, I., Mathevon, N., and Jouventin, P. 2003. Vocal signature recognition of mothers by fur seal pups. *Animal Behaviour:* 65: 543-550.

Deecke, V.B., Ford, J.K.B., and Spong, P. 2000. Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Animal Behaviour:* 60: 629-638

Evangelista, E. and Rosas, R.C.W. 2011. Breeding Behavior of Giant otter *(Pteronura brasiliensis)* in the Xixuau Reserve, Roraima, Brazil. *IUCN Otter Specialist Group Bulletin;* 28 (A).

Ey, E., Hammerschmidt, K., Seyfarth, R.M., and Fischer, J. 2007. Age and Sex-related Variations in Clear Calls of *Papio ursinus. International Journal of Primatology.* Published online.

Feighny, J.A., Williamson, K.E., and Clarke, J.A. 2006. North American Elk Bugle Vocalization: Male and Female Bugle call structure and context. *Journal of Mammalogy:* 87(6): 1072-1077.

Finerty, S.E., Wolt, R.C. and Davis, R.W. 2009. Summer activity pattern and field metabolic rate of adult male sea otters *(Enhydra lutris)* in a soft sediment habitat in Alaska. *Journal of Experimental Marine Biology and Ecology;* 377:36-42.

Gnoli, C., and Prigioni, C. 1995. Preliminary Study on the Acoustic Communication of Captive Otters *(Lutra lutra)*. *Proc.II It. Symp. On Carnivores:* 7 (1-2): 289-296

Gorman, T.A., Erb, J.D., McMillan, B.R., Martin, D.J. and Homyack, J.A. 2005. Site characteristics of River Otter *(Lontra canadensis)* natal dens in Minnesota. *The American Midland Naturalist*: 156 (1) 109-117.

Gorman, T.A, Erb, J.D., McMillian, B.R. and Martin, D.J. 2006. Space use and sociality of river otters *(Lontra candensis)* in Minnesota. *Journal of Mammalogy:* 87 (4): 740-717.

Khan, C.B., Markowitz, H., and McCowan, B. 2006. Vocal development in captive harbor seal *Phoca vitulina richardii:* Age, sex, and individual differences. *Journal of Acoustical Society of America:* 120 (3) 1684-1694

Herbinger, I., Papworth, S., Boesch, C. and Zuberbuhler, K. 2009. Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders:a playback study. *Animal Behaviour;* 78: 1389-1396.

Holst, D.V., and Eichmann, F. 1998. Sex-specific regulation of marking behavior by sex hormones and conspecifics scent in tree shrews *(Tupaia belangeri). Physiology & Behavior* 63 (2): 157-164.

Hanggi, B.E., and Schusterman, J.R. 1994. Underwater acoustic displays and individual variation in male harbour seals *Phoca vitulina*. *Animal Behavior:* 48:1275-1283.

Hansen, H., McDonald, D.B., Groves, P., Maier, J.A.K. and Ben-David, M. 2009. Social networks and the formation and maintenance of River otter groups. *Ethology;* 115:384-396.

Jouventin, P., and Aubin, T. 2002. Acoustic systems are adapted to breeding ecologies: individual recognition in nesting penguins. *Animal Behaviour:* 64: 646-757.

Knornschild, M. and Von Helversen, O. 2008. Nonmutual mother-pup recognition in the greater sac-winged bat. *Animal Behaviour;* 76:1001-1009.

Kober, M., Trillmich, F. and Naguib, M. 2007. Vocal mother-pup communication in guinea pigs: effects of call familiarity and female reproductive state. *Animal Behaviour*; 73:917-925.

Laiolo, P. and Rolando A. 2003. The evolution of vocalizations in the genus *Corvus:* effects of phylogeny, morphology and habitat. *Evolutionary Ecology;* 17:111-123.

Lehmann, J. and Boesch, C. 2009. Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes; Animal Behaviour;* 77: 377-387.

Leuchtenberger, C. and Mourao, G. 2009. Scent-Marking of Giant Otter in the Southern Pantanal, Brazil. *Ethology:* 115: 210-216.

McShane, L.J., Estes, J.A., Riedman, M.L., and Staedler, M.M. 1995. Repertoire, structure, and individual variation of vocalization in the sea otter. *Journal of Mammalogy;* 76 (2): 414-427

Molles, L.E., and Vehrencamp, S.L. 1999. Repertoire size, repertoire overlap, and singing modes in the banded wrens (*Thryothorus pleurostictus)*. *The Auk:* 116 (3): 677-689.

Nelson, D.A., and Poesel, A. 2007. Segregation of information in a complex acoustic signal: individual and dialect identity in white-crowned sparrow song. *Animal Behaviour*: 74: 1073-1084.

Rendall, D., Rodman, P.S., and Emond, R.E. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour:* 51: 1007-1015.

Rendall L.E., and Whitehead, H. 2003. Vocal clans in sperm whales *(Physeter macrocephalus). Royal Society Publishing;* http://rspb.royalsocietypublishing.org

Riesch, R., Ford, J.K.B., and Thomsen, F. 2005. Stability and group specificity whistles in resident killer whales, *Orcinus orca,* off British Columbia. *Animal Behaviour.*

Riesch, R. and Deecke, V.B. 2011. Whistle communication in mammal-eating killer whales *(Orcinus orca):* further evidence for acoustic divergence between ecotypes. *Behavior, Ecology, and Sociobiology;* DOI: 10.1007/s00265-011-1148-8.

Rostain, R.R., Ben-David, M., Groves, P., and Randall, J.A. 2004. Why do river otters scent-mark? An experimental test of several hypotheses. *Animal Behaviour* 68: 703-711.

Saulitis, E.L., Matkin C.O., and Fay, F.H. 2005. Vocal repertoire and acoustic behavior of the isolated ATI killer whale subpopulation in southern Alaska. NRC Research Press: http://cjz.nrc.ca

Sayigh, L.S., Tyack, P.L, Wells, R.S., Solows, A.R., Scott, M.D., and Irvine, A.B. 1998. Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Animal Behaviour;* 57: 41-50.

Sepulveda, M.A., Bertheld, J.L., Monsalve, V.G. and Medina-Vogel, G. 2007. Habitat uses and spatial behavior of the endangered Southern River Otter *(Lontra provocax)* in ripariaon habitats of Chile: Conservation implications. *Biological Conservation;* 140: 329-338.

Shannon, J.S. Ontogeny of behavior and self sufficiency in free-ranging otters. http://www.riverotters.net/development.html

Soltis,J., Leong K., and Savage, A., 2005. African elephant vocal communication I: antiphonal calling behaviour among affiliated females. *Animal Behaviour:* 70: 579-587.

Soltis,J., Leong K., and Savage, A., 2005. African elephant vocal communication II: rumble variation reflects the individual identity and emotional state of callers. *Animal Behaviour:* 70: 589-599.

Sousa-Lima, R.S., Paglia, A.P., and DaFonseca, G.A.B. 2002. Signature information and individual recognition in the isolation calls of Amazonian manatee, *Trichechus inunguis* (Mammalia: Sirenia). *Animal Behaviour:* 63: 301-310.

Thom, M.D., Macdonald, D.W., Mason, G.J., Pedersen, V. and Johnson, P.J. 2004. Female American mink, *Mustela vison*, mate multiply in a free-choice environment. *Animal Behaviour;* 67:975-984.

Thomas, D.A., and Kaczmarek, B.K. 2002. Scent-marking behavior by male prairie voles, *Microtus ochrogaster,* in response to the sect of opposite-and same-sex-conspecifics. *Behavioural Processes*; 60: 27-33.

Williams, T.M., Ben-David, M., Noren, S., Rutishauser, M., McDonald, K., and Heyward, W. 2002. Running energetics of the North American River Otter: do short legs necessarily reduce efficiency on land? *Comparative Biochemistry and Physiology Part A* No. 133: pp: 203-212.

Wong, J., Stewart, P.D., and MacDonald, D.W. 1999. Vocal repertoire in the European Badger *(Meles meles)*: Structure, context, and function. *Journal of Mammalogy:* 80 (2): 570-588.

Val-Laillet, D. and Nowak, R. 2008. Early discrimination of the mother by rabbit pups. *Applied Animal Behaviour Science;* 111: 173-182.

Van Opzeeland, I.C., and Van Parijs, S. 2004. Individuality in harp seal, *Phoca groenlandica*, pup vocalizations. *Animal Behaviour:* 68: 1115-1123.

Vicario, D.S., Naqvi, N.H. and Raksin, J.N. 2001. Sex discrimination of vocal communication signals in a songbird. *Animal Behaviour;* 61:805-817.

Yin, S. and McCowam, B. 2004. Barking in domestic dogs: context specificity and individual identification. *Animal Behaviour;* 68: 343-355.

Yorzinski, J.L, Vehrencamp, S.L., Clark, A.B. and McGown, K.J. 2006. The inflected alarm caw of the American Crow: Differences in acoustic structure among individuals and sexes. *The Condor;* 108:518-529.