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Spatial and Behavioral Patterns of Captive Coyotes

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SPATIAL AND BEHAVIORAL PATTERNS OF

CAPTIVE COYOTES

by

Jeffrey T. Schultz

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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in

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ABSTRACT

Spatial and Behavioral Patterns of Captive Coyotes

by

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Utah State University, 2017

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Department: Wildland Resources

Environmental enrichment can improve the well-being of animals in captivity and

promote natural behavior. Habitats that offer an assortment of choices can provide

practical ways for captive animals to cope with challenging situations. Enclosure

features, such as shelter structures, can promote wild behavior by adding complexity to

an enclosure's physical environment. Enrichment efforts are most effective when they are

specialized to the natural behavior and biological needs of the animals in captivity.

Human activity may alter captive animal behavior and utilization of various enclosure

features, and there is concern that human presence may negatively impact the welfare of

some captive animals. Captive coyotes (*Canis latrans*) at the United States Department of

Agriculture (USDA)-National Wildlife Research Center (NWRC) Predator Research

Facility in Millville, UT, USA, are maintained for research on biology, ecology,

physiology, and behavior. Coyotes at the research facility utilize simple shelter structures

to hide, rest, and display vigilant behavior. Because they regularly use these simple

structures, new and more complex enrichment structures were installed to enhance

enclosure enrichment. The objectives of this study were to assess (1) enclosure utilization

and shelter structure preferences, and (2) how human activity affects captive coyote behavior and enclosure utilization. Using 32 mated coyote pairs rotated through eight 0.6-ha enclosures for 28-day trials over the winter months (January – March) of 2015 and 2016, spatial and behavioral patterns were monitored via the implementation of GPS-collars and live scan observations. Coyotes overutilized all shelter structure areas, given their available space, but spent most of their time at the perimeter and open areas of their enclosures. Complex structures were utilized more than simple structures. Coyotes most often demonstrated inactive and vigilant behavior, but showed increased vigilance when there was human activity. Human activity also stimulated coyotes to become more active than inactive and reduce their utilization of enrichment structures. Although there was no clear preference for one specific type of complex enrichment structure, composite evidence from GPS-collars and behavioral data suggest the ramp may have heightened biological suitability. This study advances the knowledge of captive coyote spatial patterns and helps improve environmental enrichment planning for captive animals by exploring effective methods of adding complexity to animal enclosures.

(81 pages)

PUBLIC ABSTRACT

Spatial and Behavioral Patterns of Captive Coyotes

Jeffrey T. Schultz

Environmental enrichment is a technique used at many captive animal facilities that can improve the well-being of their animals. It seeks to enhance habitat features and promote natural behavior by providing a variety of practical ways for captive animals to control their environmental settings, especially during stressful circumstances. Enclosure features, such as shelter structures, are one tool that promotes wild behavior by adding complexity to an enclosure's physical environment. Enrichment efforts for captive wildlife are most effective when they are specialized to the biological needs of the animals. Human activity may alter captive animal behavior and utility of enclosure features, and there is concern that human presence can negatively impact the welfare of some captive animals. Captive coyotes (*Canis latrans*) at the USDA-National Wildlife Research Center (NWRC) Predator Research Facility in Millville, UT, USA, are maintained for research on biology, ecology, physiology and behavior. Coyotes at the research facility are routinely noticed utilizing shelter structures to hide, rest, and display vigilant behavior. Because they regularly use these simple structures, new and more complex enrichment shelter structures were installed to be evaluated. Specific research objectives aimed to assess (1) coyote enclosure utilization and shelter structure preferences, and (2) coyote spatial and behavioral responses to human activity. Using 32 mated coyote pairs rotated through eight 1.5-acre enclosures for 28-day trials over the winter months (January – March) of 2015 and 2016, spatial and behavioral patterns were

monitored via the implementation of GPS-collars and live behavioral observations.

Coyotes showed preference for shelter structure designs, but still spent most of their time

at the perimeter and open areas of their enclosures. Complex structures were preferred

over simple structures. Coyotes most often demonstrated inactive and vigilant behavior

without human activity, but showed increased vigilance when there was human activity.

Human activity also stimulated coyotes to become more active than inactive and reduce

their utilization of enrichment structures. Although there was no clear preference for one

specific type of enrichment structure, composite evidence from GPS-collars and

behavioral data suggest the ramp may have heightened biological suitability. This study

advances the knowledge of captive coyote spatial patterns and helps improve

environmental enrichment planning for captive animals by exploring effective methods of

adding complexity to animal enclosures.

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CHAPTER 1

INTRODUCTION

Animals are routinely kept in captivity, for the purposes of public education, research, rehabilitation, or species conservation (Guy et al., 2013; Mason, 2010; Rees, 2011). According to a 2010 estimate, 26 billion animals, over 10,000 species, reside in confined environments (Mason, 2010). This emphasizes the value of expending resources to measure the effectiveness and utility of captive settings, and the importance of adjusting enclosure design to enhance animal welfare. Captive facilities frequently use environmental enrichment to improve welfare by accommodating natural biological tendencies. Enrichment is defined as "a process to ensure that the behavioral and physical needs of an animal are being met by providing opportunities for species-appropriate behaviors and choices" by the Association of Zoos and Aquariums (AZA, 2017). Enrichment can also improve welfare of captive animals by reducing undesirable stereotypic behavior such as repetitive pacing (Shyne, 2006). Various methods of enrichment can be used to enhance the captive environments of animals, including variation in food delivery, provision of sensory stimulation, and alteration of physical features (Bloomsmith et al., 1991; Newberry, 1995). Captive facilities can also evaluate different aspects of enrichment programs to improve efficacy (Hoy et al., 2010).

Animals in captivity have finite resources in their enclosures and may not utilize them uniformly, resulting in preferred (overutilized) and avoided (underutilized) areas. Since captive animals are provided substantially less physical space than in the wild (Hosey, 2005), it is important to identify and alter underutilized areas which reduce the effective size of an enclosure. Resources, or features, may facilitate the utilization of an enclosure

area. Evaluating enclosure utilization can help measure the appropriateness of the

confined environment in relation to biological and behavioral needs of captive animals

(Ross et al., 2009) and help managers improve the features offered. Carnivores have been

shown to utilize complex features more than barren or less complex environments,

demonstrating that preferred features can shift enclosure utilization (Kistler et al., 2010;

Mallapur et al., 2002). Structural enrichment can increase complexity. However, the

permanent nature of structural enrichment often demands more time and money to

implement than other forms of enrichment and thus poses a greater risk of inefficient

efforts. Hence, it is important for captive facilities to assess the utility of different

structural enrichment designs and evaluate their biological value, during times with and

without human presence.

Human activity can disrupt behavior and activity levels of captive wildlife and may

therefore negatively affect animal well-being (Davey, 2007; Hosey, 2000). This is

especially of concern when animals demonstrate increased abnormal behavior or

aggression related to human presence (Mallapur et al., 2005; Wells, 2005). Some species

naturally function on low energy diets and may be physiologically impacted by increased

energy expenditures caused by stressful events, and such impacts can vary with the

number of humans present (Larsen et al., 2014). For example, larger crowds can bring

increased undesirable effects compared to smaller crowds (Woolway and Goodenough,

2017). It is strongly advised for captive animal facilities to provide environmental

enrichment that allows captive animals the opportunity to control their surroundings

when disruptive human events occur (Carder and Semple, 2008; Fernandez et al., 2009).

Predictability and control are important aspects of an animal's welfare (Bassett and

Buchanan-Smith, 2007), and human interruptions are not always clearly signaled. Metrics that gauge how captive animals respond to human activity are needed to appropriately manage the frequency and magnitude of human interaction events. In addition to monitoring animal response to human activity, recording animal responses to enrichment strategies can critically assess the overall benefit of the enrichment program (Mellen and MacPhee, 2001).

This study elucidates how spatial and behavioral ecology of a captive carnivore relates to the utility of various environmental features and human activity. Specific research objectives were to evaluate (1) enclosure utilization and shelter structure preferences, and (2) spatial and behavioral responses to human activity. I used captive coyotes (*Canis latrans*) at the United States Department of Agriculture (USDA)-National Wildlife Research Center (NWRC) Predator Research Facility in Millville, UT because it offered an ideal setting to examine enclosure utilization. The study provided the opportunity to enhance environments for over 100 animals. In chapter two, GPS-collars were used to monitor how coyote enclosure utilization related to discrete enclosure features. This information was supplemented with behavioral evidence to help clarify preferences among three novel and more complex enrichment structure designs. In chapter three, coyote behavior and enclosure utilization were compared between periods with and without human activity to further portray the utility of enclosure features and enrichment structures. Since scientists frequently use results from captive investigations to improve field experiments, it is critical that coyotes at the research facility behave similar to wild coyotes. Improving enrichment can promote natural behavior. Research

facilities can benefit from this information, especially when developing more complex features and designing future enclosures for captive canids.

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CHAPTER 2

ENCLOSURE UTILIZATION AND ENRICHMENT STRUCTURE PREFERENCES

OF CAPTIVE COYOTES[1]

ABSTRACT

Environmental enrichment improves well-being of captive animals by enhancing their ability to cope with acute stress and adapt to challenging situations. Enrichment programs utilize a variety of tools to promote wild behaviors, including adding complexity to the physical environment. Designing enrichment structures requires an understanding of behavioral and biological responses to enrichment efforts. Captive coyotes (*Canis latrans*) at the USDA-National Wildlife Research Center's (NWRC) Predator Research Facility utilize shelter structures, called shade tables, to hide, rest, and display vigilant behavior. Because these simple structures are regularly used, new and more complex enrichment structures were installed to enhance enclosure enrichment. This study examined the time captive coyotes spent at discrete enclosure features to determine: (1) how coyotes utilize enclosure space and shelter structures; and (2) if coyotes have a preferred enrichment structure design. Three enrichment structure designs (ramp, closed, and neutral) were installed simultaneously in 0.6 ha enclosures during the 2015 and 2016 breeding seasons (January – March). Additional coyote pairs were monitored in control enclosures, where the shelter structures were shade tables. GPS-collars and scan sampling was used throughout a 28-day testing period to record space use and behavior. Coyotes

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over utilized all shelter structure areas, given their availability, but spent most of their time at the perimeter and open areas of their enclosures. Coyotes utilized the complex enrichment structures in treatment enclosures more than the shade tables in control enclosures. Although there was no statistical preference for one specific type of complex enrichment structure, composite evidence from GPS-collars and behavioral data suggest the ramp may have heightened biological suitability. This study advances the knowledge of captive coyote spatial patterns while helping improve environmental enrichment planning for captive facilities through the exploration of adding complexity to animal enclosures.

1   INTRODUCTION

The Association of Zoos and Aquariums (AZA, 2017) define enrichment as "a process to ensure that the behavioral and physical needs of an animal are being met by providing opportunities for species-appropriate behaviors and choices." The implementation of environmental enrichment can improve an animal's ability to cope with acute stress and allow it to adapt to changing situations (Mellen & MacPhee, 2001). Environmental enrichment practices fall into several categories, including feeding regimes, toys, sensory stimulation, and physical environment (Bloomsmith, Brent, & Schapiro, 1991; Newberry, 1995; Wells, 2009). Recording animal responses to enrichment efforts is often used to critically assess aspects of an enrichment program (Mellen & MacPhee, 2001), although documentation procedures range from explicitly designed experiments to anecdotal annotations. Evaluation of these records can advance

an enrichment program tailored to the biological needs of the captive species, resulting in enhanced welfare and improved efficacy of husbandry efforts.

Captive animals have finite resources in their enclosures and may not utilize them uniformly, resulting in preferred (over utilized) or avoided (underutilized) areas. Underutilized areas reduce the effective size of an enclosure, making it important to identify and eliminate the causes of avoidance. Hunter, Gusset, Miller, & Somers (2014) found that captive African wild dogs (*Lycaon pictus*) preferred and avoided specific areas of their enclosures, depending on features such as substrate, slope, or proximity to zookeeper areas. Chimpanzees (*Pan troglodytes*) and lowland gorillas (*Gorilla gorilla*) underutilized a common vertical tier within a zoo enclosure, likely because it consisted mainly of ropes designed for locomotion and not resting (Ross & Lukas, 2006). Thus, preferred and avoided areas may correlate to underlying biological or social functionalities that can go undetected when using cumulative time measures. Evaluating enclosure utilization can help assess the appropriateness of the environment in relation to biological and behavioral needs of captive animals (Ross, Schapiro, Hau, & Lukas, 2009). Since natural instincts may influence a captive animal's selection of resources, evaluating the utilization and functionality of enclosure areas and associated features can help managers improve the resources they provide and accommodate for species-specific inherent behavior.

Modification to an animal's physical environment to improve environmental enrichment efforts has been explored among several captive animal species, typically by providing additional structures to stimulate active wild behavior. General activity increased in spectacled bear (*Tremarctos ornatus*) by introducing climbing structures

(Renner & Lussier, 2002) and in Indian leopards (*Panthera pardus*) with the provision of structurally enriched habitats compared to barren enclosures (Mallapur, Qureshi, & Chellam, 2002). Indian leopards housed in more complex enclosures also spent more time in the enriched zones of their enclosures compared to those in less complex enclosures (Mallapur et al., 2002). Similarly, red foxes (*Vulpes vulpes*) preferred areas having structural components over barren areas (Kistler, Hegglin, Würbel, & König, 2010). Increasing the complexity of enclosures also reduced the proportion of edge zone used by lion-tailed macaques (*Macaca silenus*) (Mallapur, Waran, & Sinha, 2005). Changes in enclosure utilization noted in these studies illustrate that enhanced areas that offer additional environmental choices are preferred by captive animals, and likely improve their welfare.

Understanding utilization of different enclosure features by captive animals can help facility managers gauge the biological relevance of unique environmental components and efficiently advance future designs of enclosures and enrichment structures. Although several studies have evaluated wild coyote space use, home ranges, and habitat selection in relation to resources (Gese, Ruff, & Crabtree, 1996; Kluever & Gese, 2016; Mills & Knowlton, 1991; Shivik, Jaeger, & Barrett, 1996; Young, Glasscock, & Shivik, 2008), none have attempted to evaluate these topics pertaining to coyotes in captivity. The United States Department of Agriculture (USDA)-National Wildlife Research Center (NWRC)-Predator Research Facility in Millville, UT, USA, houses over 100 captive coyotes for research purposes. Simple structures, called shade tables, are provided within each outdoor enclosure. Captive coyote pairs regularly utilize shade tables to hide, rest, and display vigilant behavior, so additional enrichment structures were designed for this

study to increase complexity within enclosures. To ensure new structures would be suitable and well used, three designs were tested. The objective of this study was to assess how captive coyotes utilize enclosure features, given the introduction of more complex enrichment shelter structures. Specific goals aimed to determine: (1) how coyotes utilize enclosure space and shelter structures; and (2) if coyotes have a preferred enrichment structure design. Understanding how coyotes utilize resources and enclosure space will assist captive facilities with appropriately designing new enclosures and enrichment structures.

2   MATERIALS AND METHODS

2.1 Study overview

The study was conducted at the 164-acre, USDA-NWRC Predator Research Facility in Millville, UT, USA, which houses over 100 adult coyotes in captivity as mated pairs for research purposes. Testing occurred during winter months (January – March) of 2015 and 2016. Thirty-two coyote pairs were randomly selected from all mated pairs in the captive colony, with 16 pairs tested each year. Males were vasectomized, per facility standard operating procedures, to prevent breeding prior to the study. Each pair was randomly assigned to a treatment or control enclosure. Research protocols were approved by the Institutional Animal Care and Use Committee at the National Wildlife Research Center (QA-2375) and Utah State University (Protocol #2490).

Eight 0.6 ha enclosures were utilized for this study for two 28-day periods in 2015 and 2016. The enclosures remained vacant for 1-3 days before experimental coyote pairs were released into the enclosures to allow for shelter structure construction and feces

removal. Enclosures consisted of two human access gates and an animal capture kennel (2 m x 3 m) with a concrete floor that was located at either the north or south corner (Figure 2.1). Each enclosure was comprised of natural substrate, an automatic watering device situated adjacent to one of the gates, and two den boxes made of cylindrical PVC (0.5 m high x 0.5 m diameter) providing corn cob bedding (Green Products Company, Conrad, IA, USA) in each capture kennel. Only experimental or control shelter items were provided in the main enclosure area, and in-ground den holes were collapsed or otherwise made inaccessible during the study. Coyotes were scatter-fed normal daily rations (650 g per coyote) of a commercially prepared food (Fur Breeders Agricultural Cooperative, Logan, UT, USA) in one specified area of each enclosure, and water was available *ad libitum*.

2.2 Enrichment structures

2.2.1 Control enrichment structures

Two study enclosures were randomly selected to serve as control enclosures. Control enclosures reflected shelter resources routinely available to captive coyotes by providing two wooden shade tables (0.6 m tall x 0.8 m wide x 1.2 m long) per enclosure. Shade table locations in the control enclosures were randomly assigned to two of the three locations designated for experimental shelter structures (Figure 2.1).

2.2.2 Treatment enrichment structures

Enrichment structures were randomly assigned to occupy the three predetermined shelter locations in the treatment enclosures. The structures were simultaneously offered

and spaced 40-55 m from each other and >10 m from the perimeter fence (Figure 2.1).

Middle points of the structure locations were recorded using a Garmin GPSMap 64®

handheld device. All experimental enrichment structures included two components: (1) a

wooden shade table and (2) an additional taller plywood platform (1.2 m x 1.2 m)

supported 1.2 m above the ground using four steel T-posts (Figure 2.2). Combining the

two components, each enrichment structure spanned 4 m in length. Enrichment structures

were oriented in a north-south direction, with the taller component positioned to the

north. The three structure designs were: (1) a neutral structure composed of the basic two

components, (2) a ramp structure that joined the two components using a 4 cm x 24 cm x

2.4 m wooden board, and (3) a closed structure formed by adding three plywood boards

to the T-posts underneath the taller platform (Figure 2.2). Coyotes were allowed access

into the closed cavity from the south and could access the top of the taller component

with the ramp design.

2.3 Data collection

2.3.1 Global Positioning System (GPS) collars

Each coyote was fitted with a GPS-logger (i-gotU GT-600®, Mobile Action

Technology, Inc.) for the 28-day test period. The logger was protected and attached via a

vinyl pouch to a durable leather dog collar (3 cm wide), that was placed on the coyotes

such that the device would face upward when the coyote was standing or lying in a prone

position. Geographic coordinate locations for each coyote were recorded at 5-min

intervals. Acquisition rates were also assessed for each coyote GPS-collar during each

28-day test period.

Nine GPS-collars were positioned at known geographic coordinates for accuracy testing during the second year of the study. To simulate potential positions of the GPS-logger attached to the coyotes, three collars were positioned so the GPS-logger was facing upward, three collars were set so the GPS-logger was facing parallel to the ground, and three collars were set facing the ground. Locations were recorded every five minutes for 28 days. The number of GPS points counted in a 5-m radius of the known geographic coordinate was divided by the total number of GPS points used. The resulting proportion represented the accuracy for the nine test collars, and a mean accuracy for each position was obtained by averaging the accuracies of the three collars that were set at the same position. Acquisition rates were also determined for the nine test collars and averages were obtained for the three test positions.

2.3.2 Behavioral observations

Scan sampling was used for all behavioral observations (Altmann, 1974) using an innocuous mobile observation blind. Scans of each animal were conducted at 5 min intervals for one hour per day, four days per week, over the duration of each 28-day period. Although the coyotes appeared to ignore the observation blind, the observer arrived at the designated vantage point 15 min before beginning any observations to assure coyotes resumed their normal activities if they responded to the blind. Start times were randomly selected between 08:00 and 15:00 to ensure sufficient light for visibility. At each scan, the location and behavior of the study coyote was logged. Coyotes were recorded at enrichment structures when they were within 2 m of a structure, and were considered at the perimeter when they were within 2 m of the perimeter fence. Behavior

was categorized into three groups: vigilant, inactive, and active (Table 2.1). Only one person conducted all scans to eliminate inter-observer variability.

2.4 Data analysis

GPS data were downloaded using @trip PC software (provided with the GPS-logger) and managed in ArcGIS®, version 2.2.2 (ESRI, 2014). Accuracy of the experimental collars was estimated by dividing the number of GPS points located within a 5 m buffer of a known geographic coordinate by the total number of points obtained from each collar. The first 12 hours of all GPS data used in this study was removed from analysis to allow time for the data loggers to initialize and find satellites.

Enclosure perimeters were delineated using editing tools in ArcGIS to trace the fence lines demarcated on the Environmental Systems Research Institute (ESRI) satellite basemap. Five-meter buffers were placed around the center points of each structure and along both sides of the enclosure perimeters to prevent overlapping (Figure 2.1). Coyote locations were categorized at discrete enclosure areas, including perimeter and enrichment structure, when coordinates from their GPS-collar fell within or intersected the buffer (Figure 2.1). All other locations inside the enclosure were categorized as open areas (Figure 2.1). Enclosure space comprised of 39% perimeter space, 58% open areas, and 1% per structure. Thus, in control enclosures where there were only two structures, the open area made up 59% of the enclosure. These proportions of available enclosure area space were derived using ArcGIS to represent the expected enclosure feature utilization for each individual. The proportion of time recorded at each enclosure feature for each coyote was obtained by dividing the number of GPS points at each feature by the

total number of GPS points for each individual. For all GPS data, locations that fell

outside of the perimeter buffer were excluded from analysis. Since the observed data did

not follow normal distributions, non-parametric Mann-Whitney U-tests were performed

to determine significant differences in observed proportions of GPS points at each

enclosure feature between (1) treated animals (n = 60) and control animals (n = 4), and

(2) observed and expected enclosure feature utilization for treated and control animals.

A mixed logit model was fitted using the glmer function in the lme4 package, version

1.1-12 (Bates, Maechler, Bolker, & Walker, 2015) in Program R, version 3.3.2 (R Core

Team, 2016) to compare the probability of use among shelter structure locations between

treatment and control enclosures. Using a binary response for structure use (yes/no) and

the logit link function, fixed factors included sex (female/male), enclosure type

(control/treatment), and time of day (day/night), and all interactions were included in the

model. Day locations were from 600 – 1800 and night locations were from 1800 – 600.

Random effects included individual and pair identifications to account for clustering

within these groups. Predicted probabilities were obtained using the lsmeans function in

the lsmeans package, version 2.5 (Lenth, 2016) in Program R.

To estimate coyote preferences among the three enrichment structure designs, a set of

three generalized linear mixed models (GLMMs) fitted using binomial distributions and

logit link functions were independently assembled to emulate the logistic equations that

would simultaneously be estimated in a mixed multinomial regression model (Begg &

Gray, 1984) using the GLIMMIX procedure in SAS/STAT®, version 14.2 (SAS

Institute, 2013). Only GPS points falling within enrichment structure locations were used

for the set of three GLMMs. Odds-ratio estimates were compiled to understand the

utilization of one enrichment structure design in relation to another: (1) ramp use over neutral use, (2) ramp use over closed use, and (3) neutral use over closed use. The models included the same fixed factors as the logit model comparing shelter structure utilization between the control and treatment coyotes. To accommodate correlation due to clustering of GPS points within pairs, pair was included as a random effect. Using the GPS-collar data from points only at the enrichment structures, Mann-Whitney U-tests explored significant differences in observed proportions of GPS points between (1) males and females and (2) day and night structure utilization.

An additional GLMM using behavioral scans observed at the enrichment structures was fitted with a negative binomial distribution. There was no apparent difference in behavior between the male and female coyotes within a pair, so sex was not included as a predictor variable in the model. The response variable was scan count, summed over all observations for both coyotes in a pair. Behavior type (vigilant/inactive/active) and location (closed/neutral/ramp) were fixed effects factors, and the interactions between these factors were included in the model. Pair was again included as a random effect. The model was fitted using the glmmadmb function in the glmmADMB package, version 0.8.3.3 (Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2013) in R. Means were estimated using the lsmeans function in the lsmeans package, and comparisons among means were computed using the contrast function in the lsmeans package. Family-wise Type I error was controlled using the Tukey method. The significance threshold was set at 0.05 for all statistical analysis.

3 RESULTS

3.1 GPS-collar accuracy

Mean proportions of GPS points found within a 5-m radius of a known point were 0.48 ($\pm$ 0.03) when the collar was facing the ground, 0.81 ($\pm$ 0.02) when it faced the sky, and 0.53 ($\pm$ 0.13) when the collar was facing parallel with the ground. Most GPS-collars recorded data at the programmed 5-minute intervals for the entire 28-day testing period. Acquisition rates of the GPS-collars on coyotes were 0.87 ($\pm$ 0.02), resulting in an average of 7356 ($\pm$ 150) locations per coyote. Of all acquired locations from GPS-collars on coyotes, an average of 0.83 ($\pm$ 0.01) of total GPS points fell within the enclosure area and were used for analysis. For test collars, acquisition rates were 0.96 ($\pm$ 0.003) for collars in the up position, 0.95 ($\pm$ 0.01) for collars in the side position, and 0.91 ($\pm$ 0.01) for collars that faced the ground.

3.2 Enclosure space use

Comparing coyotes in treatment enclosures to coyotes in control enclosures, treatment coyotes utilized the perimeter significantly less ($U = 50.0$, $P = 0.05$) and utilized structures significantly more ($U = 4.0$, $P < 0.01$) (Figure 2.3). Comparing observed enclosure feature utilization to expected enclosure feature utilization, control coyotes significantly overutilized shade tables ($U = 16$, $P = 0.01$). Treatment coyotes significantly overutilized enrichment structures ($U = 3480$, $P < 0.01$) and significantly underutilized open areas ($U = 1080$, $P < 0.01$) (Figure 2.4).

3.3 Enrichment structure use

In treatment enclosures, the proportion of coyote locations at an enrichment structure was 0.12 (± 0.00), while the proportion of coyote locations at a shade table in the control enclosures was 0.04 (± 0.00) (Figure 2.3). Of accounts at enrichment structures, ramp structures had the highest proportion of use (0.41 ± 0.04), followed by neutral (0.33 ± 0.03) and closed structures (0.27 ± 0.03). Experimental shelter structures were significantly overutilized (ramp, U = 2400, P < 0.01; closed, U = 2160, P = 0.04; neutral, U = 2400, P < 0.01; shade table, U = 16, P = 0.01) (Figure 2.5). No significant differences in enrichment structure utilization were noticed from the proportions of GPS-collar locations between males and females (Figure 2.6). Coyotes utilized the ramp significantly more during the day (U = 2229, P = 0.02) (Figure 2.7).

Results from the mixed logit model showed the treatment/control factor was a significant predictive term (P = 0.01). The probability that control coyotes would be located at a shade table was 0.04 (95% CI: 0.02 to 0.07) and the probability that treatment coyotes would be located at an enrichment structure higher, estimated at 0.09 (95% CI: 0.07 to 0.10).

Significant predictor variables varied among the three logistic regression models comparing the enrichment structure designs. Time of day (P < 0.01) and the interaction of time of day and sex (P < 0.01) were significant in the model to explain ramp use compared to neutral use (Table 2.2). However, the models comparing ramp over closed structures and neutral over closed structures provided no statistical evidence that enrichment structure utilization varied by sex or time of day. The relative preference for

ramp over neutral was higher during the day than at night, regardless of sex, but the

relative preference was more pronounced for females (Table 2.3).

Results from the GLMM derived from behavioral observations showed significant

differences in the distribution of coyote enrichment structure selection and behavior ($P <$

0.01), along with the distribution of behavior at the varying enrichment structures ($P =$

0.01). Pairwise comparisons show coyotes selected the ramp significantly more often

than the closed ($P < 0.01$) and neutral structures ($P < 0.01$). Inactive behavior was

significantly more frequent than vigilant behavior ($P < 0.01$), and vigilant behavior was

significantly more frequent than active behavior ($P < 0.01$). When comparing to the

closed structure, significantly more inactive behavior was associated with both the neutral

($P = 0.01$) and ramp structures ($P < 0.01$). Vigilant behavior was more frequent at the

ramp structure when compared to vigilant behavior at the closed ($P < 0.01$) and neutral

structures ($P = 0.05$).

4   DISCUSSION

Captive coyotes spent a substantial amount of time at the perimeter and open areas of

enclosures, but also overutilized structural features based on structure availability.

Coyotes housed with complex enrichment structures also spent less time at the perimeter,

an effect also noticed in lion-tailed macaques (Mallapur et al., 2005). Novel and more

complex enrichment structures were utilized more than the simple shade tables. Although

there were three enrichment structures in the treatment enclosures and only two shade

tables in the control enclosures, coyotes used enrichment structures more than twice as

much as shade tables. This suggests the importance of providing additional complex

enrichment structures for captive coyotes, and illustrates the benefits of evaluating structural designs using different monitoring techniques.

Models using the GPS and behavioral data produced similar estimates of enrichment structure preferences while providing unique predictive elements. Combining different monitoring techniques can help managers at captive animal facilities select biologically appropriate enrichment structure designs. Measuring the proportion of time at different structures is one method to spatially analyze the generic utility of a resource and decipher a preference for an area, but must rely on direct or indirect methods to obtain the data. GPS-collars in this study described both nocturnal and diurnal patterns of captive coyotes. While it is beneficial to obtain information without human disturbance (Larsen, Sherwen, & Rault, 2014; Sekar, Rajagopal, & Archunan, 2008), GPS-collars only depict location and lack information on animal behavior. Behavioral assessments can help explain the functionality of resources in relation to the animal's inherent natural tendencies. Ethograms and activity budgets portraying behavioral repertoires of animals can be applied to illustrate animal responses to changes in their environment (Kluever & Gese, 2016; Wells & Hepper, 2000). For instance, these techniques have been useful in comparing the behavior of captive and wild coyote populations (Brummer, Gese, & Shivik, 2010; Shivik, Palmer, Gese, & Osthaus, 2009). Behavioral information collected from this study showed that complex enrichment structures were associated with predominantly inactive behavior, however, vigilant behavior occurred primarily at the ramp. Thus, using two discrete metrics improved estimates of the efficacy of environmental enrichment efforts and elucidated the biological and social functionality of different enclosure features.

Overutilization and underutilization of enclosure areas have been specifically measured to assess enclosure appropriateness and animal welfare of captive wild animals (Hunter et al., 2014; Ross et al., 2009). When evaluating the utilization of features in an animal's environment, only in theory will each resource be utilized proportionately to their allocated space. Animals naturally spend varying amounts of time exploiting different resources (Bekoff & Wells, 1981; Gese et al., 1996) and correlating these intricate biological functions with often crudely delineated spatial features is challenging. While overutilized areas allude to associated features that are likely preferred, underutilized areas may suggest the avoidance of related resources and decrease the functional captive space. This study provides evidence that coyotes value shelter structures, especially those with more complex arrangements. Similar results have been found in studies of species that are prone to predation (Jensen, Gray, & Hurst, 2003; Kistler et al., 2010). Coyotes were mainly inactive at the enrichment structures, perhaps feeling more relaxed and secure in a more complex environment. Wild coyotes spend the majority of their time resting, especially in the winter months (Gese et al., 1996). Thus, any structure design that creates a more complex setting may be more amenable to a coyote's natural tendency to rest and display vigilance.

Although complex features in the enclosures were shown to be preferred, coyotes were still more frequently at the perimeter and open areas. Coyotes will routinely use howling and scent-marking for territory maintenance purposes and increase the frequency of scent-marking near territorial boundaries during the breeding season, December – February (Gese & Ruff, 1997). Perimeter areas of high intrusion are related to increased rates of raised-leg urinations (Wells & Bekoff, 1981). Similarly, captive coyotes often

scent mark their enclosures and interact with neighbors while at the periphery (Schell, Young, Lonsdorf, Mateo, & Santymire, 2016). Coyotes in treatment enclosures spent less time at the perimeter than coyotes in control pens. A similar reduction in perimeter space use was observed in lion-tailed macaques when complex enrichment structures were introduced (Mallapur et al., 2005). Although perimeter utilization serves specific biological and social functions for captive coyotes, stereotypic pacing is often related to the peripheries of enclosures (Lyons, Young, & Deag, 1997), suggesting that structural features may improve well-being.

Results showed coyotes used open areas less than expected. Open areas comprised more than half of the enclosure space and could analogously be considered as the core areas of their territories, which tend to remain stable over time (Young, Andelt, Terletzky, & Shivik, 2006). Aside from structural features, small prey such as voles and mice may naturally occur inside the enclosures and contribute to the utilization of areas. This may be why captive coyotes spend more time exploring their environment when housed in larger enclosures (Brummer et al., 2010). One would expect fewer in the open, homogenous areas and more along the periphery, where they can escape predation by exiting the enclosure. Indeed, small mammals are often at higher abundance in edge habitats relative to homogenous landscapes (Bowers, Gregario, Brame, Matter, & Dooley, 1996). Wild coyotes generally avoid grasslands and prefer habitat that provide more structural complexity (i.e., pinyon-juniper and shrubs) which may be more abundant with prey (Gese, Rongstad, & Mytton, 1988). For captive coyotes, open areas are more homogenous than perimeter or structural features. Further, the preference for enrichment structures in treatment enclosures may have resulted in less use of open areas.

While a preference for one experimental enrichment structure did not materialize, some trends appeared. Behavioral scan observations, although only clustered during brief periods of daytime hours, showed that coyotes were more likely to be at the ramp structure than at the other two enrichment structures. This coincides with GPS-based modeled and observed results that male and female coyotes used the ramp structure more during the day rather than at night. GPS data also showed that when coyotes were located at an enrichment structure, they were most frequently recorded at the ramp. This may be explained by biological reasons; coyotes were mostly inactive at the enrichment structures, implying their suitability in offering protection from harsh environmental conditions common in winter. Vigilant behavior is routinely noticed in wild coyote populations, often in conjunction with resting (Bekoff & Wells, 1981). Similarly paired correlations were found in this study where vigilance was intermittently exhibited within longer lasting inactive states, and was most frequently recorded at the ramp structure. This suggests the ramp design may be best because it protects from weather and visual exposure, provides additional resting space, and better accommodates vigilant behavior with an accessible elevated platform.

The use of GPS-collars is a novel method for monitoring enclosure utilization of captive animals. While it provided a detailed evaluation of space use, even more detailed than noted in wild studies of coyotes (e.g., Arias-Del Razo, Hernández, Laundré, & Velasco-Vázquez, 2012), it also had limitations likely related to the use of hand-made GPS-collars. The accuracy of the GPS-collars fluctuated in relation to their orientation to the sky, which would not have been known without the independent collar tests, because the GPS-loggers did not record standard metrics of error (e.g., Bowman, Kochanny,

Demarais, & Leopold, 2000; Frair, Fieberg, Hebblewhite, Cagnacci, DeCesare, & Pedrotti, 2010; Hansen & Riggs, 2008). The GPS-collars were put on the coyotes in such a way that the data logger faced the sky when they were standing, sitting, or laying prone, and the collars successfully remained in that position on the neck for the duration of the testing period. Clusters of GPS points at the structure areas were readily discernable when visually inspecting the spatial distribution of the data, supporting that the collars were sensibly portraying animal spatial patterns. The high acquisition rates of the GPS-collars produced thousands of GPS points for each coyote, which helped validate the trends observed in this study. Using comparably large enclosures at the research facility (0.6 ha enclosures rather than 0.1 ha enclosures) helped account for GPS error by enabling the application of buffer areas. Enrichment structures are likely to be visible in future ESRI basemaps, making it feasible to reduce error even further in future studies.

In summary, the provision of more complex enrichment structures increased coyote utilization of structures and reduced time spent at the enclosure perimeter. Coyotes overutilized all structure designs, and enclosures with more complex enrichment structures realized an underutilization of open areas. Since no clear enrichment structure preference was evident, all three tested designs may be considered appropriate for coyotes in captivity. However, if only one design is used, the ramp may be best because of the observed trend in greater use seen from both monitoring techniques. Further, the ramp provides easier access to the taller platform, offering additional versatility and utility for captive coyotes.

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TABLE 2.1 Description of behavior categories used for analysis from scan observations.

Behavior category	Description
Vigilant	Laying, sitting, standing, walking, or running with head raised and visually surveying the environment.
Inactive	Laying and resting with head down or eyes closed (not vigilant); laying and grooming, sniffing or biting grass; sitting; standing and drinking or grooming.
Active	
General	Running; walking; pacing; digging; sniffing with nose close to the ground while walking or standing.
Social	Breeding activities (i.e., mounting, sniffing); dominant or subordinate playing or fighting; howling.
Territorial	Marking (i.e., urinating or defecating then scratching, laying and rolling); stalking conspecifics; tail flagging; fence running with vigilance directed at conspecifics.

TABLE 2.2 Tests of main effects and interactions of three generalized linear mixed models derived from GPS-collar data and used to predict odds ratios of relative enrichment structure utilization by captive coyotes. Only GPS-collar points at enrichment structures were used.

Effect	df	X^2	*P*
Neutral over Ramp:			
Sex	1	1.18	0.29
Time of day	1	13.68	**< 0.01**
Time of day * sex	1	21.62	**< 0.01**
Closed over Ramp:			
Sex	1	1.84	0.19
Time of day	1	3.89	0.06
Time of day * sex	1	3.52	0.07
Closed over Ramp:			
Sex	1	0.15	0.70
Time of day	1	0.64	0.43
Time of day * sex	1	0.00	0.97

[a] Bold denotes significance at the 0.05 level.

TABLE 2.3 Odds ratio of enrichment structure utilization, lower and upper bounds for a 95% confidence interval for the odds ratio, and p-value for the test of whether the odds ratio is different than one. Bold denotes significance at 0.05.

Effect	Odds ratio	Lower bound	Upper bound	*P*
Ramp use over neutral use:				
Female over Male	1.12	0.91	1.37	0.29
Day over night	**2.21**	**1.43**	**3.43**	**0.00**
Day, Female over Male	**1.33**	**1.07**	**1.65**	**0.01**
Night, Female over Male	0.94	0.75	1.17	0.55
Female, Day over Night	**2.63**	**1.68**	**4.10**	**< 0.01**
Male, Day over Night	**1.86**	**1.19**	**2.90**	**0.01**
Ramp use over closed use:				
Female over Male	1.16	0.93	1.46	0.19
Day over night	1.73	0.98	3.06	0.06
Day, Female over Male	1.26	0.99	1.61	0.06
Night, Female over Male	1.07	0.84	1.37	0.58
Female, Day over Night	1.88	1.06	3.35	0.03
Male, Day over Night	1.59	0.90	2.84	0.11
Neutral use over closed use:				
Female over Male	1.06	0.76	1.48	0.70
Day over night	0.80	0.45	1.42	0.43
Day, Female over Male	1.07	0.76	1.50	0.71
Night, Female over Male	1.06	0.76	1.49	0.72
Female, Day over Night	0.80	0.45	1.43	0.44
Male, Day over Night	0.80	0.45	1.43	0.43
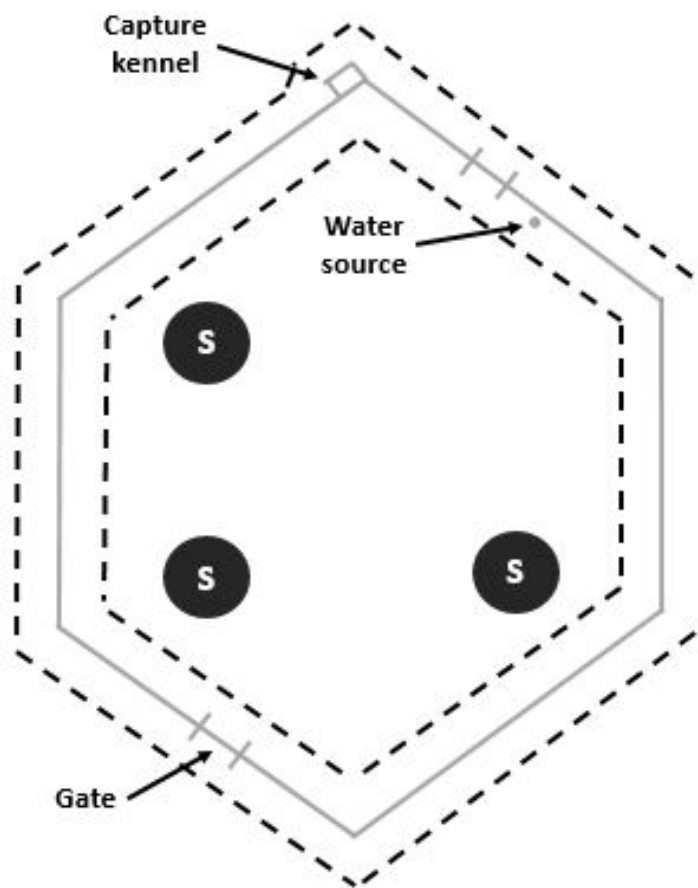
FIGURE 2.1 Enclosure used in January-March 2015 and 2016 for study on captive coyotes at the USDA-NWRC-Predator Research Facility in Millville, Utah. Locations of enrichment structures are depicted as S (dark circles denoting a 5-m buffer around the middle point of each shelter structure), perimeter as dashed lines (delineating a 5-m buffer on both sides of the enclosure fence to accommodate for GPS error), and open area as other interior space. Depiction is not to scale.

(a)

(b)

(c)
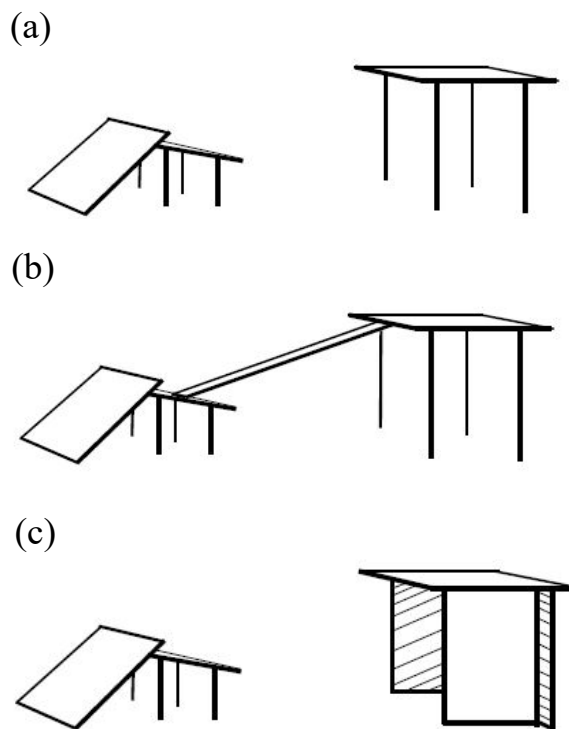
FIGURE 2.2 Sketches of three enrichment shelter structures provided to captive coyotes for testing: (a) neutral, (b) ramp, and (c) closed. Captive coyotes were previously exposed to shade tables, the shorter component of the enrichment structures, used in control enclosures.
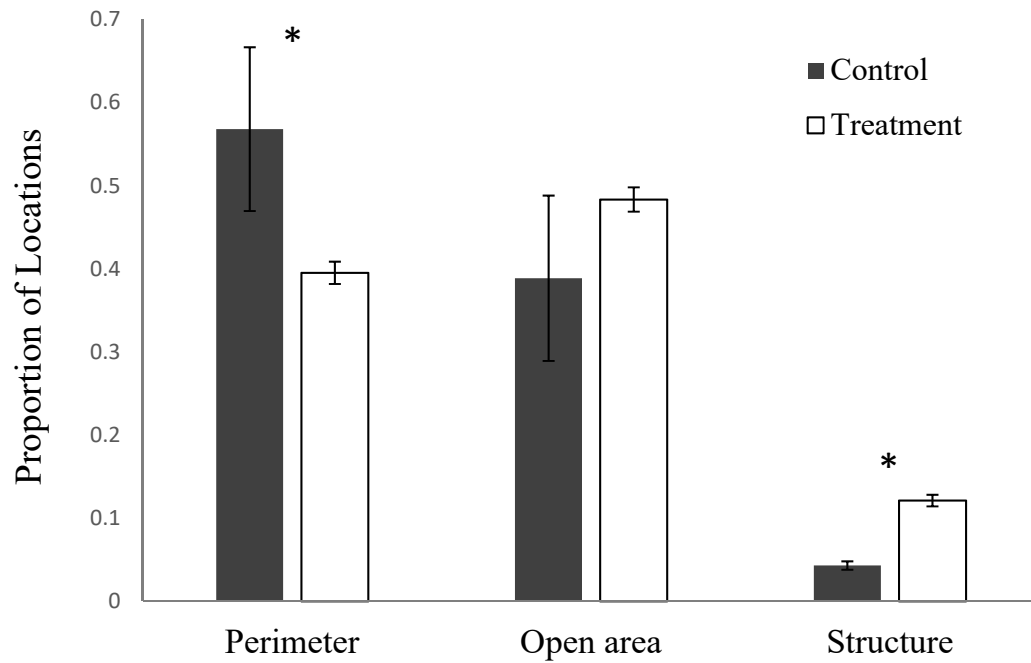
FIGURE 2.3 Average proportion of time spent at study enclosure features by mated pairs of captive coyotes. Three enrichment structures were installed in treatment enclosures while only two structures were in the control enclosures. Error bars represent standard error and (*) depict significant differences between control and treatment values.

(a)

(b)
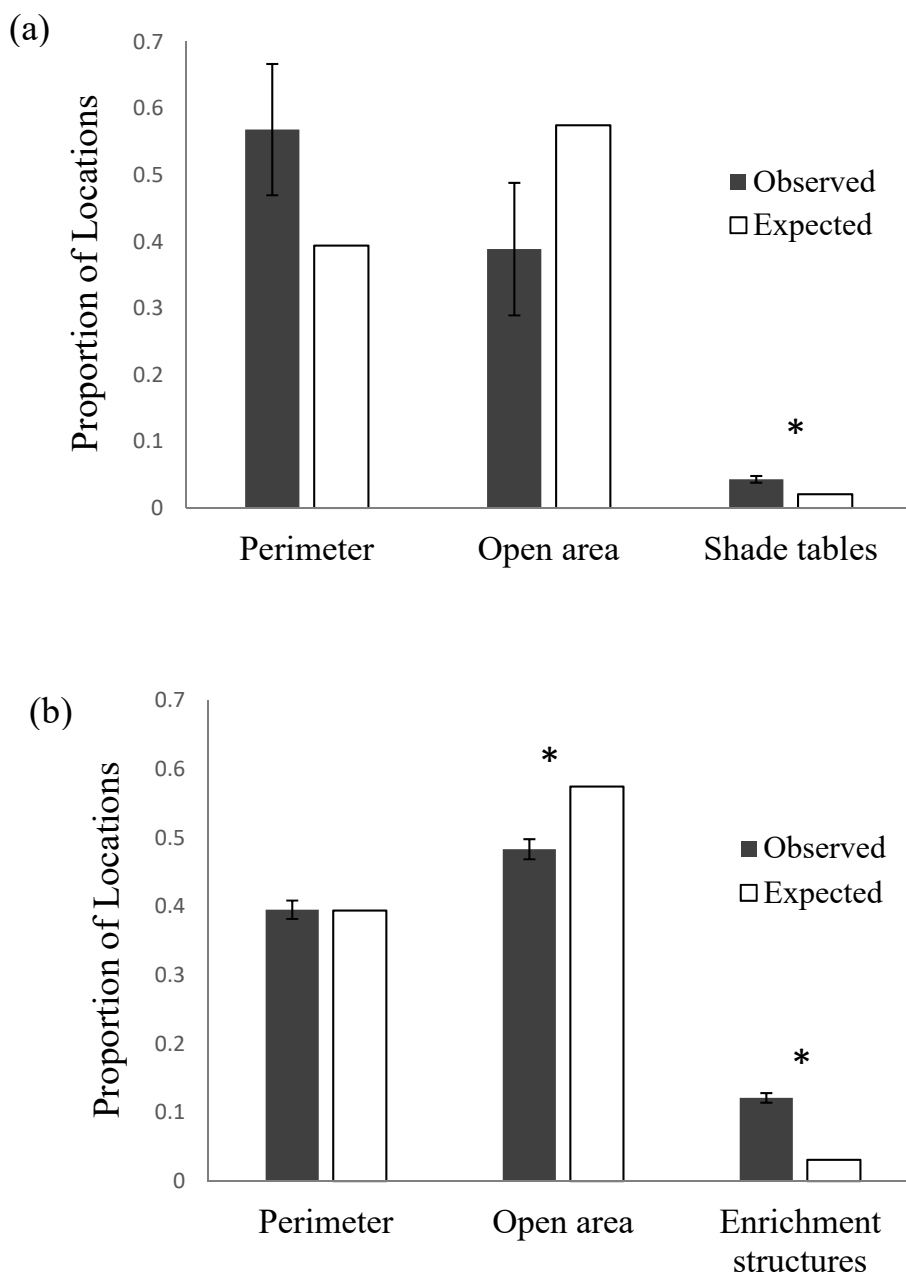
FIGURE 2.4 Average proportion of time spent at study enclosure features, compared to proportion of available space, for pairs of captive coyotes housed in (a) control and (b) treatment enclosures. Three enrichment structures were installed in treatment enclosures while only two structures were in the control enclosures. Error bars represent standard error and (*) depict significant differences between observed and expected values.
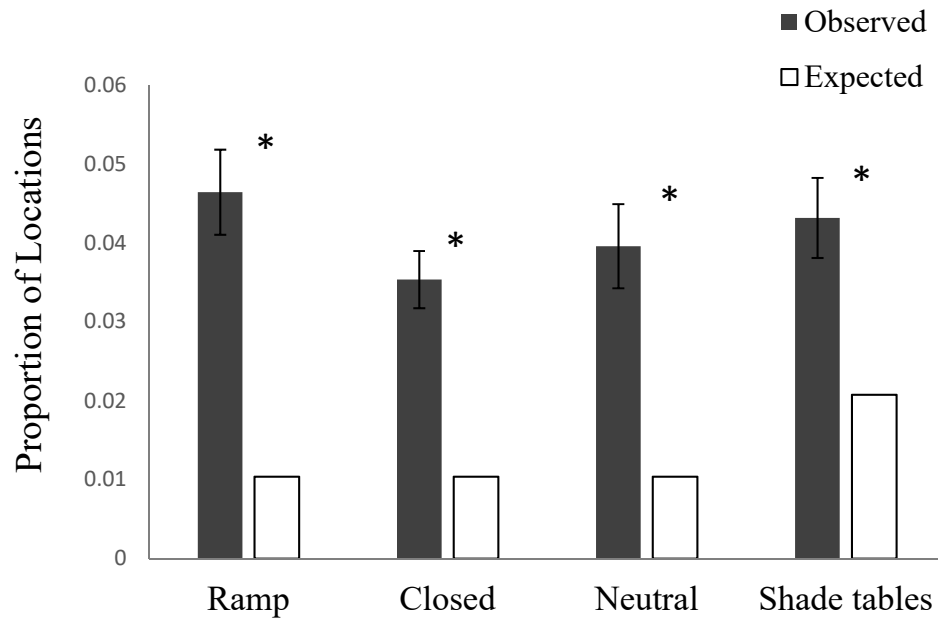
FIGURE 2.5 Average proportion of time mated pairs of captive coyotes spent at each type of shelter structure, compared to proportion of available space. One ramp, closed, and neutral structure was installed in each treatment enclosure while two shade tables were placed in each control enclosure. Error bars represent standard error and (*) depict significant differences between observed and expected values.
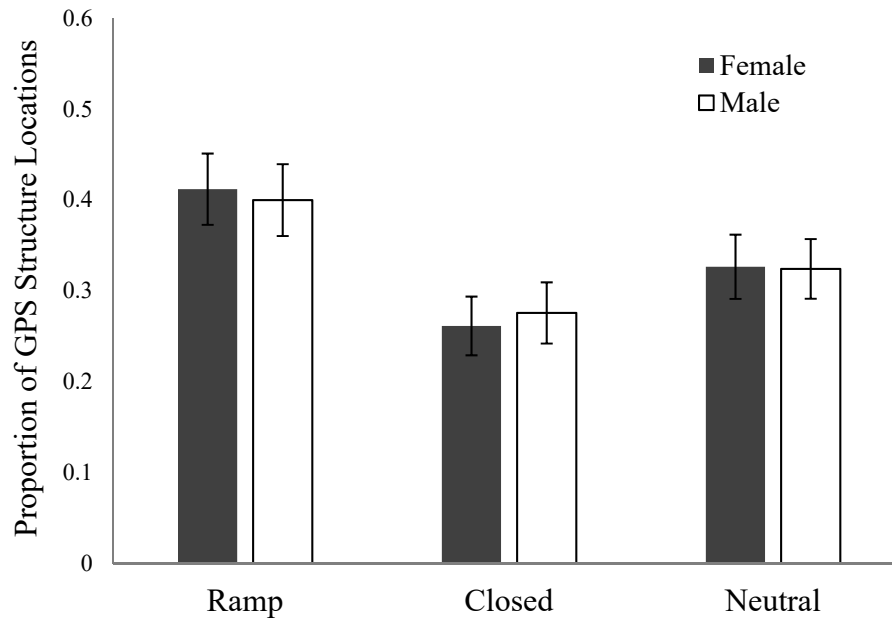
FIGURE 2.6 Mean average proportion of GPS-collar locations observed at each enrichment structure for captive male and female coyotes. Error bars represent standard error (SE) of individual mean proportions, and only GPS-collar locations at enrichment structures were used. Means and SEs shown are computed by descriptive statistics that used raw data and are not least squares means estimated by generalized linear mixed models.
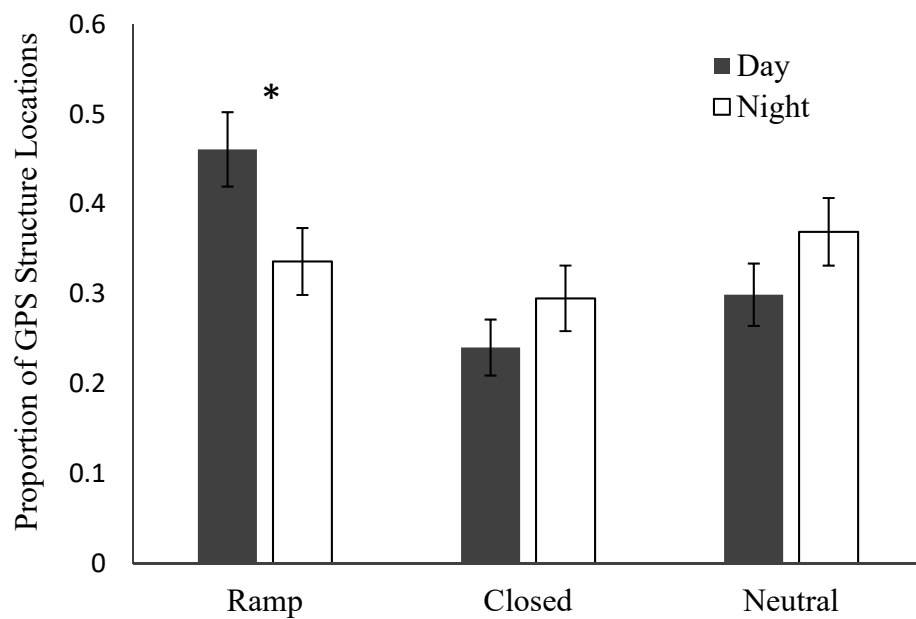
FIGURE 2.7 Mean average proportion of GPS-collar locations of captive coyotes at each enrichment structure by time of day. Error bars represent standard error (SE) of individual mean proportions, and (*) depict significant differences between daytime and nighttime values. Only GPS-collar locations at enrichment structures were used. Means and SEs shown are computed by descriptive statistics that used raw data and are not least squares means estimated by generalized linear mixed models.

CHAPTER 3

CAPTIVE COYOTE SPATIAL AND BEHAVIORAL RESPONSES

TO HUMAN ACTIVITY[2]

ABSTRACT

Human interactions can alter an animal's behavior and utilization of its surroundings, and how this impacts the welfare of some captive wild animals is of growing concern. Structural enrichment shelters offer weather protection or space for animals to separate themselves from interactions with other animals or humans. Some animals are naturally inactive for long periods of time and select for more complex environmental features. Additionally, animals may naturally utilize different features to perform specific behavior. This study addressed the effects of human activity on coyote behavioral budgeting and enclosure utilization. Coyotes were experimentally exposed to one hour of human activity and one hour with no human activity for 16 observation days. Scan sampling showed that captive coyote behavior and enclosure utilization changed in the presence of human activity. Human activity increased vigilant behavior while reducing inactive behavior. Additionally, coyotes utilized open areas and enrichment structures less and increased perimeter use during periods of human activity. This study illustrates that captive animals may switch activity levels in the presence of humans and may not choose more complex environments when active behaviors are stimulated. Thus, certain

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wild animals in captivity may benefit from having the choice to utilize multiple types of

habitat, depending upon their natural biological tendencies.

1. Introduction

Animal spatial patterns result from the availability and utility of resources, but are

also inextricably tied to behavioral motives. Correlating an animal's behavior to its use of

the landscape helps illustrate the utility associated with selected environmental features.

For instance, Gese et al. (1996) found that coyotes (*Canis latrans*) mainly rested and

hunted in grasslands and meadows and traveled on roads or riparian areas. In the winter,

coyotes actively select among available habitat for travel, disproportionately choosing to

use groomed trails (Dowd et al., 2014). An animal's behavior may change because food

resources, social organization, and physiology fluctuate across seasons (Bekoff and

Wells, 1981). It is also influenced by other species (Kitchen et al., 1999; Neale and

Sacks, 2001). For example, fine-scale environmental conditions that incorporated factors

such as predatory and anthropogenic threats best explained elk (*Cervus elaphus*)

movement patterns (Frair et al., 2005). The complexity of animal spatial and behavioral

relationships also depends on individual variability of movement strategies (Roshier et

al., 2008). Incorporating behavioral aspects into a thorough investigation of animal space

use is essential when an animal's perception and decision-making abilities can influence

selection.

Identifying the use and functionality of selected environmental features can provide

beneficial information for improving animal welfare of captive wildlife. A principal goal

of many captive animal facilities is to have behavior of captive animals resemble

behavior of wild counterparts. When captive wild animals retain wild behavior, it suggests satisfactory welfare (Gilloux et al., 1992). Where animals are captive for outreach and education, such as at zoos, animals exhibiting natural behavior will maximize visitor learning experience. Where facilities house captive animals for research, activity budgets of captive animals that mimic those of conspecifics in the wild can provide rationale to extend inference (Renner and Lussier, 2002; Shivik et al., 2009).

Captive animals may occasionally demonstrate unnatural behavior such as pacing, hair-pulling, or self-biting (Bayne, 2005). Although the occurrence of stereotypic behavior may insinuate insufficient welfare, it may be serving innate biological or physical functions (Mason, 1991). Demonstrations of non-wild behavior do not always indicate a decrease in welfare, since they may be modes for animals to attain control over their environment (Veasey et al., 1996). Even so, environmental enrichment can reduce incidences of some stereotypic behavior in captive animals (Shyne, 2006). The Association of Zoos and Aquariums (AZA, 2017) define enrichment as "a process to ensure that the behavioral and physical needs of an animal are being met by providing opportunities for species-appropriate behaviors and choices." Thus, environmental enrichment seeks to aid captive animals in matching the behavior of wild constituents by providing additional environmental choices that are biologically relevant. Enrichment can enhance an animal's ability to cope with acute stress and allow it to adapt to changing situations (Mellen and MacPhee, 2001). Evaluating spatial and behavioral animal responses to enrichment practices can improve the efficacy of enrichment programs.

Occurrences of human activity at captive animal facilities may disrupt behavior and activity levels of their inhabitants (Davey, 2007; Hosey, 2000). The presence of visitors

at zoos can influence an animal's behavior and space use (Kuhar, 2008; Mallapur et al., 2005; Sekar et al., 2008; Wells, 2005), and have additional effects when visiting groups are larger (Larsen et al., 2014; Woolway and Goodenough, 2017). Similar to zoos, animals at research laboratories must cope with human interactions caused by caretakers, researchers, maintenance crews, or visiting groups. Daily husbandry and maintenance interruptions range from being fairly innocuous to slightly intrusive. Visitor occurrences can increase abnormal behavior that ultimately impacts the welfare of some captive animals (Mallapur et al., 2005). Facilities should monitor animal responses to human activity to appropriately manage the frequency and magnitude of human interaction events. Predictability and control are important aspects of an animal's welfare (Bassett and Buchanan-Smith, 2007), and environmental enrichment may allow opportunities for captive animals to have more control of their surroundings when disruptive human activity occurs (Carder and Semple, 2008; Fernandez et al., 2009).

Coyotes are ubiquitous across the contiguous US and readily populate urban environments (Gehrt et al., 2009; Poessel et al., 2017). Responses to human interaction may vary among individual coyotes, but those living in urban areas typically co-occur with humans by partitioning their activity patterns, spatially or temporally, to maximize resources (Gehrt et al., 2009). Like urban coyotes, captive coyotes must cope with human interactions on a daily basis. To gain a clearer understanding of how captive coyotes respond to human activity, this study aimed to relate coyote behavior to the utility of different enclosure features during periods with and without human activity.

3. Material and Methods

2.1 Study overview

The study was conducted at the United States Department of Agriculture (USDA)-Wildlife Services (WS)-National Wildlife Research Center's (NWRC) Predator Research Facility in Millville, UT, USA, which houses over 100 adult coyotes in captivity as mated pairs for research purposes. Testing occurred during winter months (January – March) of 2015 and 2016. Thirty coyote pairs were randomly selected from all mated pairs in the captive colony. Males were vasectomized, per facility standard operating procedures, to prevent breeding prior to the study. Each pair was randomly assigned to an enclosure and subjected to the same treatment and control activity schedule. Research protocols were approved by the Institutional Animal Care and Use Committee at the National Wildlife Research Center (QA-2375) and Utah State University (Protocol #2490).

Eight 0.6 ha enclosures were utilized, consisting of two human access gates and an animal capture kennel (2 m x 3 m) with a concrete floor that was located at either the north or south corner (Fig. 3.1). Each enclosure was comprised of natural substrate, an automatic watering device situated adjacent to one of the gates, and two den boxes made of cylindrical PVC (0.5 m high x 0.5 m diameter) providing corn cob bedding (Green Products Company, Conrad, IA, USA) in each capture kennel. Only experimental enrichment structures were provided in the main enclosure area, and in-ground den holes were collapsed or otherwise made inaccessible during the study. The enclosures remained vacant for 1-3 days before new experimental coyote pairs were released into the enclosures to allow for shelter structure construction and feces removal. Coyotes were scatter-fed normal daily rations (650 g per animal) of a commercially prepared food (Fur

Breeders Agricultural Cooperative, Logan, UT, USA) in one specified area of each

enclosure, and water was available *ad libitum*.

2.2 Enrichment structures

Experimental enrichment structures were assigned to one of three predetermined

locations in the enclosures, spaced 40-55 m from each other and >10 m from the

perimeter fence (Fig. 3.1). They included two components: (1) a wooden shade table (to

which coyotes have had previous exposure) and (2) an additional plywood platform (1.2

m x 1.2 m) supported 1.2 m above the ground by four steel T-posts. Combining the two

components, each enrichment structure spanned 4 m in total length and were oriented in a

north-south direction. Enrichment structures either comprised of the basic two

components or had one extra feature (a ramp to access taller platform or three walls

around the T-post supports).

2.3 Behavioral observations

Scan sampling was used for all behavioral observations (Altmann, 1974) using an

innocuous mobile observation blind. Scans of each animal were conducted at 5-minute

intervals for two 1-hour blocks per day, four days per week, over the duration of a 28-day

period. One time block was randomly assigned to have human activity (i.e., driving an

ATV) among the other non-study enclosures at the facility, while human activity was

abstained during the other time block. Although the coyotes appeared to ignore the

observation blind, the observer arrived at the designated vantage point 15 minutes before

beginning observations to assure coyotes resumed their normal activities if they

responded to the blind. Start times were randomly selected between 08:00 and 15:00 to

ensure sufficient light for visibility. At each scan, the location and behavior of the study

coyote was logged. Coyotes were recorded at enrichment structures when they were

within 2 m of a structure, and were considered at the perimeter when they were within 2

m of the perimeter fence. Behavior was categorized into three groups: vigilant, inactive,

and active (Table 3.1). Only one person conducted all scans to eliminate inter-observer

variability.

2.4 Analysis

The proportion of scans at each location and behavior were averaged across all

individuals and reported with standard error (SE). Since the observed data did not follow

normal distributions, non-parametric Mann-Whitney U-tests were performed to

determine significant differences between the observed proportions at each condition of

human activity. To statistically assess how the distribution of coyote behavior differed

among locations and how human activity affected the distribution of behavior or

utilization of enclosure features, a generalized linear mixed model (GLMM) was fitted

with a negative binomial distribution. There was no apparent difference in behavior

between the male and female coyotes within a pair, so sex was not included as a predictor

variable in the model. The response variable was scan count, summed over all

observations for both coyotes in a pair. Behavior type (active/inactive/vigilant), enclosure

feature (perimeter/open/enrichment structure), and human activity (no/yes) were fixed

effects factors, and all interactions among these factors were included in the model. To

accommodate correlation due to clustering of scans within pairs, pair was included as a

random effects factor. Models were fitted using the glmmadmb function in the

glmmADMB package (Skaug et al., 2013) in Program R, version 3.3.2 (R Core Team, 2016). Means were estimated using the lsmeans function in the lsmeans package (Lenth, 2016), and comparisons among means were computed using the contrast function in the lsmeans package. Family-wise Type I error was controlled using the Tukey method. The significance threshold was set at 0.05.

4. Results

Human activity significantly increased perimeter utilization (U = 379.5, P < 0.01) while coyotes significantly decreased utilization of open areas (U = 2630, P < 0.01) and enrichment structures (U = 2763.5, P < 0.01) (Fig. 3.2a). Human activity significantly increased vigilant behavior (U = 30, P < 0.01) and significantly decreased inactive behavior (U = 3599, P < 0.01) (Fig. 3.2b).

The GLMM showed human activity significantly affecting coyote behavior and utilization of different enclosure features (Table 3.2). When there was no human activity, coyotes utilized open areas significantly more than enrichment structures (P < 0.01) and the perimeter (P = 0.02), with enrichment structures being used significantly less than the perimeter (P = 0.02). Vigilant and inactive behavior occurred significantly more than active behavior (P < 0.01) when there was no human activity. When human activity occurred, coyotes utilized perimeter and open areas significantly more than enrichment structures (P < 0.01). Human activity resulted in significantly more vigilant behavior than active or inactive behavior (P < 0.01), and coyotes were significantly more active than inactive with human activity (P < 0.01).

The GLMM also indicated significant variation in behavior at the different enclosure features (Table 3.2). At enrichment structures, coyotes were significantly more inactive and vigilant than active ($P < 0.01$). Open areas realized significantly more vigilance than active ($P < 0.01$) and inactive behavior ($P = 0.01$). Coyotes at the perimeter were also significantly more vigilant than active ($P = 0.0013$) or inactive ($P < 0.0001$), but were significantly more active than inactive ($P < 0.0001$). Although the GLMM did not support the significance of the third order interaction, proportions of behavior at each location were calculated for each condition of human activity (Fig. 3.3).

4. Discussion

This study examined the relationship between coyote behavior and their selection of certain environmental features. It also explored how behavior and utilization of different enclosure features changed with the presence or absence of human activity. Results show that captive coyotes dynamically respond to the presence of human activity, altering behavior and utilization of different features. Human activity notably generated higher occurrences of vigilant behavior and caused coyotes to utilize perimeters and open areas more than enrichment structures. Coyotes often appeared to be vigilant, regardless of their surrounding environmental conditions, and mainly inactive at enrichment structures and open areas. Behavior at the perimeter, aside from being mostly vigilant, was more active than inactive.

Understanding the relationships of how human activity affected coyote behavior at different enclosure features was interesting to explore. Coyotes may have been more active at the perimeter when humans were present to gain a better vantage point for

observing the human, which is supported by the accompanying increase in vigilant state, or it could be related to a natural tendency for coyotes to perform scent-marking behavior along the periphery of their territories (Gese and Ruff, 1997). Captive coyotes will often scent mark their enclosures and interact with neighbors while at the periphery (Schell et al., 2016). Although the third order interaction was not statistically significant in the GLMM, the model did support that behavioral and spatial distributions were each independently affected by human activity, and behavior was related to enclosure features.

Coyotes in this study spent slightly less than half of their time being inactive when there was no human activity. This is less time than observations of wild coyotes that reportedly spend upwards of 59% of their time resting (Gese et al., 1996). One possible explanation could be the differences in diurnal activity budgets between captive and wild coyotes. Another possible explanation could simply be due to slight differences in defining inactive behavior between studies. For example, captive coyotes that were laying but also displaying vigilance were recorded as being vigilant as opposed to inactive. Nonetheless, inactivity is a predominant natural behavior for coyotes, and captive facilities aiming to match wild behavior should monitor this phenomenon while not confusing it with the concept of animal boredom (Wemelsfelder, 1984).

When human activity occurred, coyotes shifted behavior from being highly inactive to predominantly vigilant, mostly with coyotes located at the perimeter instead of at enrichment structures. Accounts of vigilance toward humans by other wild animals in captivity have been interpreted to portray that the animals perceive humans as enemies, but have partially habituated to the circumstance (Hosey, 2013). A vigilant behavioral response differs from primates that may display increased aggressive behavior or felids

that typically remain unaffected by visitor presence (Hosey, 2013, 2008). Further examination into which direction (i.e., further from, closer to) coyotes moved in relation to the sources of human activity could better describe how they perceived human activity.

Some stereotypic behaviors (i.e., pacing, aggressive digging, grass pulling) were occasionally observed, insinuating a decrease in well-being (Mason, 1991; Shepherdson et al., 1993). Coyotes have been found to decrease the frequency of these non-wild behaviors with increased enclosure space (Brummer et al., 2010), and thus conducted the experiment in the largest enclosures at the research facility. Stereotypic behavior was more often observed with the presence of human activity and may be related to predictable signals (Bassett and Buchanan-Smith, 2007). Stereotypic behaviors in captive animals can result from excitement, anxiety, or frustration (Mason, 1991). Coyotes at the research facility are fed once daily from caretakers using ATVs. Even though ATVs are used outside of feeding, coyotes may still highly anticipate a feeding event and it is likely that stereotypic behavior in this study was food-related. Captive coyote behavior has been noticed to differ with the predictability of food (Gilbert-Norton et al., 2009), which may cause shifts in the utilization of different enclosure features.

Coyotes were located at enrichment structures more often and were mainly inactive when there was no human activity. Enrichment structures and open areas had similar counts of inactive behavior when no human activity was occurring. Since the enrichment structures occupied a comparably small proportion of enclosure space, it appears that coyotes actively selected for complex environmental features when resting during undisturbed conditions. Other species of captive animals have been shown to exhibit preferences for more complex environments. Indian leopards (*Panthera pardus*) housed

in more complex enclosures spent more time in the enriched areas compared to leopards

housed in less complex enclosures (Mallapur et al., 2002). Captive red foxes (*Vulpes*

vulpes) were also observed to utilize structurally enriched areas more than barren areas

(Kistler et al., 2010). This study found that enrichment structures were used less during

human activity events. Even though no in-ground dens were accessible, coyotes did not

appear to hide at the structures when human disruption occurred. Instead, the enrichment

structures were utilized for resting during periods of no human activity.

Recording and analyzing responses to environmental enrichment is critical for

evaluating and refining enrichment programs (Mellen and MacPhee, 2001). This study

will help to advance environmental enrichment practices for captive coyotes and possibly

other canids. Enrichment structures appear to be utilized for resting and vigilance. While

these results provide insight into winter responses of captive coyotes to human activity,

their behavior and enclosure utilization should also be evaluated in other seasons.

Coyotes clearly alter their behavioral and spatial tendencies in response to human

activity, indicating an inherent capacity to quickly adapt to changing environments. This

poses questions regarding their perception of humans and any risks or rewards they may

associate with instances of human interaction. Researchers could consider this when

designing future studies. Correlating animal behavior to the utilization of environmental

features adds an informative and realistic dimension to captive animal care and welfare.

Captive facilities should provide features that accommodate the natural tendencies of

their animals, and monitor behavioral responses to human activity events. This study

illustrates that captive animals may switch activity levels in the presence of humans and

may not utilize complex environments when active behaviors are stimulated. Thus, most

wild animals in captivity may benefit from having the choice to utilize multiple types of habitat.

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Table 3.1. Description of behavior categories from scan observations of captive coyotes during two, 1-hr blocks where one was with and one without human activity.

Behavior Category	Description
Vigilant	Laying, sitting, standing, walking, or running with head raised and visually surveying the environment.
Inactive	Laying and resting with head down or eyes closed (not vigilant); laying and grooming, sniffing or biting grass; sitting; standing and drinking or grooming.
Active	
General	Running; walking; pacing; digging; sniffing with nose close to the ground while walking or standing.
Social	Breeding activities (i.e., mounting, sniffing); dominant or subordinate playing or fighting; howling.
Territorial	Marking (i.e., urinating or defecating then scratching, laying and rolling); stalking conspecifics; tail flagging; fence running with vigilance directed at conspecifics.

Table 3.2. Tests of main effects and interactions of generalized linear mixed model derived from scan data and used to predict frequencies of enclosure feature and behavior distributions in relation to the absence or presence of human activity.

Effect	df	X^2	*P*
Human activity	1	41.1	**< 0.01**
Enclosure feature	2	115.7	**< 0.01**
Behavior	2	168.6	**< 0.01**
Human activity * behavior	2	182.6	**< 0.01**
Human activity * enclosure feature	2	10.6	**< 0.01**
Behavior * enclosure feature	4	226.2	**< 0.01**
Human activity * behavior * enclosure feature	4	3.1	0.53

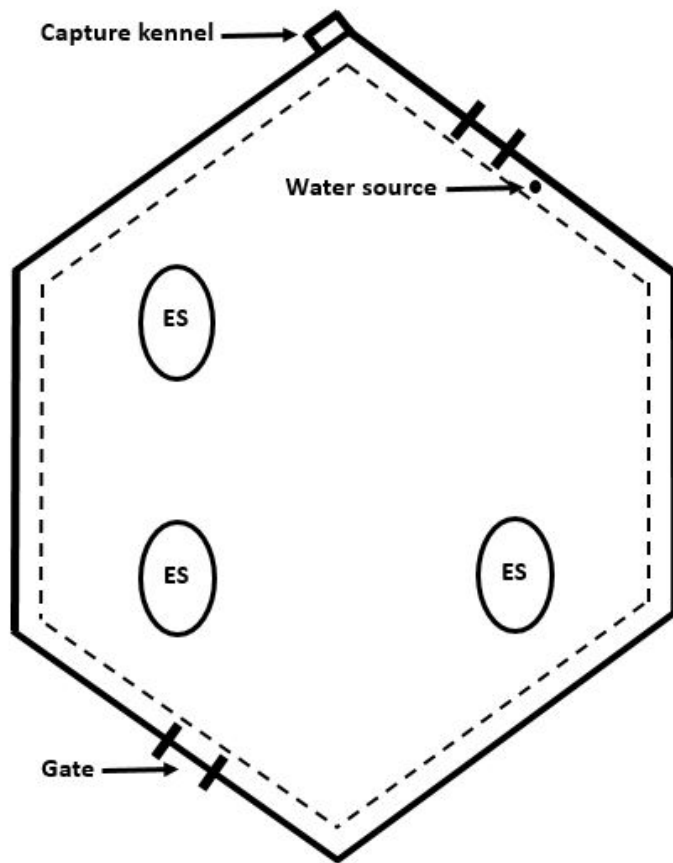[a] Bold denotes significance at the 0.05 level.

Fig. 3.1. Study enclosure for captive coyotes at the USDA-NWRC-Predator Research Facility. Enclosure features are depicted as ES (ovals denoting enrichment structure locations, perimeter (dashed lines delineating a 2-m perimeter zone that also incorporated a capture kennel located at one corner), and open area (other interior space). Depiction is not to scale.
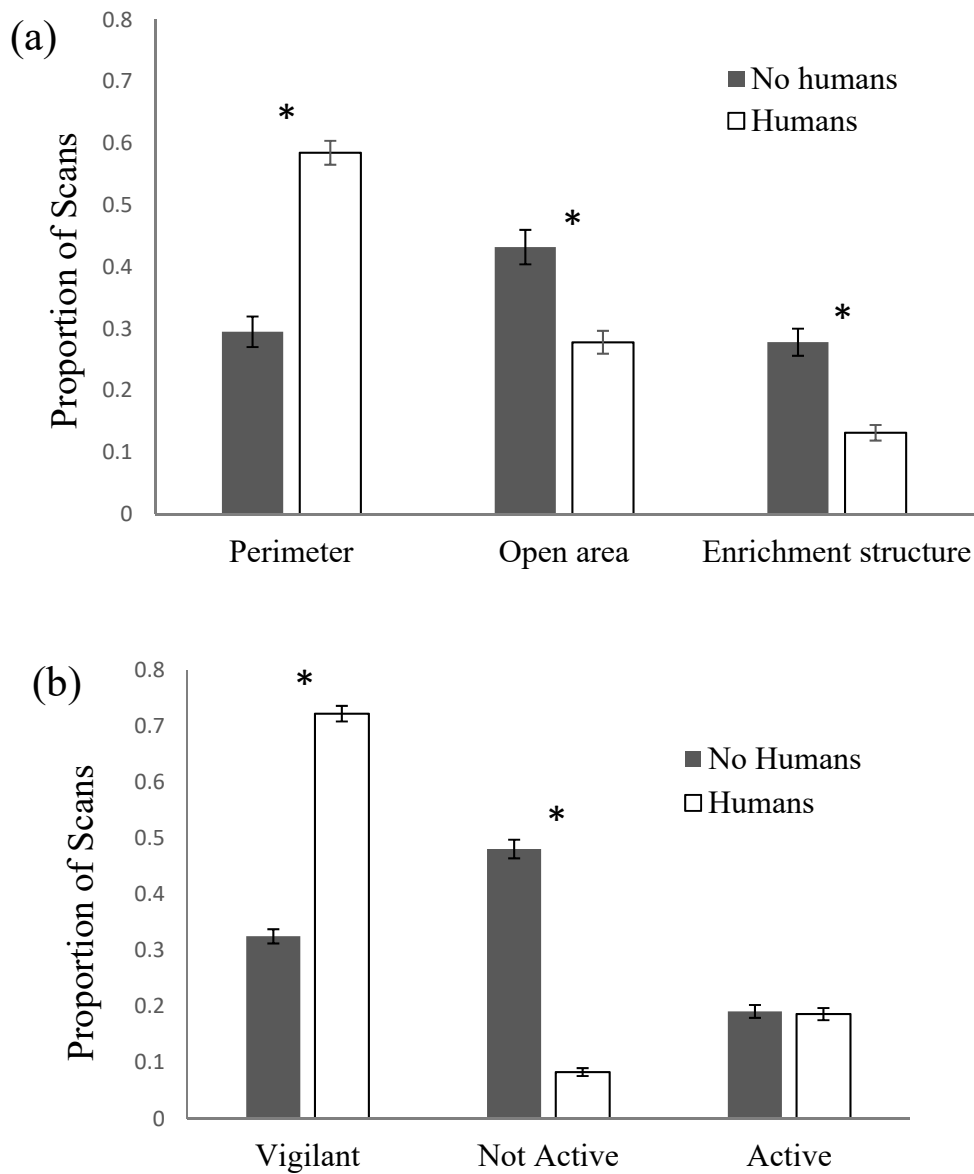
Fig. 3.2. Mean proportions of observed animal (a) enclosure features and (b) behavior with and without human activity. Error bars represent standard error (SE) of individual mean proportions and (*) signifies significant differences between periods with and without human activity. Means and SEs shown are computed by descriptive statistics that used raw data and are not least squares means estimated by the generalized linear mixed model.

Fig. 3.3. Mean average proportion of behaviors observed at each enclosure feature (a) without human activity and (b) with human activity. Error bars represent standard error (SE) of individual mean proportions. Means and SEs shown are computed by descriptive statistics that used raw data and are not least squares means estimated by the generalized linear mixed model.
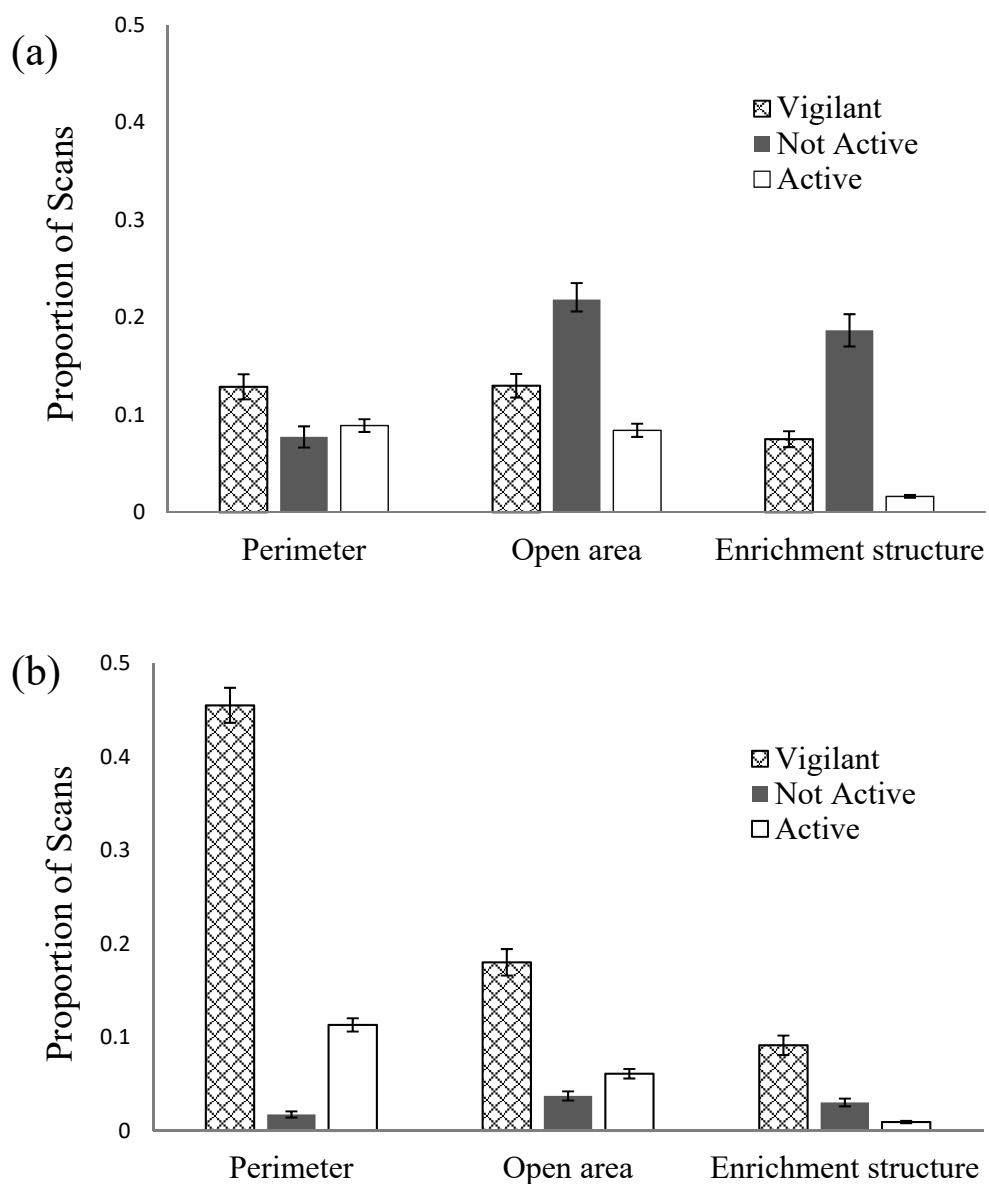
CHAPTER 4

CONCLUSIONS

This study provides valuable information on spatial and behavioral patterns

demonstrated by coyotes in captivity, and was the first to document the space use of

captive wildlife through the utilization of GPS-collars. Nearly two-thirds of the captive

population at the USDA-NWRC Predator Research Facility were examined. Each coyote

contributed up to 672 hours of GPS-collar data and 32 hours of behavioral information,

providing a robust sample from which conclusions were formulated. GPS-collars allowed

for the analysis of enclosure utilization throughout a 24-hour period, but lacked evidence

of animal behavior. Scan sampling revealed behavioral information to inform biological

functionality of different enclosure features, and compared behavior between periods

with and without human activity. Thus, both data recording methods had benefits and

limitations, that when combined, improved the evaluation of enclosure feature utilization,

enrichment structure preference, and the influence of human activity on these two

metrics.

Chapter two examined captive coyote enclosure utilization, focusing on selection of

discrete environmental features and whether captive coyotes showed a preference for a

particular enrichment structure design. Overutilization and underutilization of enclosure

areas have been specifically measured to describe enclosure appropriateness and animal

welfare of captive wild animals (Hunter et al., 2014; Ross et al., 2009). Although coyotes

naturally spend varying amounts of time exploiting different resources (Bekoff and

Wells, 1981; Gese et al., 1996), overutilization and underutilization of resources within

captive facilities change the functional size of enclosures. Comparing the proportion of time spent at enclosure features to the proportion of available space of the resource is a practical method to discern the selection of certain environmental features. Other captive animals have been shown to exhibit preferences for more complex environments (Kistler et al., 2010; Mallapur et al., 2002). Although coyotes were mainly located at perimeter and open areas of the enclosure, they overutilized shelter resources, suggesting these features have high biological value. Coyotes spent about twice as much time at the novel, more complex enrichment structures than at the smaller, familiar shade tables. Utilization of enclosure areas differed between enclosures with or without complex structures. Coyotes underutilized open areas in the treatment enclosures, and this may be due to a stronger selection for enrichment structures. Coyotes in treatment enclosures also spent less time at the perimeter than coyotes in control pens. A similar reduction in perimeter space use was observed in lion-tailed macaques when complex enrichment structures were introduced (Mallapur et al., 2005). This suggests structures improved well-being, since stereotypic pacing is often related to the peripheries of enclosures (Lyons et al., 1997).

Evaluating responses to environmental enrichment is critical for effective enrichment programs (Mellen and MacPhee, 2001). While a preference for one experimental enrichment structure did not materialize, some trends appeared. Behavioral scan observations, although only clustered during brief periods of daytime hours, showed that coyotes were more likely to be at the ramp structure than at the other two enrichment structures. This coincides with GPS-based model results that male and female coyotes used the ramp structure more during the day rather than at night. GPS data also showed

that when coyotes were located at an enrichment structure, they were more often at the ramp and least often at closed structures. Coyotes were mostly inactive at the enrichment structures, implying their suitability in offering comfortable protection from harsh environmental conditions common in winter. Vigilant behavior is routinely noticed in wild coyote populations, often in conjunction with resting (Bekoff and Wells, 1981). Similarly paired correlations were found in this study where vigilance was intermittently exhibited within longer-lasting inactive states, and was most frequently recorded at the ramp structure. In sum, all three complex enrichment structure designs may be considered appropriate for coyotes in captivity since they were each overutilized. All the tested enrichment structures provided additional protection from weather and visual exposure. However, if only one design is to be used, the ramp may be best because it provides additional resting space and better accommodates vigilant behavior with an accessible elevated platform.

Chapter three focused on captive coyote behavior in relation to human activity. When there was human activity, captive coyotes increased vigilant behavior and perimeter utilization. Perimeter utilization was associated with more active behavior than inactive behavior. This observation could be related to a natural tendency for coyotes to perform scent-marking behavior along the periphery of their territories (Gese and Ruff, 1997), as they often scent mark their enclosures and interact with neighbors while at the enclosure edges (Schell et al., 2016). Alternatively, coyotes use enclosure perimeters to gain a better vantage point to observe human activity. Accounts of vigilance toward humans by other wild captive animals have been interpreted to portray that the animals perceived humans as enemies, but have partially habituated to the circumstance (Hosey, 2013). A

vigilant response in canids differs from primates that can demonstrate aggressive behavior, or felids that typically remain unaffected by visitor presence (Hosey, 2008, 2013). Captive coyotes have been found to have increased heart rates at times of human interactions such as food delivery (Brummer et al., 2010). This response may occur whenever ATVs are operated and may be related to increased physical activity. Even when they are not being fed, they may still have elevated heart rates because of the association between ATVs and highly anticipated feeding events. With no human activity, coyotes exhibited inactive behavior nearly half the time, which has similarly been observed in wild coyotes (Gese et al., 1996). Thus, it is natural for some wild animals to rest for long periods and facility managers should not confuse this phenomenon with animal boredom (Wemelsfelder, 1984). Coyotes were observed at enrichment structures less frequently during human activity events, suggesting coyotes did not choose to retreat to the structures when human activity occurred. Instead, the enrichment structures were mainly utilized for resting during periods with no human activity. Behavioral evidence from this study suggests that while human activity reduces inactivity and enrichment structure utilization, coyote well-being did not appear to be impacted.

This study conveyed interesting patterns of enclosure utilization and behavior. Managers at this facility can feel confident about enhancing other enclosures with any of the three tested designs, although the ramp may be considered the most functional. A ramp design with a wall feature may also beneficially serve dual purposes of additional protection from weather and a top platform for vigilant and resting behavior. While GPS-collars provided insight into enclosure space use, future studies could depict fine-scale

distribution of coyote spatial utilization in relation to enclosure areas, rather than a broad focus on features. Because the GPS-collars in this study had unaccounted for error around GPS locations, it was not possible to analyze fine-scale space use, even though this approach could provide a clearer picture of where coyotes were positioned in relation to sources of human activity. Alternative modes and frequencies of human activity could also be explored, along with measurements of how coyotes respond to enrichment structures and human activity when housed in smaller enclosures.

By studying spatial and behavioral responses of captive coyotes, this study evaluated the functionality and biological value of features in their enclosures. Information presented from this research can be used to improve structural enrichment at other captive facilities and to guide similar assessments of the utility of environments provided.

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