

RESEARCH ARTICLE

An Investigation Into The Prevalence of Exploratory Behavior in Captive Cheetahs (*Acinonyx jubatus*)

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Exploratory behavior in the wild is fundamentally linked to an animal's survival and natural life history. The ability to gather information about their environment, establish territories, assert dominance, communicate information regarding reproductive status and locate mates are closely associated with a range of exploratory behaviors. Understanding how these behaviors are performed within the captive setting is crucial in order to create a captive environment in which these behaviors can be expressed, and their function conserved. The objective of this research was to highlight the factors of captive husbandry and management that influence the occurrence of exploratory behaviour of cheetahs (*Acinonyx jubatus*) in captivity. One hundred and twelve cheetahs in 88 enclosures across nine zoological institutions in five countries were the subjects of this study. The presence of raised areas, number of movements between enclosures, group composition, sex and an interaction between group composition and the ability to view cheetahs in adjacent enclosures, all significantly influenced the prevalence of exploratory behavior in captive cheetahs. The presence of raised areas and an increasing number of movements between enclosures significantly increased the probability of observing exploratory behaviour, while this probability was significantly decreased for female cheetahs, when cheetahs were able to view conspecifics in adjacent enclosures, and were maintained in groups. A number of recommendations are discussed in relation to promoting exploratory behavior in captive cheetahs. Zoo Biol. 34:130–138, 2015. © 2014 Wiley Periodicals, Inc.

INTRODUCTION

Exploratory behavior is an essential type of information gathering and presentation behavior. Toates [1983] stated that 'exploration serves to establish and continuously refine the animal's 'cognitive map' with respect to food sources, aversive stimuli and other relevant dimensions of the environment'. Of particular significance is exploratory behavior in the form of olfaction and scent-marking which can serve to advertise an animal's reproductive status, delineate territories, assert dominance and locate mates. Additionally, the presentation of scents and faeces, in combination with scuffing, cheek rubbing and tree scratching contribute to an animal's exploration of an area by allowing an animal to gather information on when and where it has previously been on territory patrols in a given area. Providing a captive environment within which these behaviors can be performed is highly desirable, as it allows animals to express a full array of natural behaviors. Olfactory stimuli are often integrated into environmental enrichment programmes within zoos in order to increase levels of exploratory behavior. This olfactory enrichment can refer to the addition of scents or scented material to enclosures [Swaigood and Shepherdson, 2005]. Scents include food scents, herbs and spices, essential oils and faeces/urine of other animals. A

number of experiments utilizing olfactory enrichment as well as food enrichment have reported changes in levels of exploratory behavior within the captive setting [Shepherdson et al., 1993; Powell, 1995; Schuett and Frase, 2001; Pearson, 2002; Wells and Egly, 2004; Quirke and O' Riordan, 2011a, b]. These studies demonstrated that exploratory behavior can be significantly influenced by environmental enrichment. However, very few studies have examined in detail what other factors within the captive environment impact upon the prevalence of exploratory behaviors.

Scent-marking via urine spraying is the main form of olfactory communication in felids [Estes, 1992]. The basic marking technique begins with the cat intently sniffing the place to be marked. If the area has been marked before, the

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cat will often grimace, which may then be followed by rubbing its head against the object in question. Finally, the cat backs up and sprays its urine on the spot [Estes, 1992]. Other olfactory communication behaviors include scuffing, which can be described as a rhythmic treading and forward kicking motion of the hind feet. This may be accompanied by urination which mixes the urine with the substrate and impregnates the hind feet with odour [Estes, 1992]. Head rubbing, rolling, defecation and claw sharpening also serve as forms of olfactory communication, with the significance and frequency of occurrence of each dependent upon species [Eaton, 1970; Schaller, 1972; Leyhausen, 1979; Estes, 1992; Bothma and Le Riche, 1995]. Cheetahs (*Acinonyx jubatus*) in the wild spend much time searching for, smelling and depositing their own scent on previously marked places, with elevated areas and other landmarks such as trees or boulders frequently used as both observation and scent posts [Eaton, 1974; Estes, 1992].

In recent years, there has been substantial research carried out on the causes, possible functions and methods with which to minimize or eradicate stereotypical behavior in captive animals. Undoubtedly, this animal welfare issue is highly important, but so too is an understanding of the factors determining the prevalence of natural species-typical behaviors within the captive setting. Conserving the natural repertoire of behaviors is as crucial as the conservation of the species. The performance of natural behaviors in captivity represents an opportunity for researchers and zoological institutions to gain knowledge about these behaviors and to educate the public, while also ensuring that the animals are experiencing conditions indicative of good welfare. The objectives of this research were to 1) highlight which factors relating to captive husbandry and management influence the occurrence of exploratory behavior and 2) discuss how these could be altered or manipulated in order to promote the occurrence of natural exploratory behaviors.

METHODS

Study Sites and Animals

One hundred and twelve cheetahs, maintained in 88 enclosures were the subjects of this study. Data were collected on cheetahs kept in nine zoological institutions namely, Africa Alive, Banham Zoo, Chester Zoo, Colchester Zoo, ZSL Whipsnade Zoo in the UK, Fota Wildlife Park in Ireland, Toronto Zoo in Canada, the Cheetah Conservation Fund in Namibia and the Ann van Dyk Cheetah Centre in South Africa. Institutions had been selected based on the number of cheetahs they maintained, as well as differences in the factors examined during the study (Table 1). Fifty-seven cheetahs were male and fifty-five were female. Forty five were solitary and sixty seven were maintained in groups during the duration of the study. Table 2 highlights the composition of the groups. Of these, ten of the animals belong to the northern subspecies of cheetah (*Acinonyx*

jubatus soemmeringii) and the remainder belong to the southern subspecies (*Acinonyx jubatus jubatus*). Ages ranged from 1 year to 15 years of age. Throughout the study, no cheetahs were on contraceptives, were involved in breeding introductions or were pregnant. In terms of seasonality, data were collected in Summer and Winter in the five institutions in Ireland and the UK, Autumn in Toronto Zoo and Winter in the two southern African institutions. Each enclosure experienced low temperatures and high temperatures throughout data collection. Temperature data were collected at one point (1pm) each day of data collection. The minimum temperatures recorded ranged from 3°C (Toronto zoo – Canada) to 9°C (Cheetah Conservation Fund – Namibia) whilst maximum temperatures recorded ranged from 18°C (Fota Wildlife Park – Ireland) to 26°C (Cheetah Conservation Fund – Namibia). This resulted in a narrow mean temperature range (10°C (Fota Wildlife Park – Ireland) – 17°C (Cheetah Conservation Fund – Namibia)) across the nine institutions during data collection periods.

Data Collection

Data were collected on exploratory behavior using instantaneous scan sampling with a 5 minute inter-scan interval. Exploratory behavior included olfaction, which was defined as the sniffing of any object within an enclosure, and also scent-marking, which was defined as the spraying of urine on or towards any prominent feature within an enclosure as well as scuffing, tree scratching and cheek rubbing. At Africa Alive, Banham Zoo, Colchester Zoo, Chester Zoo, ZSL Whipsnade, Toronto Zoo and Fota Wildlife Park, data were collected between 08:00 hr and 18:00 hr. Data collection during the winter months in Africa Alive, Banham Zoo, Colchester Zoo and Fota Wildlife Park was shortened to between 08:00 hr and 17:00 hr due to closing times of the zoos, cheetahs being put in their night dens, and the fact that no researchers were permitted to remain on zoo grounds after closing hours. Behavior data were collected between November 2008 and October 2010. Data were collected between 07:00 hr and 17:00 hr at the Ann van Dyk Cheetah Centre and at the Cheetah Conservation Fund. Each day was divided into a number of 2 hr periods (e.g.; 08:00–10:00 hr, 10:00–12:00 hr, 12:00–14:00 hr, 14:00–16:00 hr, 16:00–18:00 hr), consisting of eight 15-min time periods. For each day of data collection, a random number generator was utilised in order to select the time period in which data collection would occur for an enclosure, the start time of sampling for each enclosure and the number of samples to be collected in that time period for that enclosure. A maximum of ten scan samples were carried out in each time period for each enclosure in 1 day. No more than three time periods were sampled in any one day. This was to ensure even distribution of data collection during the hours of the day and days of the week throughout this research. A total of thirty scan samples were carried out for each two-hour period for each enclosure in each institution. For enclosures

TABLE 1. List of covariates recorded at each institution. Categorical covariates coded as factors in lme4 in R

Covariate	Abbreviation	Continuous/Categorical
Enclosure size	Size	Continuous
Visual barriers	Visual	Continuous (1–10 scale, 10 being many visual barriers)
Presence of raised areas	Raised	Categorical (1 = not present, 2 = present)
Visitor numbers	Visitors	Continuous
Feeding predictability	Feeding	Categorical (1 = predictable, 2 = unpredictable)
Ability to view cheetahs in other enclosures	Oc	Categorical (1 = no, 2 = yes)
Ability to view other animals other than cheetahs	Other	Categorical (1 = no, 2 = yes)
Presence of enrichment	Enrichment	Categorical (1 = not present, 2 = present)
Group composition	Group	Categorical (1 = solitary, 2 = in group)
Sex	Sex	Categorical (1 = male, 2 = female)
Enclosure movements	Enclosure	Continuous
Vehicle disturbance	Vehicle	Continuous
Diet diversity	Diet	Continuous
Age	Age	Continuous

with more than one individual, a scan was conducted for the entire enclosure to create a single data point for behavior within a given enclosure and its associated factors. Each enclosure represents an observation (unit) in this study.

Data Analysis

Before applying any statistical models, data exploration was carried out following the protocol described in Zuur et al. [2010]. The presence of outliers in the response and

continuous covariates was investigated with Cleveland dotplots. Scatterplots between each continuous covariate and the response variable were made to detect the type of relationships. A list of all covariates is presented in Table 1.

Collinearity (relationships between covariates) was assessed with variance inflation factors (VIF). Temperature was not included as a covariate for a number of reasons. Firstly, temperature data were collected at one point per day so the temperature data did not match the structure of behavioral observations which were randomly assigned to

TABLE 2. Description of cheetah groups

Group	Group size	In group with	Location
Males groups			
1	2	Siblings	Banham Zoo
2	2	Siblings	Whipsnade ZSL
3	2	Siblings	Africa Alive
4	3	Siblings	Chester Zoo
5	3	Sibling and non-sibling	Fota Wildlife Park
6	2	Siblings	Ann van Dyk
7	2	Siblings	Ann van Dyk
8	2	Siblings	Ann van Dyk
9	2	Siblings	Ann van Dyk
10	2	Siblings	Ann van Dyk
11	4	Siblings and non-siblings	CCF
12	5	Siblings and non-siblings	CCF
13	3	Siblings	CCF
14	2	Siblings	CCF
15	2	Siblings	Toronto Zoo
Female groups			
1	2	Siblings	Africa Alive
2	2	Siblings	Fota Wildlife Park
3	3	Siblings	Fota Wildlife Park
4	2	Siblings	CCF
5	2	Siblings	CCF
6	4	Sibling and non-sibling	CCF
7	2	Siblings	CCF
8	3	Siblings	Toronto Zoo
Mixed sex groups			
1	2	Non-sibling	Africa Alive
2	5	Mother and cubs	Fota Wildlife Park

different times of day. Additionally, within-day variability in temperature meant that accurate temperature data was not available for all time periods in which behavioral observations were carried out. The narrow average temperature range (10–17°C) across the institutions also contributed to temperature being omitted as a covariate.

The total number of times exploratory behavior was observed for each enclosure was modelled using a generalized linear mixed model (GLMM) with a binomial distribution:

$$SB_{ij} \sim \text{Bin}(\pi_{ij}, N_{ij})$$

SB_{ij} is the number of times that exploratory behavior was observed for the j th observation in zoo i , out of the N_{ij} number of scan samples conducted, and π_{ij} is the probability of success (i.e., the probability that exploratory behavior is observed for observation j in zoo i). To model this probability, the following logistic link function was used:

$$\text{logit}(\pi_{ij}) = \text{Covariates} + a_i + \epsilon_{ij} \sim N(0, \sigma_{zoo}^2) \text{ and } \epsilon_{ij} \sim N(0, \sigma^2)$$

The random intercept a_i introduces a correlation structure between all observations (enclosures) from the same zoo, and ϵ_{ij} allows for overdispersion [Zuur et al., 2009] and is also called an observation level random effect. All continuous covariates were standardised as this improves the numerical optimisation process of the GLMM. To find the optimal set of covariates, an Information Theory approach was followed [Burnham and Anderson, 2002]. Table 3 shows the 10 models that were applied. All 10 models were decided upon a priori. The package lme4 [Bates and Maechler, 2011] in the software R version 3.0.1 was used to estimate the parameters of the GLMMs. Degrees of freedom were calculated based upon the number of enclosures (88) in the

study. The alpha level for statistical significance was taken to be <0.01 .

RESULTS

All forms of exploratory behavior, namely, olfaction and scent-marking via urine spraying, tree scratching and cheek rubbing were observed throughout the study. Exploratory behavior was observed in 81 of 88 enclosures. The mean proportion (\pm SE) of scan samples in which this behavior was observed was 0.02 (\pm 0.002). The highest proportion of exploratory behavior observed in a single enclosure was 0.11. The use of an information theory approach, utilizing a collection of models with a variety of combinations of covariates, was in order to identify the optimal set of factors which determine the prevalence of exploratory behavior in captivity (Table 3).

The data exploration indicated that none of the variables contained outliers. VIF values indicated the presence of collinearity and we decided not to include the covariates, visual barriers and diet diversity. VIF values of all remaining covariates were smaller than 3. The scatterplots indicated no strong non-linear patterns between the continuous covariates and the response variable. Application of initial models without the observation level random effects resulted in over dispersed GLMMs, hence the reason we included ϵ_{ij} . The number of regression parameters, AICs, difference in AIC values and Akaike weights for each model are given in Table 4.

The Akaike weights of models M2, M1 and M6 are 0.543, 0.254 and 0.105, respectively (Table 4). A value of 1 signified the perfect model. Therefore, this means, that if similar behavioral sampling would take place a large number of times, then in 54.3% of the cases, model M2 (All zoo factor model with selected interactions) is the most optimal

TABLE 3. Models applied

Model	Code	Description
M1	Size+Raised+Visitors+Feeding+Oc+Other+Enrichment+Group+Sex+Enclosure+Vehicle+Age	All zoo factor model
M2	Size+Raised+Visitors+Feeding+Oc+Other+Enrichment+Group+Sex+Enclosure+Vehicle+Age+Size:Oc+Group:Sex+Size:Sex+Oc:Group+Sex:Age+Enrichment:Sex	All zoo factor model with selected interactions
M3	Sex+Group+Age+Oc	Sex/Group/Age model
M4	Sex+Group+Age+Oc+Sex:Group+Sex:Age+Sex:Oc+Group:Age+Group:Oc+Age:Oc	Sex/Group/Age model with interactions
M5	Vehicle+Visitors+Other+Group+Oc+Enclosure	Disturbance model
M6	Group+Sex+Age+Raised+Enrichment	Enrichment model
M7	Group+Sex+Age+Raised+Enrichment+Enrichment:Sex+Enrichment:Group+Enrichment:Age+Enrichment:Raised	Enrichment model with interactions
M8	Size+Oc+Other+Feeding+Group+Sex+Age+Enclosure	Ranging model
M9	Size+Oc+Other+Feeding+Group+Sex+Age+Enclosure+Size:Oc+Group:Sex+Size:Sex+Oc:Group+Sex:Age	Ranging model with selected interactions
M10	Feeding+Size+Sex+Enrichment+Feeding:Size+Feeding:Sex+Feeding:Enrichment+Sex:Enrichment+Size:Sex	Feeding model with selected interactions

: indicates an interaction between covariates

TABLE 4. Comparison of alternative models for exploratory behavior

Model	<i>df</i>	AIC	AIC differences	Akaike weights (<i>w</i>)
M1	15	139.082	1.519	0.254
M2	21	137.562	0	0.543
M3	7	144.446	6.883	0.017
M4	13	143.592	6.029	0.027
M5	9	159.223	21.660	0
M6	8	140.853	3.290	0.105
M7	12	144.630	7.068	0.016
M8	11	146.890	9.328	0.005
M9	16	143.313	5.751	0.031
M10	12	147.750	10.188	0.003

model, and in 25.4% and 10.5% of cases, models M1 (All zoo factor model) and M6 (Enrichment model) respectively are the most optimal models.

The covariates, presence of raised areas (raised), the ability to view other cheetahs in adjacent enclosures (oc), group composition (group), sex (sex), enclosure movements (enclosure) and the interaction between group composition (group) and the ability to view other cheetahs in adjacent enclosures (oc) were significantly different from 0 at the 1% level in model M2 (Table 5). The covariates, presence of raised areas (raised), sex (sex) and enclosure movements (enclosure) were significantly different from 0 at the 1% level in model M1, while the covariates, presence of raised areas (raised) and sex (sex) were significantly different from 0 at the 1% level in model M6 (Table 5).

Figure 1 shows a visual representation of the most optimal model (M2). The probability of observing exploratory behavior increased with the presence of raised areas and an increased number of enclosure movements (Fig. 1). The probability of observing exploratory behavior was lower for female cheetahs, cheetahs who had the ability to view other

cheetahs in adjacent enclosures, and cheetahs maintained in a group (Fig. 1).

Figure 2 highlights that solitary cheetahs perform more exploratory behaviors compared to those in groups when other cheetahs in adjacent enclosures cannot be seen. Solitary cheetahs who cannot view other cheetahs in adjacent enclosures also perform more exploratory behaviors than those solitary cheetahs that can view other cheetahs. In contrast, cheetahs maintained in groups show a higher level of exploratory behavior when they can view other cheetahs compared to other cheetahs in groups who cannot view other cheetahs in adjacent enclosures.

DISCUSSION

Swaigood [2007] highlighted that good welfare is often associated with a diversity of 'normal' behaviors. During this study, a diverse array of natural cheetah behaviors were observed. Although exploratory behavior was not a very common behavior, on average, accounting for 2% of the activity budget across 88 enclosures, it was significantly influenced by a number of factors. Olfaction,

TABLE 5. Estimated parameters and *p* values for each covariate for the three most optimal models for exploratory behavior

	M2	M1	M6
Size	0.002 (0.98)	-0.084 (0.37)	—
Raised	0.586 (0.00005)	0.59 (0.00004)	0.348 (0.01)
Visitors	-0.114 (0.09)	-0.125 (0.06)	—
Feeding	-0.458 (0.02)	-0.442 (0.02)	—
Oc	-0.715 (0.006)	-0.220 (0.25)	—
Other	0.059 (0.74)	0.018 (0.92)	—
Enrichment	0.011 (0.95)	-0.057 (0.72)	0.048 (0.75)
Group	-0.822 (0.007)	0.014 (0.92)	0.110 (0.46)
Sex	-0.661 (0.001)	-0.371 (0.001)	-0.477 (0.0002)
Enclosure	0.181 (0.01)	0.189 (0.01)	—
Vehicle	0.106 (0.10)	0.141 (0.03)	—
Age	0.078 (0.31)	0.055 (0.38)	-0.026 (0.71)
Size: Oc	-0.025 (0.85)	—	—
Group: Sex	0.631 (0.02)	—	—
Size: Sex	-0.187 (0.10)	—	—
Group: Oc	0.859 (0.006)	—	—
Sex: Age	0.138 (0.26)	—	—
Enrichment: Sex	-0.047 (0.85)	—	—

Values in bold represent values that were significant at the 1% level.

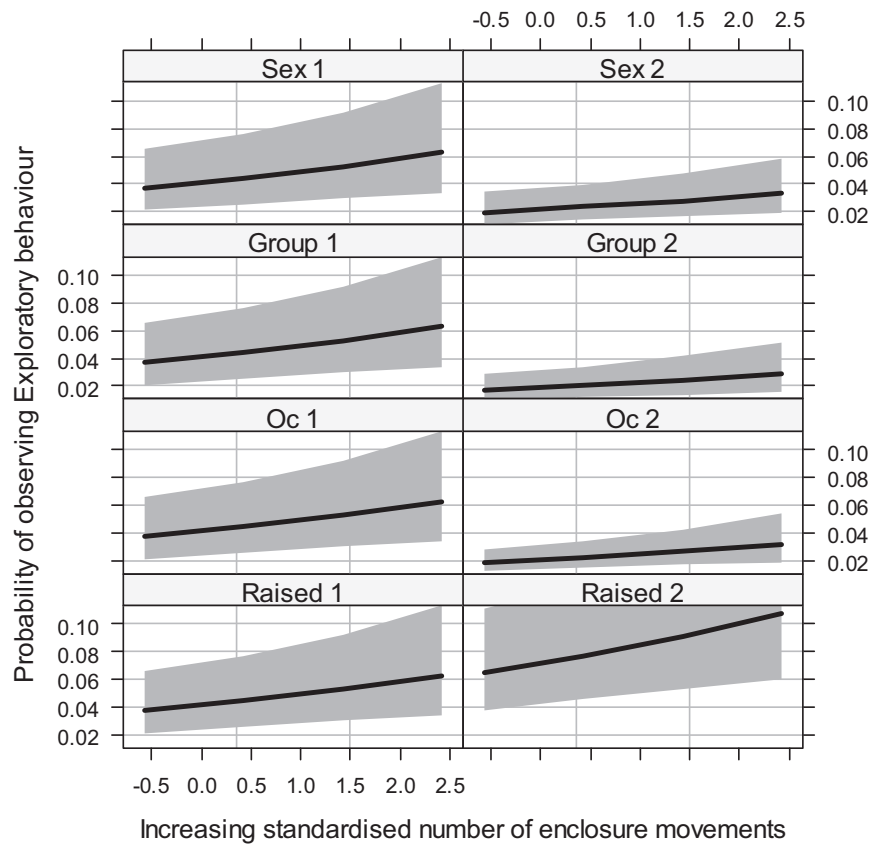


Fig. 1. Visual representation of optimal model, M2 showing the effect of raised areas, ability to view other cheetahs, group membership, sex and enclosure movements on the probability of observing exploratory behavior. (Raised 1 = Raised areas absent, Raised 2 = Raised areas present, Oc 1 = cannot view other cheetahs in adjacent enclosures, Oc 2 = can view other cheetahs in adjacent enclosures, Group 1 = solitary, Group 2 = maintained in a group, Sex 1 = male, Sex 2 = female).

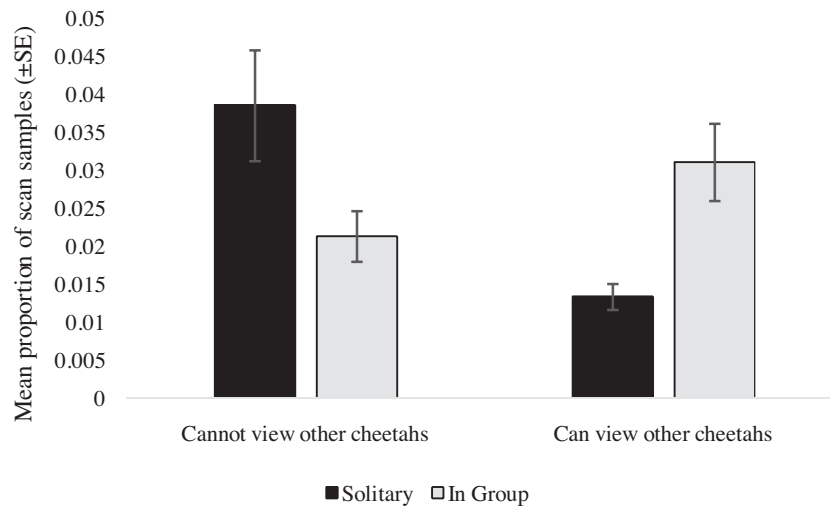


Fig. 2. Mean proportion of scan samples (\pm SE) in which exploratory behavior was observed for solitary cheetahs (Group 1) and cheetahs in groups (Group 2) when other cheetahs cannot be seen in adjacent enclosures (Oc 1) and can be seen in adjacent enclosures (Oc 2).

then scent-marking were the most common forms of exploratory behavior observed, followed by scuffing, tree-scratching and cheek-rubbing. It is important to note that, in the wild, behaviors which make up exploratory behavior, in particular, olfaction and scent-marking, both precede and facilitate the occurrence of mate location, assessment of reproductive status and territory delineation, each of which is of fundamental importance in the life history of cheetahs. Therefore, it is a priority to understand how these behaviors are expressed in captivity and to ensure that they can be continually expressed in an appropriate way within the captive setting.

The presence of raised areas within an enclosure resulted in a significant increase in levels of exploratory behavior with cheetahs frequently utilizing raised areas for olfaction and scent-marking. Raised areas were classified as platforms, high mounds, strategically placed logs, and trees in which access to lower branches could easily be reached. Caro [1994] regularly observed cheetahs in the Serengeti scent-marking prominent landmarks such as solitary trees, rocks, termite mounds and branches of fallen trees. In Namibia, 'play trees' which are particular trees used for scent-marking, are important locations for territorial and communication behaviors [Marker-Kraus et al., 1996; Marker et al., 2003]. Lyons et al., [1997] found that raised areas were preferred sites within enclosures for captive felids, particularly for observation. This was also the case during the present study. Cheetahs were frequently observed sitting and lying upon these raised areas, using them as vantage points to survey the surrounding areas. The addition of raised areas to cheetah enclosures is recommended, as they function as a form of structural enrichment, creating prominent locations, promoting the occurrence of species-typical exploratory behavior, in addition to providing a means for cheetahs to gather information and assess their surrounding environs.

An increased number of movements between enclosures presented the cheetahs with novel olfactory, visual and structural stimuli which significantly increased olfactory and scent-marking behavior. Upon movement into a new enclosure, which frequently had been previously occupied by conspecifics, cheetahs spent prolonged periods of time thoroughly investigating the new enclosure. Males in particular, were observed sniffing and scent-marking multiple areas whereas females predominantly engaged in olfactory behavior. Wild felids frequently patrol their home range and they regularly will investigate scent-marks of others and will also often leave their own [Kitchener, 1991; Estes, 1992]. Moving cheetahs between enclosures effectively simulated the introduction of environmental enrichment incorporating novel olfactory stimuli which has previously been shown to encourage exploratory and active behaviors in captive felids. Wells and Egli [2004] observed increases in levels of enclosure exploration in black-footed cats (*Felis nigripes*) in response to a number of different odours. Other studies on cheetahs (*A. jubatus*) [Quirke and

O'Riordan, 2011a, b) and African wild dogs (*Lycaon pictus*) [Rafacz and Santymire, 2013] reported significant increases in exploratory behaviors, activity levels and positive social behaviors respectively, when scents from prey species were added to enclosures. An increasing number of movements between enclosures also resulted in significant increases in locomotory behavior (pers obs). When feasible, the utilisation of enclosure movements can be an effective way to stimulate the expression of exploratory behaviors and to provide captive cheetahs with novel stimuli akin to the introduction of environmental enrichment. However, care must be taken in relation to stress caused by unknown individuals encroaching on marked and established 'territories' within enclosures. Further studies are required to ascertain the balance between an enriching and stressful number of enclosure movements.

Males were observed to engage in exploratory behavior more frequently than females. They also differed in the type of exploratory behavior performed. Olfaction and scent-marking via urine spraying was most common in males whereas olfaction, defecation on raised areas while urinating and scuffing was more common in females. Cheek-rubbing, most often on trees or along fence lines was only observed in females, albeit extremely rarely. In contrast to solitary males or coalitions of males in the wild, who often hold territories, female cheetahs live in large home ranges varying in size from 830 km² in the Serengeti to 1600 km² in Namibia [Caro, 1994; Marker, 2002]. Therefore, the need to scent-mark in order to delineate a territory is not necessary. Cheetahs are known to inspect faeces but little is known about whether faeces carry specific information, or about their territorial significance [Eaton, 1974; Estes, 1992]. The observations of females defecating on raised areas while urinating and scuffing their hind feet may suggest that faeces carry some olfactory information because as mentioned earlier, raised areas are important locations for communicative behaviors. It is also of particular importance to monitor a number of exploratory behaviors in captive female cheetahs. An increase in several types of behaviors including rubbing, sniffing and urine-spraying have been correlated with increases in estradiol concentrations and therefore can be an indicator of estrus [Wielebnowski and Brown, 1998]. For a species that is not regarded as self-sustaining in captivity, the monitoring of these behaviors may prove effective in ensuring an increased number of successful breeding introductions between estrus females and breeding males.

The interaction between the covariates group membership and the ability to view other cheetahs offered an interesting insight into the maintenance of neighbouring groups or individual cheetahs in captivity. Solitary cheetahs which had the ability to view other cheetahs in adjacent enclosures were observed performing exploratory behavior less often compared to when they could not observe other cheetahs. Caro [1994] observed non-territorial males which are predominantly solitary, examining prominent locations intensely but urinating less frequently compared to territorial

males. He also reported that territorial behavior was effective at intimidating adolescent and single males. Solitary cheetahs in captivity which could view other cheetahs may have performed exploratory behavior less often so as not to advertize their presence to other possibly territorial males in order to avoid conflict. In contrast, those solitary individuals who could not view other cheetahs in adjacent enclosures were able to advertize their presence through scent-marking and extensive exploration within their enclosure (territory) without fear of encroaching upon other males' territories. It must also be noted that Quirke et al., [2012] reported that levels of stereotypical behavior were significantly higher when cheetahs could view conspecifics in adjacent enclosures. Therefore, the reduction in levels of exploratory behavior may also be associated with the increase in stereotypical behavior when cheetahs can view conspecifics. Groups of cheetahs which could view others in adjacent enclosures had slightly higher but comparable levels of exploratory behavior compared to other groups which could not view others in adjacent enclosures. Cheetahs in groups showed a much lower level of exploratory behavior compared to solitary cheetahs when both configurations could not observe others, but the opposite was the case when those configurations could view others. This would suggest that within the captive setting, solitary cheetahs are inclined to be territorial (increased scent-marking) when the presence of other males is not detected and that groups of males become more territorial when other males are detected. Caro [1994] observed that coalitions of males were better able to hold territories and gain access to females compared to solitary males, therefore, groups of males only showed a slight increase in exploratory behavior, in particular, scent-marking, when other males could be observed. Quirke et al., [2012] also reported that cheetahs maintained in groups were less likely to engage in stereotypical behavior, allowing more time to perform exploratory behavior in response to detecting neighbouring males. This variation in reactions to the presence of other cheetahs shows rather encouragingly, how cheetah behavior in captivity can mirror that of wild counterparts, but also how it can be greatly influenced by the husbandry practice within zoological institutions. In relation to increasing the prevalence of exploratory behavior in captive male cheetahs, it may be beneficial to keep solitary males in enclosures which are not adjacent to other male enclosures.

CONCLUSION

1. On average, across the 88 enclosures in this study, exploratory behavior accounted for 2% of the activity budget of captive cheetahs with the highest level observed in a single enclosure accounting for 11% of the activity budget.
2. The presence of raised areas and an increasing number of movements between enclosures significantly increased the probability of observing exploratory behavior.
3. The probability of observing exploratory behavior is significantly decreased when cheetahs are female, can

view conspecifics in adjacent enclosures and are maintained in groups.

4. The addition of raised areas to cheetah enclosures is recommended as they facilitate the performance of a range of natural species-typical behaviors in captivity. Increasing movements between enclosure stimulated exploratory behavior but further studies are required in order to determine an appropriate number of enclosure movements in a given time period.
5. A significant interaction between the covariates group composition and the ability to view conspecifics in adjacent enclosures highlighted that cheetah behavior in captivity can closely mirror that of wild counterparts but can be greatly influenced by husbandry practice.
6. The use of an information theory approach, comparing a number of different models in order to decipher behavior patterns, clearly reveals the dynamics of behavior within the captive setting.

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