

Behavioral Comparison of Cougars (*Puma concolor*) and Lions (*Panthera leo*) between Zoo and Sanctuary

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Abstract

Maintaining captive animal populations possesses many benefits to conservation, education, and research, but at a cost of reduced animal freedom and welfare. Due to the many geographical, social, and behavioral restrictions placed on captive animals, it is important to study their welfare so that facilities can improve the lives and health of their captive populations. One reliable factor which has been used as a real-time indicator of an animal's well-being is stereotypic behavior. Stereotypies are repetitive, unvarying behavior patterns performed with no purpose or goal that develop as a result of various negative environmental factors. They often represent animal distress when present at high rates. Currently, there are few studies that analyze the effects that exhibit design and spatial distributions (i.e. where and what animals are doing at different locations in their enclosures) have on these behaviors. We hypothesized that exhibit design and the spatial distributions of stereotypies are important factors to consider when trying to manage captive animal welfare. To test our hypothesis, we analyzed the behavior profiles, exhibit-use, and pacing routes of five individual African lions (*Panthera leo*) and four individual cougars (*Puma concolor*) housed in two different facilities. Through the use of video observation, modified ethograms, and spatial tracking we found a strong correlation between the location of stereotypic behavior and the amount of visual stimulation available at those locations. Animals performed stereotypic behaviors significantly more along guest viewing areas and at places in the exhibit where other animals were visible to each individual. We also analyzed the effects of temperature, facility type, and exhibit size and found trends that can be explored in future research. These results provide new ways to effectively manage captive felid populations and have potential implications for improving captive animal welfare in the future.

I. Introduction

Members of the felidae family have long been housed in captive facilities all across the United States because they serve a vital role in the conservation efforts of their clade. The International Union for the Conservation of Nature (IUCN) lists 29 of the 36 species of the felidae family as having a decreasing population trend (IUCN, 2020; Bauer et al. 2016; Nielsen et al. 2015; Lamberski, 2015) and captivity can provide benefits to counteract this problem. Some of the benefits of captivity include controlled breeding programs that reduce the threat of extinction, protection from predation and competition (CBSG, 2017; Conde et al., 2011; Tribe and Booth, 2003), and increased lifespans (Tidière et al. 2016). Captivity also provides increased funding of conservation projects in the wild (Gusset and Dick, 2011; Tribe and Booth, 2003), and has helped researchers understand the basic zoology and biology of related species.

However, maintaining these animals in captivity in a way that maximizes welfare is difficult. This study focused on two felids: the African lion (*Panthera leo*) and the cougar (*Puma concolor*), both of which are often subject to captive conditions that are very different from the environments in which they naturally evolved (Carlstead, 1996). African lions, for example, usually travel in social groups, known as prides, which average 15 or more individuals (Schaller, 1972) and occupy territories of roughly 25 km² (Van Hooft et al. 2018). Cougars on the other hand, remain mostly solitary, but will frequently overlap and socialize with other conspecifics in the area (Elbroch et al. 2017). Estimations of their territory size are variable: with some as large as 1,300 km² and others as small as 25 km² (Utah Wildlife Resources, 1999). In captivity, these social dynamics and habitat ranges are rarely met (Carlstead, 1996). In addition to these environmental and social restrictions, felids are also behaviorally restricted - unable to perform naturally occurring behaviors like stalking, hunting, and, in some cases, copulation (McPhee, 2002).

In order to cope with all of these restrictions, animals inside of captivity often perform abnormal behaviors (Mason, 1991). One particular behavior that is often highlighted in observational studies is stereotypic behavior. Stereotypies are repetitive behaviors that occur with no obvious purpose or intended goal, and they are signals of animal distress when they occur at high rates (Mason and Rushen, 2006 ; Mason et al. 2007). Some common examples of stereotypic behavior in felids include pacing, digging, fur-plucking, head-rolling, self-mutilation, and excessive grooming (Stanton et al., 2015; Shyne, 2006). Although many facilities that house felids are aware of these abnormal behaviors and we understand that both previous experience and current environments affect them (Mohapatra et al., 2013; Mason et al., 2007; Bashaw, 2007; Ahola et al., 2017), more research needs to be done to understand what causes reduced animal welfare and how we can mitigate it in future populations.

In this study, we sought to understand the impact that exhibit design, space use, and facility type can have on felid welfare, so we examined lions and cougars at two different facilities. Lions and cougars were chosen because of their availability and popularity inside of captive settings and because both species are in need of conservation help (Bauer et al. 2016; Nielsen et al. 2015). The two facilities chosen were a zoological park and a wildlife rescue sanctuary. Zoological parks are captive facilities that exhibit animals to the public and are involved in collecting, trading, and breeding animals for conservation and educational purposes. Wildlife sanctuaries are captive facilities that only acquire animals for rescue and rehabilitation purposes, and typically do not breed or trade animals (Shea, 2014; AZA, 2020; SNZCBI, 2020). There is a solid body of research investigating how environmental cues influence stereotypies (Liu, 2007; Mohapatra et al., 2014; Greco et al., 2016), but currently the field of animal welfare lacks any research on how facility type and the spatial distributions of stereotypies relate to

animal welfare. We hypothesized that these two under-researched variables are also important factors to consider when trying to manage a captive population.

To test this hypothesis, we used an observational study approach combined with a spatial tracking methodology to understand what behaviors the animals were performing, when they were performing them, and where inside their enclosures these behaviors were occurring at high rates. By studying the stereotypic behavior and the spatial distributions of these animals we accomplished (1) a new avenue for studying stereotypic behavior and the factors that influence it and (2) a better understanding of how other variables such as temperature, sex, and time of day affect an animal's welfare. Lastly, our results can improve the lives of the specific subjects of this study as well as the lives of other members of the felidae clade in the future.

II. Methods

This study was approved by the Zoological Park's Institutional Animal Care and Use Committee and by the Sanctuary's animal care and research staff. All observations were performed by the primary author of this paper.

Study Sites

This study was conducted at two independent facilities located in the United States. Specific facility information will remain anonymous due to privacy concerns. The first facility was a zoological park (hereafter, zoo) accredited by the Association of Zoos and Aquariums (AZA) and operated on over 500 acres of land (Source 1). In order to be accredited by the AZA, the facility underwent a lengthy and rigorous inspection of its veterinary care, animal welfare, conservation, education, and operating procedures (AZA, 2020). The second facility was a wildlife rescue sanctuary (hereafter, sanctuary). The sanctuary was a 501(c)3 nonprofit organization certified by the Global Federation of Animal Sanctuaries (GFAS) and it was located on 55 acres of land (Source 2). GFAS provides verification for and support to animal sanctuaries that uphold their rigorous standards of operations, animal care, and education (sanctuaryfederation.org, 2020). Both the AZA and GFAS certifications are considered to be the top levels of accreditation in their respective fields.

Animal Housing

In total, we studied nine individuals, five lions and four cougars. All enclosures at both facilities were open-air exhibits that had endemic substrate and a combination of natural and synthetic environmental elements. All animals were fed six days of the week and were assigned one day for fasting. All animals had unlimited access to water at at least one location in the

exhibit. Enrichment schedules varied by facility: the zoo animals received enrichment four days per week and the sanctuary animals received enrichment seven days per week. These species were chosen due to their availability at both facilities and because of their popularity in captive facilities such as zoos, sanctuaries, reserves, and circuses. Each animal's social relationships, medical history, and previous circumstances can be found in Table 1.

Zoo Felids

Two of the lions were housed at the zoo in a 790.0 m² exhibit. The exhibit was regressed roughly 5 m below the guest viewing area and held one male, RIL (born: Toledo Zoo; age: 20 years; weight: 186 kg), and one female, MAK (born: Columbus Zoo; age: 9 years; weight: 131.5 kg). Both lions were on exhibit for the entirety of each day, and only came off exhibit for feeding and inclement weather. Feeding always occurred off exhibit in separated areas to reduce aggression. On normal feeding days, animals received one portion at around 8:00 am EST before entering the enclosure and one portion at around 5:00 pm EST after leaving the enclosure.

Two of the cougars were housed at the zoo in a 278.7 m² exhibit. This exhibit was not regressed into the ground and only had one glass viewing area on its South West side. This exhibit housed two siblings; one male, HEA (born: wild; age: 5.5 years; weight: 63.5 kg) and one female, OLI (born: wild; age 5.5 years; weight 45.4 kg). Both cougars were on exhibit from 8:00 am EST to 5:00 pm EST and came off exhibit overnight. On normal feeding days, they received one portion at 7:00 am EST and one portion at 5:00 pm EST off exhibit.

Sanctuary Felids

The remaining three lions were housed at the sanctuary in two separate exhibits. All exhibits at the sanctuary were surrounded by two chain-link fences and were between 1451.0 m² and 1160.1 m². Neither of the exhibits were regressed below the guest viewing area and both were located along the main route for the facility's walking tours. The first exhibit housed one male lion named SEB (born: captive facility in Texas; age: 18 years; weight: 215.5 kg). The second exhibit housed one male, ROM (born: Zanesville, Ohio; age: 10 years; weight 144.7 kg) and one female, REI (born: Zanesville, Ohio; age: 10 years; weight: 135.6 kg). All three lions at the sanctuary remained on their exhibits 24 hours per day. Food was distributed to each animal through PVC pipe food shoots located throughout the exhibits.

The remaining two cougars were housed at the sanctuary in separate exhibits; between 371.0 m² and 169.4 m². Both exhibits were surrounded by two sets of chain-link fences and were along the main tour route for the facility. The first exhibit housed one female named STA (born: Collins Zoo in Mississippi; age 22 years; weight 39.5 kg) and the second exhibit housed one male named NAK (born: Zanesville, Ohio; age 15 years; weight 61.7 kg). Both cougars at the

sanctuary remained on exhibit 24 hours per day. Food was distributed in the same manner as the sanctuary lions (see above).

Table 1. Animal Subject Information

Individual	Species	Facility	Exhibit Size (m ²)	Age	Social Relationships	Medical History	Born
RIL	Lion	Zoo	790.0	20 years	Mate: MAK, they have had two litters together	Fractured tail, removal of two teeth due to infection, and treatment for kidney disease	Captivity: Toledo Zoo
MAK	Lion	Zoo	790.0	9 years	Mate: RIL, they have had two litters together	Puncture wound to her trachea, sepsis, and a fractured pelvic bone. Throughout the study, she had a <i>deslorelin</i> contraceptive implant	Captivity: Columbus Zoo
ROM	Lion	Sanctuary	1451.0	11 years	Mate: REI	Rescued as a result of the Zanesville, OH massacre	Unknown
REI	Lion	Sanctuary	1451.0	11 years	Mate: ROM	Rescued as a result of the Zanesville, OH massacre	Unknown
SEB	Lion	Sanctuary	1160.1	18 years	Mate: Sheba, who passed away in July 2019	Deterioration of spine; euthanized due to quality of life in December 2019	Captivity: used as prop in haunted house
HEA	Cougar	Zoo	278.7	5.5 years	Sibling: OLI	Hand reared since cub stage, surgical removal of tail digits, kidney disease for which he receives prescription medication	Wild: taken as a cub from mother after she was killed.
OLI	Cougar	Zoo	278.7	5.5 years	Sibling: HEA	Ovariohysterectomy	Wild: taken as a cub from mother after she was killed.
STA	Cougar	Sanctuary	371.0	23 years	None		Captivity: Collins Zoo, MS
NAK	Cougar	Sanctuary	169.4	15 years	None	Rescued as a result of the Zanesville, OH massacre. Diagnosed with a helicobacter infection in his stomach which has since been treated. Altered diet consists of diced meat for easier digestion.	Unknown

Observational Data Collection

The nine captive felids were observed for a total of 58 hours between June 2019 and November 2019. We observed each exhibit during a randomly assigned two-hour session and the order of exhibits observed was randomized whenever possible to avoid bias. Due to management constraints, random assignment of order was not always possible. Each set of observations were performed by the same researcher and only occurred during the facility's public hours of operation.

We used an observational study approach because behavioral phenotypes are profoundly affected by the environment in which an animal lives. Therefore it is the preferred method for understanding animal welfare as it relates to captivity (Kleiman 1992; Carlstead and Shepherdson, 1994; Lindburg and Fitch-Snyder, 1994; Watters et al. 2009; Watters 2014). Additionally, it is often chosen over other methodologies because it is cost-effective, requires no specialized equipment, and is non-invasive to its subjects (Watters 2014).

To accurately perform observations, we modified two pre-existing ethograms (Stanton et al., 2015 and Cruz, n.p.) to best fit the subjects we were studying. We identified 18 behaviors and categorized them into three categories (Active, Restful, and Stereotypic). Once the modified ethogram was finalized, we began the official data collection. Sampling was done throughout the entire two-hour session on a 2-minute fixed interval schedule. The fixed interval schedule was dictated by a two-minute repeating timer. At the end of each 2-minute interval, we recorded the animal's behavior and its location within the exhibit. Table 2 shows the behaviors that were seen commonly on the interval. Table 3 shows the behaviors that occurred infrequently on the interval and were therefore classified under the 'Other' behavior in Table 2.

Concurrent with all observations, each session was recorded using a Canon PowerShot SX530 HS video camera and reexamined for later analysis. The video footage was analyzed using ImageJ and Behavioral Observation Research Interactive Software (BORIS) to corroborate the data collected by the live recordings and to record any missed observations. We also recorded time of day, average temperature, average humidity, and average UV index for each two-hour session in order to detect any relationship between these variables and the behaviors performed.

Spatial Tracking and Heat Maps

Using reference photographs from the surroundings of each exhibit, we constructed a bird's eye view schematic using Adobe Illustrator 2019 (Adobe Inc. 2019). We summed the animal locations at every 2-min interval from the HD video footage and used the data to create heat maps. These heat maps indicated the proportion of time spent at each location within each exhibit. After summing the locations at each 2-minute interval, we isolated the intervals at which

a pacing behavior occurred. We summed these pacing locations to create a second set of heat maps that displayed the animals' pacing routes (Fig 4 and 5).

Data Analysis

Each observational period had 60 total intervals. Total behavior occurrences were converted to frequencies and averaged to obtain behavioral distribution profiles of each animal. The bar graphs in the results section compare the average number of behaviors occurring per two-hour observational session. The data was analyzed using R Studio and Microsoft Excel 2016 (Microsoft, Redmond, Washington DC; RStudio Team, Boston, MA). Each categorical variable between individuals was compared using a Wilcoxin paired difference test.

Table 2. Interval Behaviors

Behavior	Category	Description.
Vigilant/Inactive	Rest	Animal is in a stationary position either standing, sitting, or lying down but eyes are open and the animal is not asleep. This behavior is often associated with scanning or looking around the exhibit.
Sleep	Rest	The animal is in a stationary position lying down with its eyes closed.
Locomotion	Active	Animal is moving in a direction using its legs. The animal must be on the ground and not balancing on a structure. Not exclusive to running or walking.
Pace	Stereotypic	Animal performs a repetitive motion that is repeated three or more times in a row uninterrupted by any other behavior. Pauses in the behavior of more than 10 seconds ends the pace behavior.
Feed/Forage	Active	Animal is searching for or eating a food item. Behaviors that fall under this category include digging, searching with snout, biting a food item, or covering.
Self-groom	Rest	Licking or chewing on a part of the animal's own body with the intention of cleaning.
Allogroom	Rest	Licking or chewing on a part of another animal's body with the intention of cleaning or making affectionate contact. Does not include biting or aggressing on other animals.
Other Behavior	n/a	Any behavior not listed in this ethogram. See Table 3 for full list of behaviors performed in this study.
Not Visible	n/a	Animal is not visible from the recorders point of view.
Location		The location of the animal within each exhibit

Table 3. Other Behaviors

Behavior	Category	Description
Aggression	Active	Any negative interaction performed by the felid toward either another animal or human spectators. Often classified by swatting, growling, vocalizations, biting, scratching, or attacking with the intention of causing harm.
Play	Active	Animal performs a positive social interaction with other animal in enclosure that does not have the intent to harm or injure. This behavior can include chasing, play bows, wrestling, or pouncing.
Sniff	Active	Animal uses nose to smell ground, air, or object in enclosure.
Object Manipulation	Active	Animal moves, carries, or pushes non-food object with mouth, snout, or paws.
Jump/Climb	Active	Any vertical movement of the animal. This is usually seen by the animal in an attempt to get on an elevated surface such as a log or platform.
Scratch	Active or Stereotypic	Animal uses claws to scratch ground or other object in enclosure. If done repetitively for no purpose, this behavior is considered stereotypic.
Fur-Plucking	Stereotypic	Animal repetitively uses mouth or limbs to pull hair off of its own body. This behavior is different from self-grooming in that teeth are used and fur is visibly removed from the animal's coat.
Urinate	Active	Animal discharges liquid waste.
Vocalize	Active	Any vocalization made from the animal including roars, growls, chirps, and meows.
Yawn	n/a	Animal involuntarily open its mouth wide and inhale deeply. Animal must open mouth to full or almost full extension to be considered.
Flehmen	n/a	Animal curls back its upper lip exposing front teeth followed by inhalation with nostrils closed. Whiskers often flare back during this behavior.
Other	n/a	Any behavior not stated on this ethogram.

III. Results

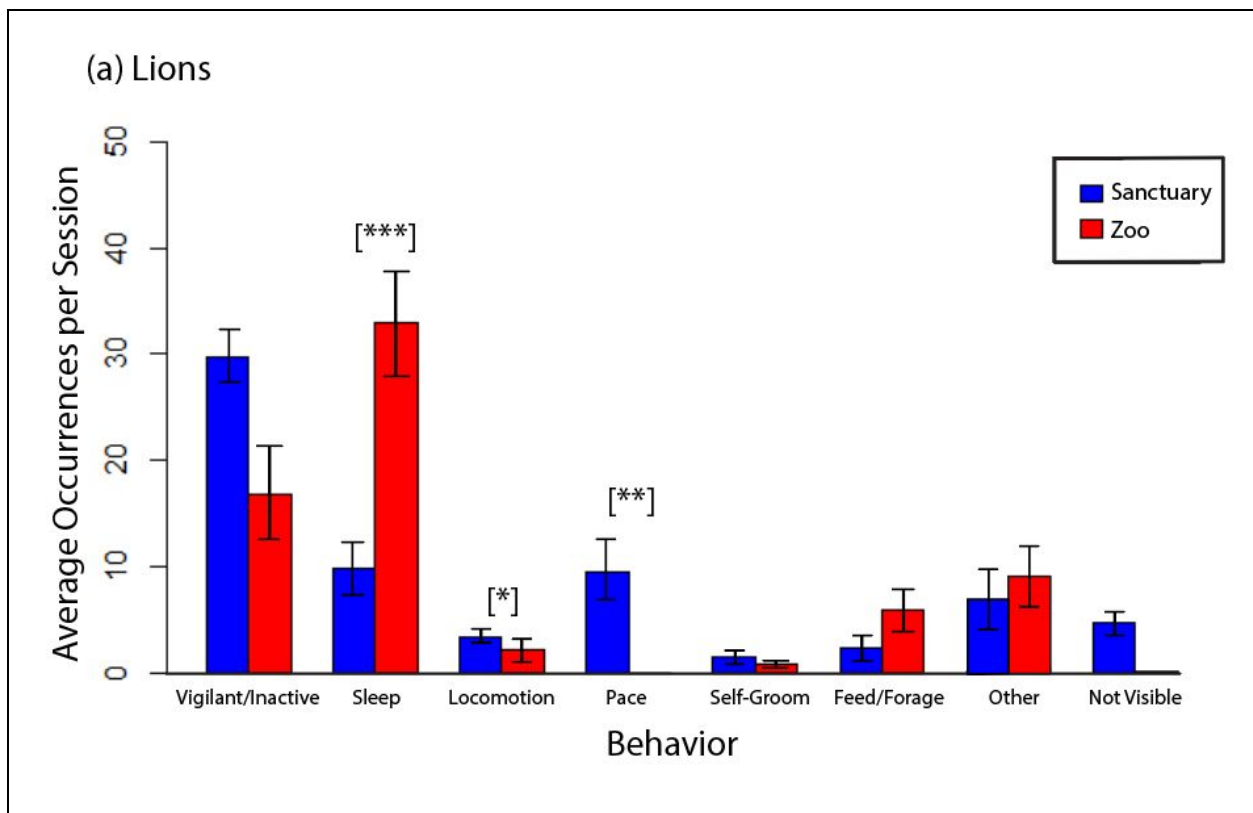
Behavior Profiles and Facility Comparison

For the 5 individual lions, we analyzed 30 hours of HD footage between June 2019 and November 2019. All 5 lions spent the most time engaged in restful behavior (Zoo: 84.0% ± 15.5% and Sanctuary: 68.2% ± 13.9%) - which is expected considering lions sleep roughly 20

hours per day in the wild and are usually most active at night (Schaller, 1972). The lions at the Zoo spent the remainder of their time engaged in active behavior ($13.9\% \pm 7.82\%$) whereas, the lions at the Sanctuary split the remainder of their time between active and stereotypic behavior (active: $9.86\% \pm 3.08\%$ and stereotypic: $15.7\% \pm 5.6\%$). The lions at the Sanctuary were the only individuals who engaged in stereotypies more than active behavior.

For the 4 individual cougars, we analyzed 28 hours of HD footage over the same 6 month period. On average, all 4 cougars spent the most time engaged in restful behavior (Zoo: $69.1\% \pm 15.3\%$ and Sanctuary: $66.7\% \pm 13.1\%$). For the majority of the remaining time, the cougars engaged in active behavior (Zoo: $19.6\% \pm 6.13\%$ and Sanctuary: $24.2\% \pm 6.40\%$) and only spent a small portion of their time engaged in stereotypic behavior (Zoo: $3.71\% \pm 2.3\%$ and Sanctuary: $6.46\% \pm 3.80\%$). None of the results were significantly different between the cougar populations. The behavior distributions for each facility based on species can be seen in Figure 1. Categories of each behavior can be seen in Table 2.

Using a Wilcoxin paired difference test, we found that the lions in the Sanctuary engaged in the sleep behavior less ($p = 0.0005$) and the locomotion ($p = 0.044$) and pace behavior ($p = 0.0017$) more than the lions at the Zoo. Using the same test, we found that there were no significant differences between the Zoo and the Sanctuary cougar populations for any behaviors.



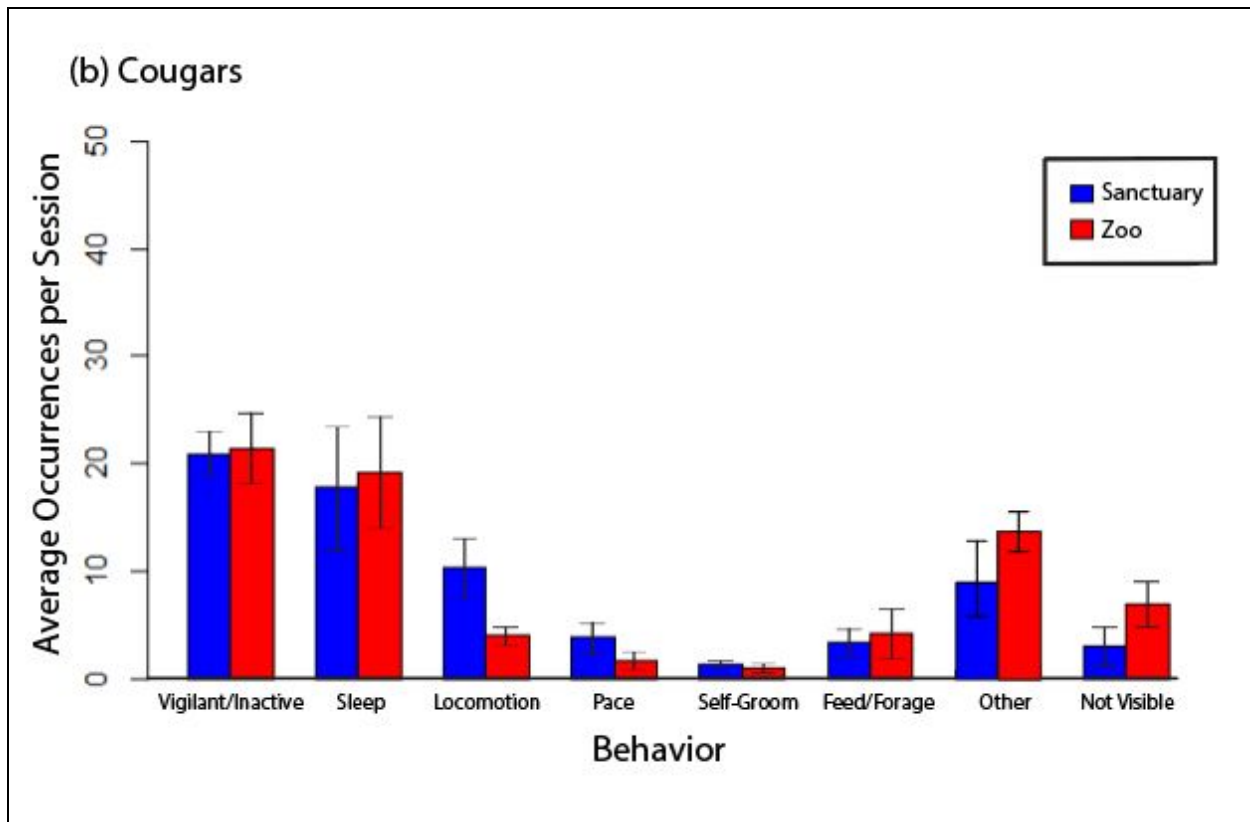


Figure 1. Average Behavioral Distributions between the Zoo and the Sanctuary. (a) The average occurrences of interval behaviors(\pm SEM) for the lions. Values indicate the average number of occurrences per 2 hour session. (b)The average occurrences of interval behaviors(\pm SEM) for the cougars. Values indicate the average number of occurrences per 2 hour session. Sanctuary bars are blue in color and are always found on the left side of the pair. Zoo bars are red in color and are always found on the right side of the pair. Asterisks indicate significance [*] = $p < 0.05$, [**] = $p < 0.01$, [***] = $p < 0.001$.

Spatial Distributions - Exhibit Use

Examining exhibit use and pacing routes has never been done in captive lion or cougar populations, but is important because it can increase our understanding of individual animal preferences and reveal possible causes of animal stress (Carlstead, 1996). This study provided an effective way of mapping out exhibits, recording location, and displaying the information in a clear discernable manner. Using the methods above (*See Spatial Tracking*) we examined where the animals spent their time throughout the exhibits and tracked the pacing routes of each individual throughout the study.

Based on the spatial distributions (Figure 2-3) the exhibit use of the Zoo animals was more widespread whereas the exhibit use of the animals at the Sanctuary was relatively sparse.

The majority of the exhibits at the Sanctuary were never used and the animals spent most of their time around either one or a few common areas.

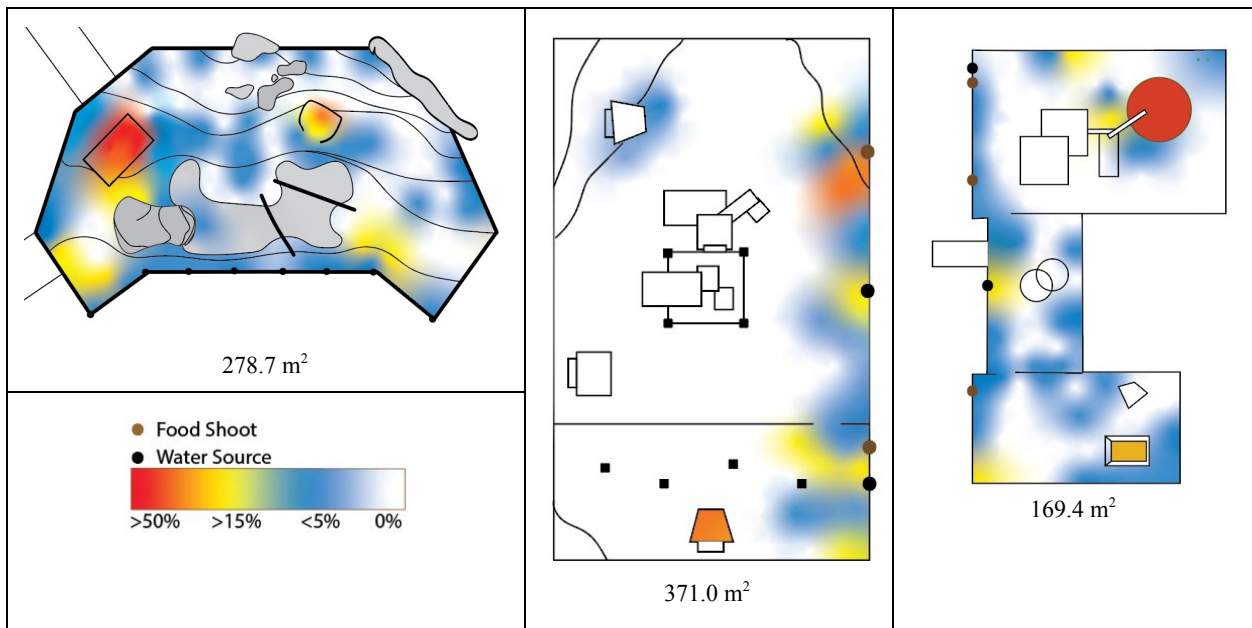
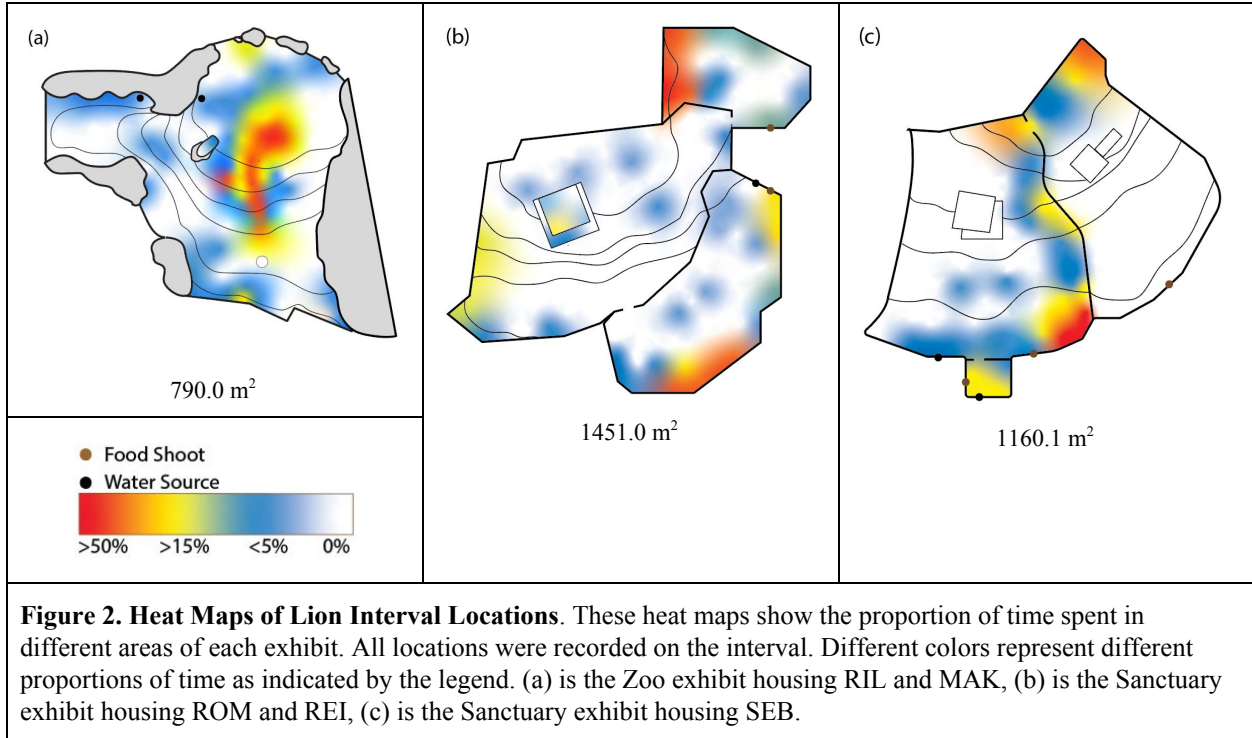
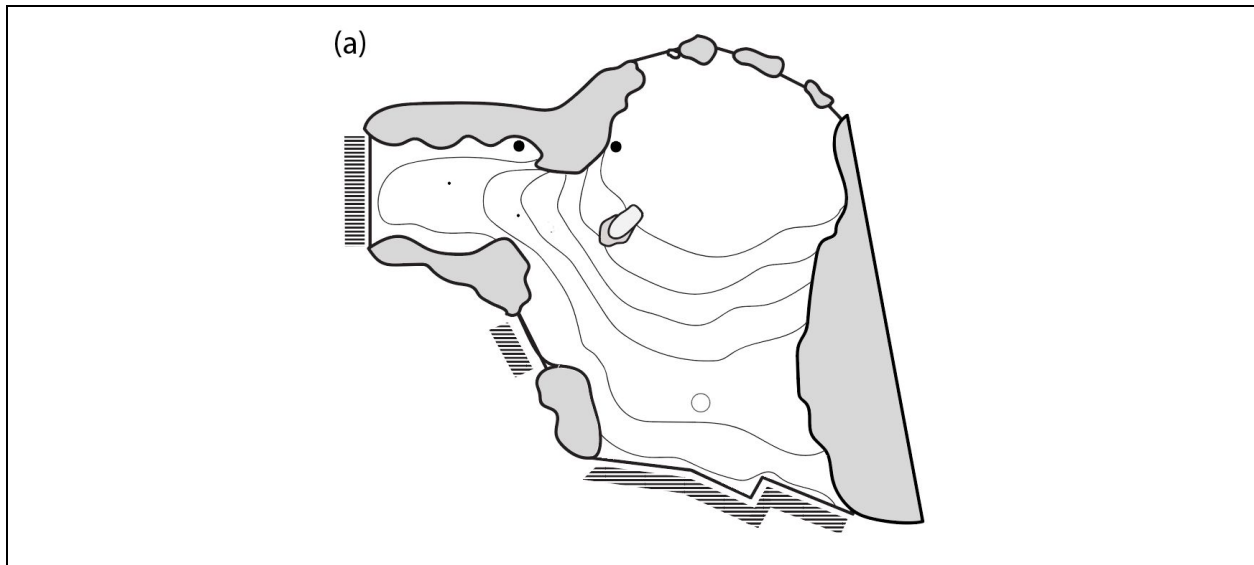
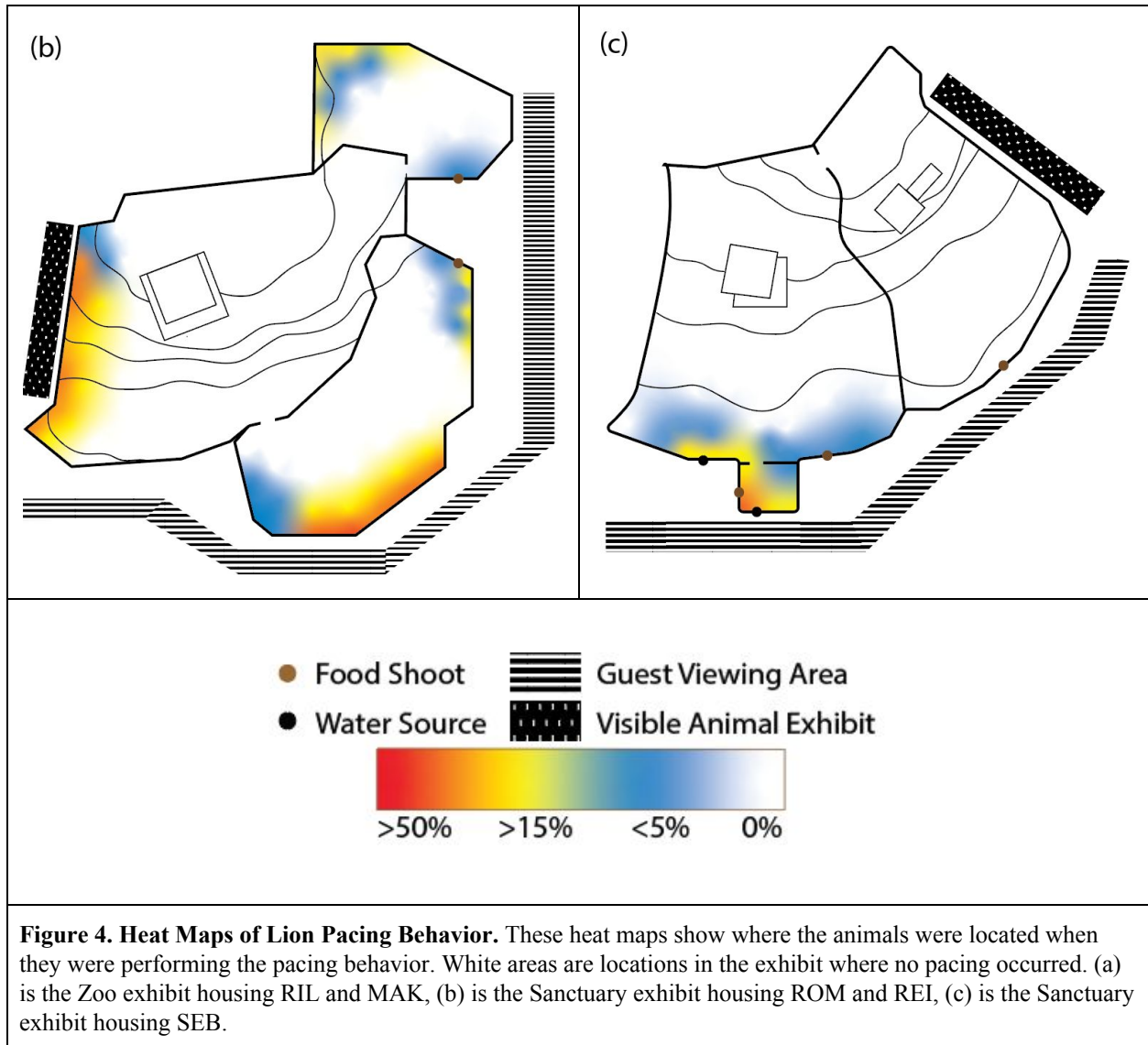


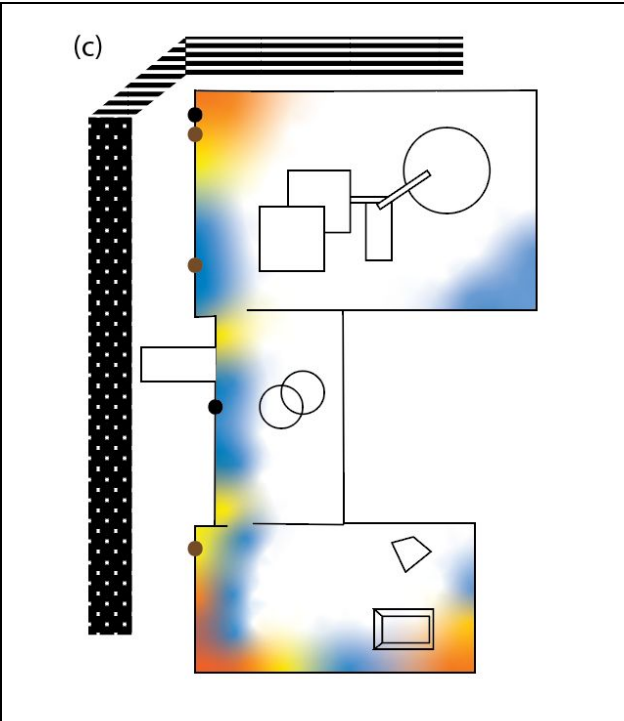
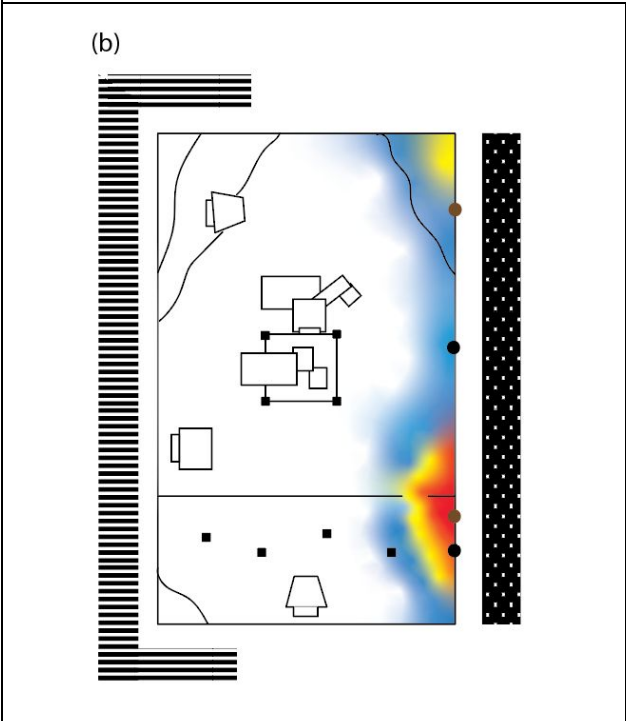
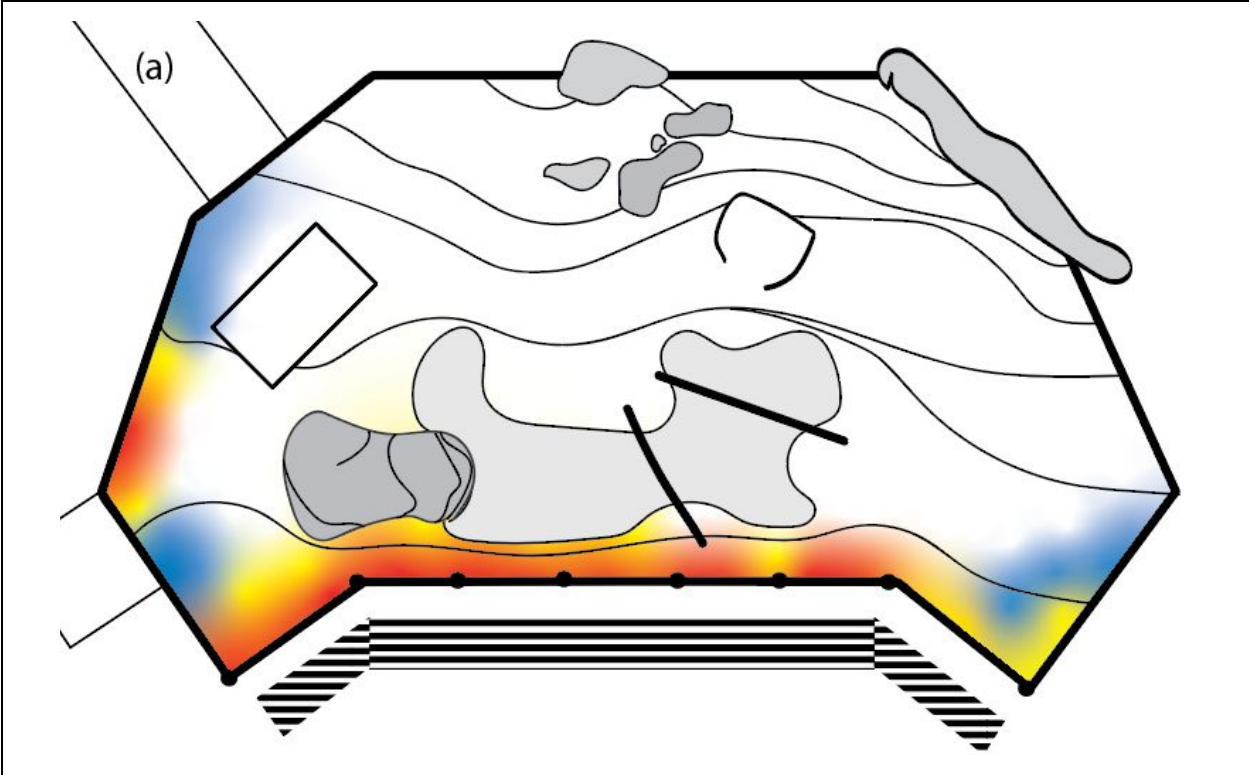
Figure 3. Heat Maps of Cougar Interval Locations. These heat maps show the proportion of time spent in different areas of each exhibit. All locations were recorded on the interval. (a) is the Zoo exhibit housing HEA and OLI, (b) is the Sanctuary exhibit housing STA, (c) is the Sanctuary exhibit housing NAK.

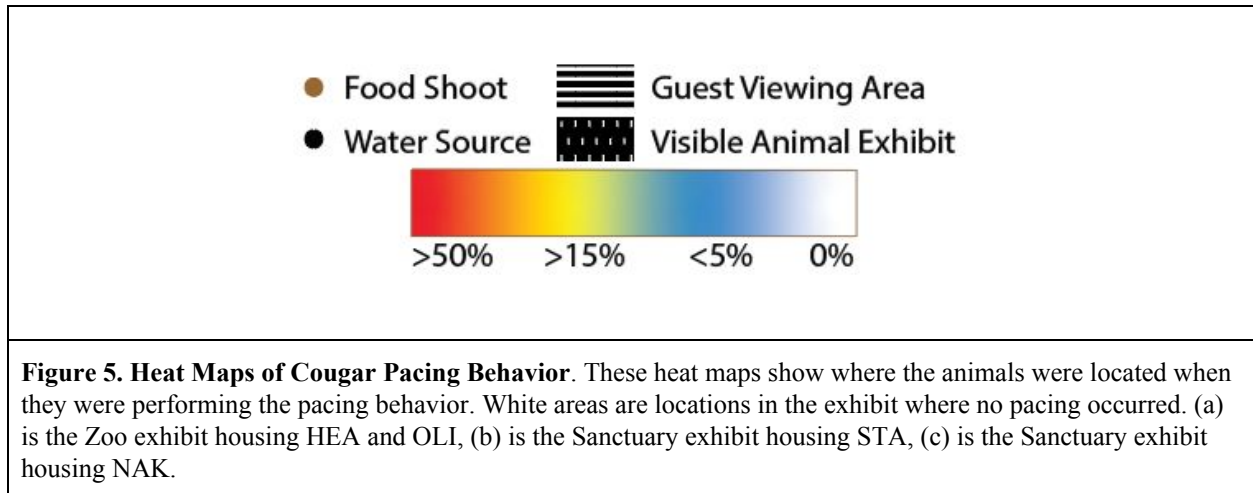
Spatial Distributions - Pacing Routes

Through analyzing the pacing routes (Figure 4-5), we found a unique trend in the location of pacing across both facilities. The majority of pacing occurred along one of two areas in the exhibit. The first area of pacing occurred near the *Guest Viewing Areas*. Figure 5a exemplifies this trend. The majority of all pacing performed by HEA and OLI occurred along the viewing glass where guests were observing the animals. The second area of pacing occurred alongside *Adjacent Animal Exhibits*. Figure 4b exemplifies this trend. One of the pacing routes that occurred with high frequency correlated with the visibility of another animal's exhibit. These results contrast some of the results found in a previous study (Bashaw, 2007), so these conclusions could have important applications for managing captive animal populations.









Species, Sex, Social Grouping, and Other Variables

Because of previous work that identified differences in sex (Beatty and Holzer, 1978) and social grouping (Ncube and Ndagurwa, 2010; Marsden & Wood-Gush, 1986) as they relate to stereotypic behavior, we compared different variables within our population ($n = 9$) to see if any had an effect on rates of stereotypic behavior. We found no significant effect of species ($p = 0.3209$), sex ($p = 0.156$), or social grouping ($p = 0.223$) on the rates of stereotypic behavior. Females appear to perform stereotypic behavior at much lower rates (17.5%) than males (26%) which opposes previous work in other mammals (Beatty and Holzer, 1978). It is important to note, these tests do not take into account all concurrent effects and therefore are only suggestive of future research directions. Further investigation into the effect of sex on stereotypic behavior in other facilities and across more species is warranted. These results demonstrate that species, social grouping, and sex likely play no role in the animal's abnormal behavior.

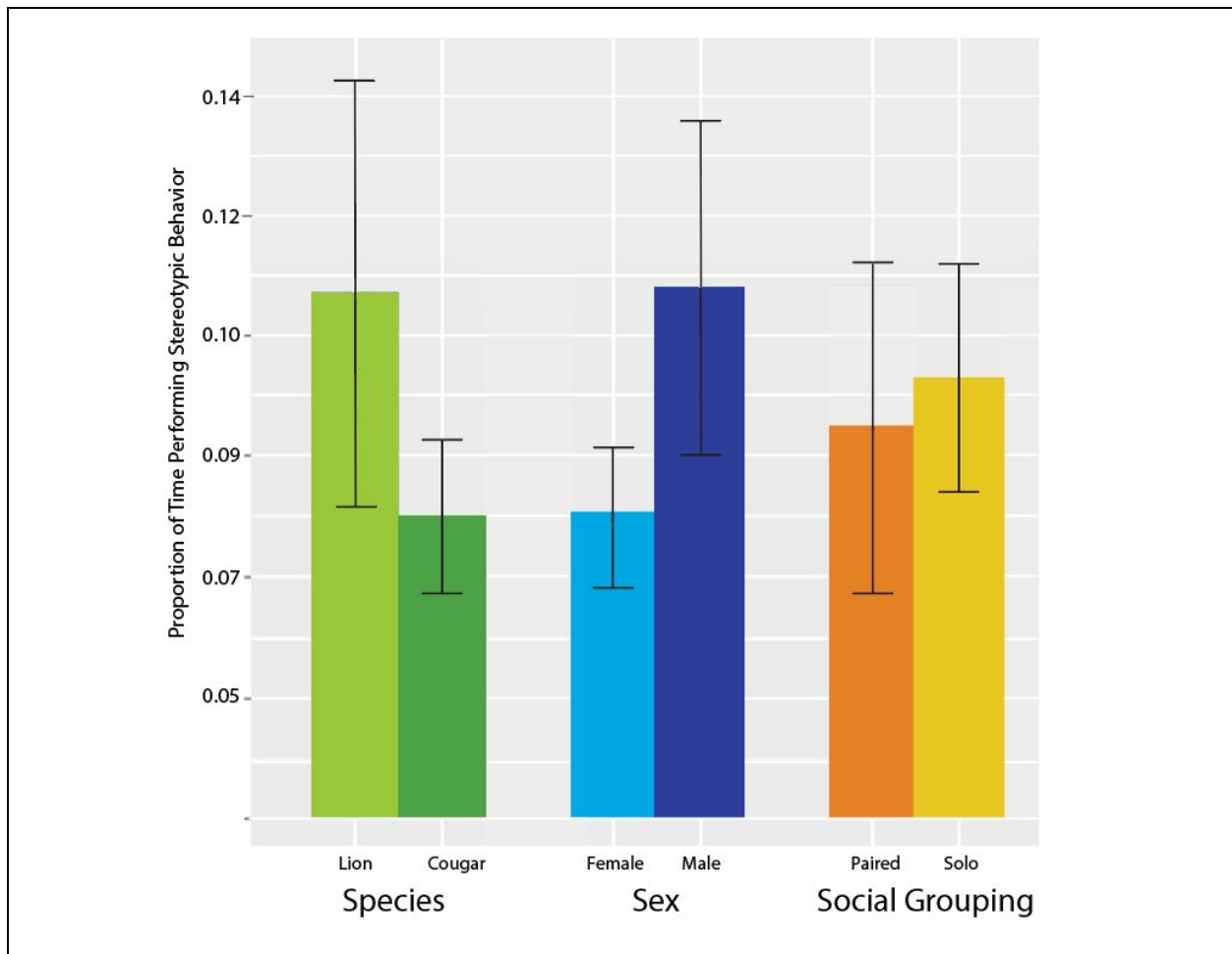


Figure 6. Comparison of Stereotypic Behavior based on Species, Sex, and Social Grouping. This graph shows the average proportion of time (\pm SEM) that each group was performing stereotypy per 2 hour session. Values are based on interval data only.

Temperature Effects

We collected observations from the month of June to November, and individuals experienced temperatures ranging from 7.22 °C to 33.3 °C. Given this wide range of temperatures, we compared the occurrences of stereotypic behavior to the average temperature during the session. We found there was a moderately negative association between stereotypic behavior and temperature ($y = -1.266x + 37.333$; $R^2 = 0.371$) and a weakly negative association between active behavior and temperature ($y = -0.7075x + 29.274$; $R^2 = 0.0671$). We also found that there was a moderately positive association between restful behavior and temperature ($y = 1.03x + 19.478$; $R^2 = 0.2603$) that reflects the negative correlations of active and stereotypic behavior. These trends suggest increases in temperature cause animals to become more restful, less active, and less likely to engage in abnormal behaviors - which matches previous research in

other large captive mammals (Liu et al., 2017). There were no effects of UV index nor humidity on stereotypic behavior.

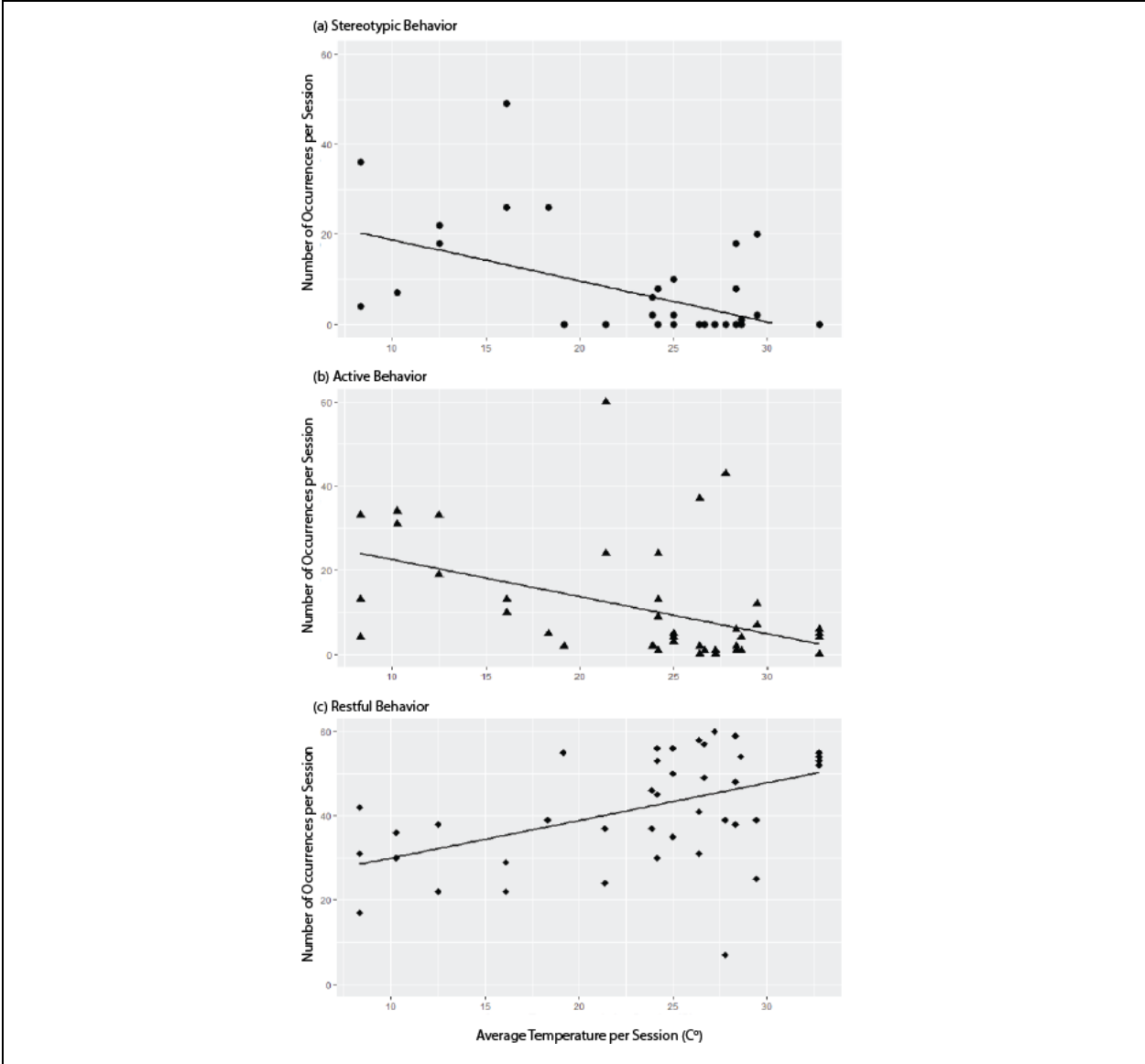


Figure 7. Occurrences of Different Behaviors based on Average Temperature. (a) the effect of temperature on stereotypic behavior occurrences per session (b)the effect of temperature on active behavior occurrences per session (c) the effect of temperature on restful behavior occurrences per session.

Time of Day

Previous studies on other captive felids (Mohapatra et al., 2014) and other mammals (Greco et al., 2016) examined the effects that time of day have on rates of stereotypic behaviors. Since both facilities followed similar feeding schedules and operating hours we averaged the occurrences of stereotypic behavior and examined the times during the day they occurred (Figure 8). We found that the animals have the highest levels of stereotypic behavior in the mornings with peak levels occurring between 11:00 and 11:59.

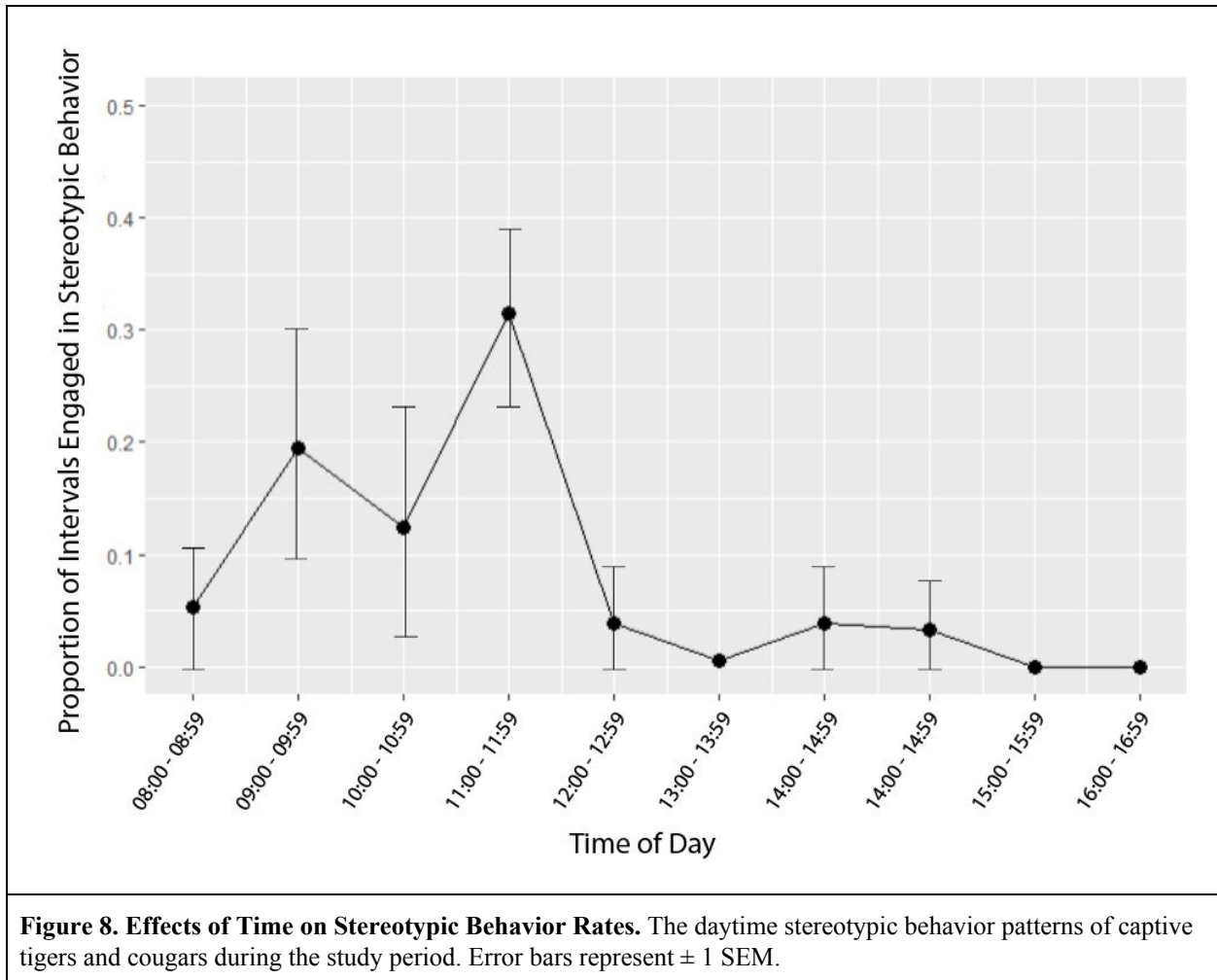


Exhibit Size

Restricted exhibit space could be a cause for increased stereotypic behavior, but there are many conflicting studies across different species (Mason and Rushen, 2006). To test this idea, we compared the average number of stereotypies performed per 2-hour session to exhibit size (m^2) and found that there was a weak positive correlation between the two variables. Animals

located in larger exhibits engaged in stereotypic behavior more often ($y = 0.0054x + 0.251$; $R^2 = 0.1097$) However, we only examined 6 total exhibits, so these results are not conclusive. Future research could aim to understand the relationship between exhibit size and stereotypic behavior in felids.

IV. Discussion

Using an observational approach and a spatial tracking methodology, we evaluated and compared the behaviors of 9 individual felids between two different facilities. Although our study had a limited sample size of 9, all of which varied in species, sex, life experience, and housing conditions, we found several interesting results which may help to improve felid welfare in the future.

A main goal of our study was to determine the welfare differences between zoos and sanctuaries. We were motivated to investigate this comparison because it could provide insight into the captive conditions best fit for felids. At both facilities, all enclosures were open-air exhibits that had endemic substrate and contained both synthetic (buildings, structures, fake rocks, large plastic enrichment, etc.) and natural environmental elements (trees, bushes, shelter, etc.). However, the zoo limited guest viewing areas to only a few locations and had clear plexiglass viewing barriers, while the sanctuary's exhibits had larger guest viewing areas and were only surrounded by two chain-link fences.

When comparing facilities, we found that lions in the sanctuary engaged in more stereotypic behavior and less restful behavior than those at the zoo, while the cougars of both facilities were not significantly different. In terms of exhibit-use between facilities, the heat maps (Figure 2 and 3) indicated that the zoo animals used a larger proportion of their exhibits than the sanctuary animals. Widespread exhibit-use could be indicative of more exploratory and comfortable animals, but in most cases it is a poor proxy for determining an animal's welfare. For example, some animals may have personal preferences with regards to temperature, substrate, or sensory access, and these preferences could cause them to stay in a centralized area. This does not mean the animal is stressed or uncomfortable. Therefore these results are not conclusive nor can they be generalized to other facilities. These results, however, can be used by both facilities to better understand each individual animal's preferences. Both facilities can use this information as a gauge of an animal's well-being from day to day, and it can also be used to improve the location of training sessions and the placement of food and enrichment (Troxell-Smith et al., 2017).

On the other hand the spatial distributions of the stereotypic behavior can be used to conclude causes of reduced animal welfare. The spatial tracking analysis of pacing routes (Figure 4 and 5) indicated a strong correlation between the stereotypic behavior of pacing and the visual stimuli available at the pacing locations. Animals who engaged in pacing ($n = 7$) performed the majority of their pacing alongside either *Guest Viewing Areas* or *Adjacent Animal Exhibits*. The animals that did not engage in pacing ($n = 2$) were exposed to *Guest Viewing Areas*, but these areas were raised above the animals' enclosure by a distance of roughly 5m. Therefore, the visual stimulation available to these subjects was significantly reduced compared to the other animals. These results match the conclusions of previous studies that indicate pacing as a means to cope with excessive sensory access (Bashaw, 2007). The subjects of this study paced along parts of the exhibit where they had uncontrolled sensory contact.

These findings provide potential solutions for improving welfare of large felids in captivity. First, facility type likely plays little to no role in the actual welfare of the animals. The differences we found were likely attributed to environmental differences that were simply a byproduct of the facility type. Second, the visual stimuli available to each animal may need to be managed with more care in order to reduce an animal's compulsion to perform stereotypies. Designing exhibits in a way that maximizes animal privacy through either regressed exhibits or visual barriers may increase the inhabitants' welfare. A previous study on captive Sumatran tigers and African lions (Bashaw, 2007) found that adding visual barriers did not significantly reduce pacing in their subjects, but these solutions are still worth considering given small sample sizes and restrictions of the previous study.

Lastly, other factors including temperature and time of day should also be considered when trying to manage a captive population's well-being. Figure 7 showed that there is an inverse relationship between temperature and stereotypic behavior occurrences. Based on this result, indoor temperature controlled enclosures that mimic the temperatures of each species' natural environment could mitigate stereotypic behavior, but this solution needs further investigation (Liu, 2007). Figure 8 showed that time of day also influenced the occurrences of stereotypies, so the facilities can use this information to understand any other underlying causes of their animals' distress.

While we were able to draw some interesting conclusions from this study, it is important to recognize its limitations. Due to the inherent restrictions of captive animal research, our sample size was small. This could have been the reason that most of the data did not produce statistically significant results. However, it is equally likely that the lack of significance was also due to no difference at all. Regardless of which possibility is true, future research should work to compile more large scale studies across more facilities and members of the felidae family. Second, the lions showed a significant difference in abnormal behavior between the two facilities, but this could be due to previous life experience rather than facility type. In Table 1,

the life experiences of each individual are shown. The animals at the sanctuary were obtained for rescue purposes because they were in need of captive assistance. The animals in the zoo were either obtained at a young age or were bred in captivity. Perhaps these previous experiences play a larger role in an animal's state of welfare than their current environment. Once again, a larger scale study could help verify this conclusion. Lastly, our study was only conducted during the operating hours of each facility and only from public viewing areas. This limited our sampling window. Lions and cougars are nocturnal animals (Schaller, 1972; Nielsen et al. 2015) and therefore a restricted sample window of 8:00 - 17:00 may belie the true behavioral profiles of these animals. Additionally, Bashaw 2007 found that pacing in other felids occurred at higher rates in off-exhibit housing, but our study was unable to examine these conditions in the zoo population.

Because this study only focused on 9 individuals of 2 different species at 2 different facilities, it is difficult to generalize the results to the entire felidae family. However, these results do point out some previously unknown trends that warrant future research. A large scale study that investigates privacy within exhibits is needed. We suggest an experimental approach that involves shifting animals to different exhibits and observing their behavioral changes in order to maximize each individual animal's welfare. Further investigation into other factors like sex, temperature, and time of day could also prove useful in understanding the trends of this study further. In addition to these future research ideas, this study can help evaluate the preferences at an individual level. It is known that individuals within the same species respond and perceive their captive spaces differently (Tetley & O'Hara, 2012), therefore the results from this study can be used by both facilities to improve the lives of their own respective collections of animals. In summary, stereotypic behavior in captive felids is a complex issue with a plethora of influencing factors. However, this study demonstrates the need to consider both the spatial distributions of stereotypic behavior and exhibit design when trying to maximize captive felid welfare in the future.

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VI. References

Source 1. Available upon request. Kept anonymous for privacy concerns.

Source 2. Available upon request. Kept anonymous for privacy concerns.

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