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The effect of a randomised enrichment treatment schedule on the behaviour of cheetahs (*Acinonyx jubatus*)

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ABSTRACT

A range of types of enrichment have been shown to enhance activity levels, reduce stereotypical behaviours and increase levels of natural behaviour, subsequently improving the welfare of many species of captive animals. However, it is important to utilise effective forms of enrichment in a manner which will sustain their future use. The continuous use of particular types of enrichment in a regular, predictable, schedule may negatively impact upon the efficacy of the enrichment over a period of time. The objective of the present study is to introduce temporal feeding variation, spatial feeding variation and olfactory enrichment to cheetahs on a completely randomised schedule, in order to reduce levels of pacing and to increase active and exploratory behaviours. This study was carried out on ten cheetahs at Fota Wildlife Park, Ireland. Eight baseline days with no enrichment, eight days of no data collection and eight days for each of the three types of enrichment were assigned. Behaviour data were collected on baseline and enrichment days during either 09:00–13:00 h or 13:00–17:00 h, using instantaneous scan sampling with a 5 min interval. A Friedmann ANOVA was used to analyse behaviour data. Overall, a significant increase in exploratory and other behaviours was observed along with a significant decrease in pacing behaviour. Between 09:00 and 13:00 h, exploratory, other and inactive behaviour were significantly affected. Between 13:00 and 17:00 h, other, inactive and pacing behaviour were significantly affected. The lowest level of pacing behaviour was observed during the temporal feeding variation days and the highest level of exploratory behaviour was observed during olfactory enrichment days. Highlighting times of day when abnormal and inactive behaviours are prevalent will be beneficial in order to determine how and when enrichment should be provisioned. The use of a randomised schedule of enrichment also provides a greater degree of novelty and does not allow the animals to habituate to any single form of enrichment. The authors would recommend the use of temporal feeding variation, spatial feeding variation and olfactory enrichment, introduced to cheetahs on a random schedule.

1. Introduction

The current trend in zoological institutions worldwide is a move towards more enriched, more naturalistic enclosures (Young, 2003). This follows research documenting the positive behavioural and welfare effects of environmental enrichment for captive animals. Over the past two decades, a myriad of enrichment experiments have been carried out on a wide range of species from bank voles (*Clethrionomys glareolus*) (Cooper et al., 1996) to red foxes (*Vulpes vulpes*) (Kistler et al., 2009), large felids (Skibiel et al., 2007) and gorillas (*Gorilla gorilla*) (Wells et al., 2007). A GAP analysis by De Azevedo et al. (2007) reported that 744 articles related to environmental enrichment have been published between 1985 and 2004. These involved

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the use of a range of different types of enrichment including the simple addition of vegetation to an enclosure, the alteration of feeding regimes, the addition of novel objects or novel scents to enclosures. Many forms of enrichment have been shown to enhance activity levels, reduce stereotypical behaviours and increase levels of natural behaviour, subsequently improving the welfare of captive animals. Swaisgood and Shepherdson (2005) reported that 53% of the time, stereotypical behaviour was reduced significantly through the use of environmental enrichment. However, a finite number of effective forms of enrichment exist for each individual species. Therefore it is important to utilise effective forms of enrichment in a manner which will sustain their future use. Clubb and Mason (2007) highlighted the importance of increasing environmental variability and novelty for animals in captive environments, while Bassett and Buchanan-Smith (2007) also highlighted evidence suggesting that temporal unpredictability of feeding can enhance welfare of certain species in captivity. There is a possibility that the continuous use of particular types of enrichment in a regular, predictable schedule may negatively impact upon the efficacy of the enrichment over a period of time. Habituation has been previously defined as 'response decrement as a result of repeated stimulation' (Harris, 1943). Murphy et al. (2003) stated that habituation is specific to characteristics of the stimulus and that the response not only habituates to the exact stimulus but also to similar stimuli. This 'generalisation' (Tarou and Bashaw, 2007) can pose problems for zoo staff which incorporate similar types of enrichment in a predictable manner. Murphy et al. (2003) also highlighted that habituation to an enrichment that previously elicited a particular behavioural response can undergo spontaneous recovery if the enrichment is withheld for a period of time. This spontaneous recovery along with the phenomenon of 'dishabituation' (Tarou and Bashaw, 2007), whereby a new enrichment may cause the return of a response towards the older enrichment, combine to strengthen the claim that randomised enrichment schedules with a number of types of enrichment may effectively minimise habituation to each form of enrichment.

Enrichment for felids which have reduced levels of pacing and increased levels of active behaviour has tended to focus on feeding (Jenny and Schmid, 2002; Shepherdson et al., 1993; McPhee, 2002). Other non-food related enrichment for felids which have contributed to improved welfare and behavioural diversity include the introduction of novel objects such as bones (Skibiel et al., 2007) as well as olfactory enrichment using novel scents (Wells and Egli, 2004; Powell, 1995; Ellis and Wells, 2010). Cheetahs have previously been described as 'near average pacers' in a study on a range of felids in captivity (Lyons et al., 1997). Enrichment experiments on cheetahs are relatively rare in the literature. Skibiel et al. (2007) noted that cheetahs showed an increase in active behaviours when provisioned with bones and frozen fish. In an experiment designed to non-invasively collect hair samples from cheetahs, Balme et al. (2005) observed that cheetahs investigated 21 of 24 perfume and cologne scents presented to them, therefore highlighting the possibility of utilising a range of olfactory enrichments for cheetahs. Quirke and O'Riordan (2011) recently carried out enrichment experiments on cheetahs (*Acinonyx jubatus*) utilising temporal feeding variation, spatial feeding variation and olfactory enrichment, introduced to the cheetahs sequentially, in order to assess the influence of these enrichments on their behaviour. The objective of the present study is to introduce the same three enrichment treatments to cheetahs, on a completely randomised schedule, in order to determine their effect on cheetah behaviour. The aim is to decrease levels of pacing, increase active and exploratory behaviours and, to highlight the benefits of provisioning captive animals with enrichment at particular times of day. The main hypothesis for this research is that pacing will decrease, with active and exploratory behaviours both increasing. The second aim is to compare the random schedule from the current study to the sequential schedule used by Quirke and O'Riordan (2011) in terms of the difference in behaviours from baseline to enrichment phases of each schedule. Thirdly, levels of habituation to the enrichment in the random schedule are investigated. The goal is also to provide zoological institutions with information on the efficacy of randomised enrichment schedules for cheetahs in captivity and to also stimulate debate on how enrichment will develop as a husbandry practice in the future.

2. Methods

2.1. Study site and animals

This research was carried out at Fota Wildlife Park (51.8992°N, 8.2982°W), Carrigtwohill, Co. Cork, Ireland, for 40 days between March 2010 and May 2010. This study was carried out on ten cheetahs maintained in five enclosures at the Park. The five enclosures ranged in size from 420 m^2 to 3500 m^2 and contained grass, tall trees, numerous small shrubs and bushes as well as wooden sheds for shelter. The ten cheetahs consisted of a solitary male, a coalition of two males, a group consisting of a mother and four old cubs, and two solitary females. The cheetahs were aged between 1 and 11 years. The cheetahs were usually fed at a regular time (around 16:00 h) once daily, six days a week on whole dead rabbits or chickens.

2.2. Procedure

Three different types of enrichment, namely, temporal feeding variation, spatial feeding variation and olfactory enrichment using fresh oryx (*Oryx dammah*) faeces were introduced to the cheetahs on a completely randomised schedule. Out of the 40 days of this experiment, random number tables were utilised to assign eight baseline days with no enrichment and eight days for each of the three types of enrichment. There were also eight days when no data were collected. Each day when data were collected was divided into two 4 h periods, namely period 1, 09:00–13:00 h and period 2, 13:00–17:00 h. These time periods were chosen on the basis that the enrichments introduced had the possibility to alter the temporal dynamics of the entire activity budget of the cheetahs. Therefore, collecting data over 4 h daily increased the likelihood of detecting these changes. Random number tables were used

Table 1
Ethogram of behaviours recorded in the study.

Behaviour	Definition
Locomotion	Movement from one location to another at any speed.
Vigilance	Eyes focused on animal/visitor/location, head rigid, ears back.
Other	Vocalisation, affiliative behaviour, standing, feeding, aggression.
Exploratory	Olfaction and scent-marking.
Inactive	Lying down, sitting, shelter, auto-grooming.
Pacing	Repetitive locomotory movement along a given route (up/down fence line, around enclosure or object in enclosure) uninterrupted by other behaviours.

to assign either period 1 or period 2 to each enrichment and baseline day. For temporal feeding variation days, feeding was carried out randomly within either period 1 or period 2 on the specific days at a time which was different to the regular feeding time (around 16:00 h). Spatial feeding variation involved changing the feeding position from the back of the enclosures to the front. Feeding was always carried out at the normal feeding time (around 16:00 h) during spatial feeding variation days. Oryx faeces were added to enclosures from various points along the fence line at random times within period 1 or period 2 on the specific days. Six behaviours were recorded during this study; locomotion, vigilance, other, exploratory, inactive and pacing (Table 1). Behaviour data were collected for 4 h on baseline and enrichment days during period 1 or 2 using instantaneous scan sampling with a 5 min inter-scan interval. For enclosures with more than one individual, scan samples were carried out on all individuals and data were pooled in order to accurately assess the behaviour within the enclosure. A total of 48 scan samples were carried out per enclosure each day in which data were collected.

2.3. Data analysis

The overall frequencies for each behaviour, were expressed as proportions of the total number of scans carried out during baseline days and each of temporal feeding variation, spatial feeding variation and olfactory enrichment days for all cheetah enclosures ($n = 5$). This resulted in data which showed the proportion of scan samples in which each cheetah enclosure were observed performing each behaviour for baseline days and each of temporal feeding variation, spatial feeding variation and olfactory enrichment days. Since the data violated normality and homogeneity of variance assumptions, a non-parametric test, namely, a Friedmann ANOVA was conducted for each behaviour using the proportion of scan samples to determine if cheetah behaviour was influenced by the enrichment treatments. If the Friedman's tests were significant, a Wilcoxon signed rank test was performed to determine significant pair-wise relationships between baseline days and each of the three enrichment days. Secondly, the same procedure was carried out for each individual time period, namely, period 1 (09:00–13:00 h) and period 2 (13:00–17:00 h). A Friedmann ANOVA was undertaken separately for period 1 and period 2 to determine if cheetah behaviour was influenced by the enrichment treatments during each time period. If the Friedmann's tests were significant, a Wilcoxon signed rank test was performed to determine significant pair-wise relationships.

In order to compare the effects of both schedules, levels of each behaviour were collapsed across all enrichment days for the random schedule and the sequential schedule of Quirke and O'Riordan (2011). The difference in the proportion of scan samples between baseline and enrichment days for both schedules was calculated. Randomisation tests using 1000 re-randomised pseudosamples were used to compare the levels of difference in order to determine which behaviours were more significantly affected by the two schedules (Plowman, 2008; Todman and Dugard, 2001). In order to measure levels of habituation during the random schedule, levels of pacing and exploratory behaviour were compared from day 1 of presentation to day 8 of presentation for temporal feeding variation and olfactory enrichment days, respectively. The difference in levels between day 1 and day 8 were analysed using randomisation tests with 1000 re-randomised pseudosamples.

3. Results

3.1. Effects of enrichment on cheetah behaviour at Fota Wildlife Park

The introduction of the three enrichment treatments in a random design over 40 days had a significant effect on the behaviour of cheetahs at Fota Wildlife Park. Exploratory ($\chi^2 = 11.291$, d.f. = 3, $p < 0.01$), other ($\chi^2 = 15.610$, d.f. = 3, $p < 0.001$) and pacing ($\chi^2 = 11.034$, d.f. = 3, $p < 0.01$) behaviour were significantly affected (Table 2). Exploratory behaviour remained at levels between 1% and 2% of scan samples during baseline days, temporal feeding variation and spatial feeding variation days (Table 2). The highest level of exploratory behaviour (5%) was observed during the olfactory enrichment treatment days (Table 2). Multiple comparisons revealed a significant difference between baseline and olfactory enrichment days ($z = -2.201$, $p < 0.05$). Other behaviour remained at levels between 5% and 9% during baseline, spatial feeding variation and olfactory enrichment days (Table 2). Levels increased to 17% of scan samples during temporal feeding variation days (Table 2). Multiple comparisons revealed a significant difference between baseline and temporal feeding variation days ($z = -2.301$, $p < 0.05$) Pacing behaviour was consistently observed less frequently during each of the enrichment treatments (2–4%) compared to baseline days (8%) (Table 2). The lowest levels of pacing behaviour were observed during temporal feeding variation days (Table 2). Multiple comparisons revealed significant differences between baseline and temporal feeding variation days ($z = -2.422$, $p < 0.05$) and between baseline and spatial feeding variation days ($z = -2.201$, $p < 0.05$).

Table 2
The mean (±SD) proportion of scan samples in which cheetahs were recorded exhibiting each behaviour during the phases of study. *p* value indicates the result of a Friedmann ANOVA. Significant multiple comparisons highlight which phase differed to the baseline phase.

Behaviour/phase	Baseline (B)	Temporal (T1)	Spatial (T2)	Olfactory (T3)	*p*	Significant multiple comparisons
Overall						
Locomotion	0.20 (0.04)	0.16 (0.07)	0.19 (0.04)	0.19 (0.04)	0.334	–
Exploratory	0.01 (0.01)	0.02 (0.02)	0.01 (0.01)	0.05 (0.03)	**0.01**	B vs T3
Vigilance	0.09 (0.04)	0.07 (0.03)	0.09 (0.05)	0.09 (0.04)	0.361	–
Other	0.07 (0.04)	0.17 (0.01)	0.05 (0.02)	0.09 (0.02)	**0.001**	B vs T1
Inactive	0.53 (0.10)	0.53 (0.08)	0.58 (0.11)	0.52 (0.08)	0.08	–
Pacing	0.08 (0.06)	0.02 (0.02)	0.04 (0.03)	0.05 (0.04)	**0.01**	B vs T1, B vs T2
09:00–13:00 h						
Locomotion	0.15 (0.05)	0.16 (0.07)	0.18 (0.07)	0.15 (0.05)	0.622	–
Exploratory	0.02 (0.01)	0.03 (0.02)	0.02 (0.02)	0.06 (0.03)	**0.004**	B vs T3
Vigilance	0.07 (0.05)	0.06 (0.05)	0.09 (0.03)	0.09 (0.04)	0.271	–
Other	0.02 (0.02)	0.16 (0.02)	0.03 (0.02)	0.02 (0.02)	**0.005**	B vs T1
Inactive	0.68 (0.12)	0.53 (0.12)	0.66 (0.12)	0.67 (0.11)	**0.023**	B vs T1
Pacing	0.03 (0.03)	0.03 (0.03)	0.02 (0.04)	0.01 (0.01)	0.379	–
13:00–17:00 h						
Locomotion	0.23 (0.06)	0.15 (0.06)	0.19 (0.03)	0.23 (0.07)	0.094	–
Exploratory	0.01 (0.01)	0.02 (0.01)	0.02 (0.01)	0.04 (0.03)	0.130	–
Vigilance	0.11 (0.06)	0.08 (0.04)	0.09 (0.08)	0.09 (0.06)	0.873	–
Other	0.11 (0.03)	0.19 (0.02)	0.09 (0.03)	0.15 (0.02)	**0.003**	B vs T1, B vs T3
Inactive	0.42 (0.11)	0.53 (0.10)	0.51 (0.11)	0.39 (0.09)	**0.012**	B vs T1
Pacing	0.10 (0.07)	0.02 (0.03)	0.06 (0.04)	0.08 (0.07)	**0.014**	B vs T1

3.2. Effect of enrichment treatments on cheetah behaviour during period 1 (09:00–13:00 h)

Between 09:00 and 13:00 h, exploratory ($\chi^2 = 13.473$, d.f. = 3, $p < 0.01$), other ($\chi^2 = 12.889$, d.f. = 3, $p < 0.01$) and inactive ($\chi^2 = 9.508$, d.f. = 3, $p < 0.05$) behaviour were significantly affected (Table 2). Levels of exploratory behaviour were between 2% and 3% of scan samples during baseline, temporal and spatial feeding variation days but reached 6% during olfactory enrichment (Table 2). Multiple comparisons revealed significant differences between baseline and olfactory enrichment days ($z = -2.060$, $p < 0.05$) Levels of other behaviour were highest during temporal feeding variation days at 16% of scan samples between 09:00 and 13:00 h with levels for baseline and other treatment days remaining between 2% and 3% (Table 2). Multiple comparisons revealed significant differences between baseline and temporal feeding variation days ($z = -2.220$, $p < 0.05$). Inactive behaviour was lowest (53% of scan samples) during temporal feeding variation compared to levels of between 66% and 68% during baseline, spatial feeding variation and olfactory enrichment days (Table 2). Multiple comparisons revealed significant differences between baseline and temporal feeding variation days ($z = -2.282$, $p < 0.05$). Pacing behaviour remained at similar levels of between 1% and 3% during baseline and the enrichment days (Table 2).

3.3. Effect of enrichment treatments on cheetah behaviour during period 2 (13:00–17:00 h)

Between 13:00 and 17:00 h, other ($\chi^2 = 14.040$, d.f. = 3, $p < 0.01$), inactive ($\chi^2 = 10.920$, d.f. = 3, $p < 0.05$) and pacing ($\chi^2 = 10.660$, d.f. = 3, $p < 0.05$) behaviour were significantly affected (Table 2). Other behaviour levels were highest during temporal feeding variation (19% of scan samples) and olfactory enrichment (15% of scan samples) and lowest during the spatial feeding variation (9%) (Table 2). Multiple comparisons revealed significant differences between baseline and temporal feeding variation days ($z = -2.233$, $p < 0.05$) and between baseline and olfactory enrichment days ($z = -2.200$, $p < 0.05$). Inactive behaviour was highest during temporal feeding variation days (53% of scan samples) and lowest during olfactory enrichment days (39% of scan samples) (Table 2). Multiple comparisons revealed significant differences between baseline and temporal feeding variation days ($z = -2.322$, $p < 0.05$). Between 13:00 and 17:00 h, pacing behaviour was consistently lower during the enrichment days (2–8% of scan samples) compared to the baseline days (10% of scan samples) (Table 2). The lowest level of pacing behaviour was observed during the temporal feeding variation days (Table 2). Multiple comparisons revealed significant differences between baseline and temporal feeding variation days ($z = -2.201$, $p < 0.05$).

3.4. Comparison of random schedule and sequential schedule

The mean difference in levels of other behaviour between baseline and enrichment days was significantly ($p < 0.01$; two-tailed) higher during the sequential schedule (7% of scans) compared to the random schedule (2% of scans) (Fig. 1). The mean difference in levels of inactive and exploratory behaviour between baseline and enrichment days were higher during the random schedule, but not significantly so ($p > 0.05$; two-tailed) (Fig. 1). Levels of pacing behaviour were lower on enrichment days for both schedules with the sequential schedule showing a slightly higher decrease but not significantly so ($p > 0.05$; two-tailed) (Fig. 1). The mean difference in levels of vigilance was close to zero for the random schedule but a decrease in levels of vigilance on enrichment days was observed during the sequential schedule (Fig. 1). The difference between the two schedules was not statistically significant ($p > 0.05$; two-tailed). For locomotion behaviour, levels were lower on enrichment days during the random schedule and higher on enrichment days during the sequential

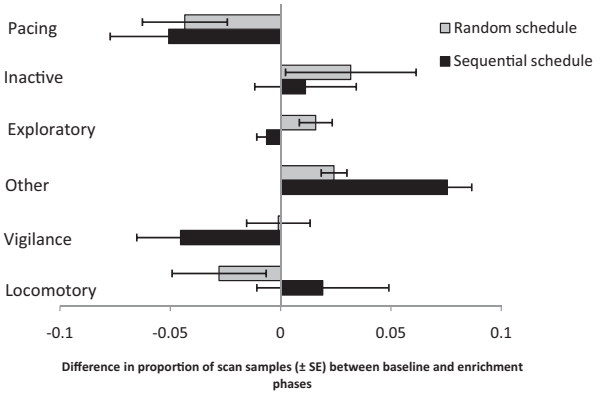

Fig. 1. Mean difference in the proportion of scans samples between baseline and enrichment phases for each behaviour.

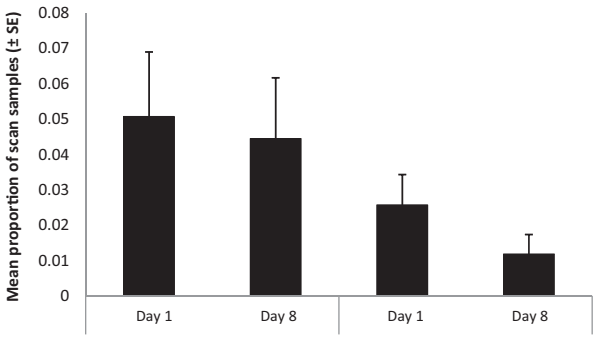

Fig. 2. Mean proportion of scan sample sin which pacing and exploratory behaviour were observed on day 1 and day 8 of temporal feeding variation and olfactory enrichment presentation, respectively.

schedule (Fig. 1). However, the difference between the two schedules was not statistically significant ($p > 0.05$; two-tailed).

3.5. Habituation during the random schedule of enrichment

There were no significant differences in levels of pacing ($p > 0.05$; two-tailed) between day 1 and day 8 of presentation of temporal feeding variation. Levels of pacing were lower on day 8 of presentation (Fig. 2). There were also no significant differences in levels of exploratory behaviour between day 1 and day 8 of presentation of olfactory enrichment. Levels were lower on day 8 of presentation (Fig. 2).

4. Discussion

The use of temporal feeding variation, spatial feeding variation and olfactory enrichment using fresh oryx faeces in a randomised schedule had a significant effect on the levels of pacing, other and exploratory behaviour of captive cheetahs at Fota Wildlife Park. The presence of pacing behaviour is often associated with a sub-optimal, stressful captive environment and is commonly used as an indicator of poor welfare (Mason et al., 2007). In carnivores, pacing is also hypothesised to develop from appetitive foraging behaviour (Mason, 1993). Captive ocelots (*Leopardus pardalis*) (Weller and Bennett, 2001), fennec foxes (*Vulpes zerda*) (Carlstead, 1991), American black bear (*Ursus americanus*) (Carlstead et al., 1991), tigrinas (*Leopardus tigrinus*) and margays (*Leopardus wiedii*) (Moreira et al., 2007) have all been observed to show high levels of pre-feeding pacing. During the present study, the cheetahs at Fota Wildlife Park also showed high levels of arousal and activity expressed as pacing behaviour prior to feeding during baseline observations. However, days with temporal feeding variation showed the lowest levels of pacing, followed by spatial feeding variation and finally olfactory enrichment days.

The use of a temporally unpredictable feeding schedule introduced novelty and did not allow food anticipatory activity (FAA) and subsequent pacing behaviour (Bassett and Buchanan-Smith, 2007) to develop at the regular feeding time, therefore significantly reducing levels of pacing behaviour on temporal feeding variation days. Law et al. (1990) also observed decreased levels of pacing in polar bears (*Ursinus maritimus*) when they were fed earlier in the day. Cheetahs in the present study also engaged in an increased amount of active behaviours such as allo-grooming, vocalising and feeding during temporal feeding variation days as recorded in the higher levels of other behaviour which were observed. As mentioned earlier, the regular feeding time at Fota Wildlife Park is around 16:00 h. As behavioural observations were concluded daily at 17:00 h, this effectively minimised the time available to record other behaviour on baseline days. During temporal feeding variation days where feeding time was earlier in the day, levels of vocalisation and post-feeding allo-grooming were observed more frequently as the post-feeding observation period was extended, therefore contributing to significantly higher levels of other behaviour during temporal feeding variation days. Therefore, the results in this respect may be due to the limitations of the sampling regime but this also provides an insight into increasing the levels of active species-typical behaviours at particular times of the day. Quirke and O'Riordan (2011) observed different behaviours being significantly affected by the enrichment treatments during different time periods. Gilbert-Norton et al. (2009) also observed temporal differences in the behaviour of coyotes (*Canis latrans*) between the am and pm conditions in their study which randomly altered time and location of feeding. The current study also revealed that a range of behaviours was significantly affected at different times of the day by the enrichment treatments. These findings once again highlight that enrichment, particularly focused on a changing of feeding time, may be used at pre-selected times of day in order to stimulate particular behavioural patterns and to improve welfare in captive cheetahs. In a study on stump-tailed macaques (*Macaca arctoides*), delays in feeding routine and subsequent prolonged anticipation of feeding resulted in increased abnormal, self-directed and inactive behaviours (Waitt and Buchanan-Smith, 2001). Changes in feeding time in the current study were prior to the scheduled feeding time during the baseline days. Therefore, the cheetahs were not subject to prolonged anticipation of feeding and subsequently the effects of delayed feeding cannot be determined from the current

study but the authors hypothesise that delayed feeding would result in a significant increase in pacing in this species. Margulis et al. (2003) highlighted that visitor interest in felid exhibits was higher when the animals were active. One of the main goals of zoological institutions is education. It is possible that visitors can learn more about animals when they are active and performing natural species-specific behaviours. Altman (1998) reported that conversation among visitors relating to behaviour was highest when polar bears were active. Her findings also suggested that visitor attention and thus, possibly visitor learning were elicited by animated animal activity. The use of temporal feeding variation and other forms of enrichment at times of day with high visitor numbers therefore may, increase visitor interest and positively impact upon education goals in addition to directly improving welfare of the animals in captivity.

The use of spatial feeding variation also had a similar effect in terms of reducing FAA pacing, though not as powerful an effect on levels of pacing. By increasing the number of the possible feeding locations, the cheetahs were unable to focus their pre-feeding arousal on a small area where food was normally dispensed, and spent a greater amount of time vigilant compared to temporal feeding variation days, therefore reducing levels of pacing behaviour. Jenny and Schmid (2002) also observed reductions in pacing behaviour upon the implementation of temporally and spatially unpredictable feeding regimes using feeding boxes for Amur tigers (*Panthera tigris altaica*). Olfactory enrichment significantly increased levels of exploratory behaviour. In contrast to Quirke and O'Riordan (2011), where fresh oryx faeces were added to enclosures by keepers moving within enclosures and placing the faeces, this study did not involve entering the enclosure and faeces were added at random locations all around the borders of enclosures. The introduction of olfactory enrichment has been shown to increase activity levels in lions (*Panthera leo*) (Powell, 1995) and black-footed cats (*Felis nigripes*) (Wells and Egli, 2004). A study conducted in the Bronx zoo recently revealed that a male and female cheetah investigated 87.5% of sites scented with colognes and perfumes placed in different locations around their enclosure (Balme et al., 2005). The cheetahs in the present study showed lower levels of inactive behaviour, albeit very slightly, when compared to days without olfactory enrichment. Increased levels of scent-marking and olfaction in the areas where the oryx faeces had been added to enclosures were observed at Fota Wildlife Park. The greater amount of time spent investigating the novel odours also resulted in decreased levels of pacing. Quirke and O'Riordan (2011) had partly attributed the increase in exploratory behaviour in their experiment to the movement of keepers within the enclosures while placing the faeces. The present study revealed that the novel scent alone can increase levels of natural behaviour and reduce pacing in cheetahs. The use of oryx faeces or the faeces of other prey animals, which are widely available in captivity, can be an easily introduced form of olfactory enrichment to improve levels of active species-typical behaviour of cheetahs in captivity. However, care must be taken in order to not provide a vector for the spread of pathogens between species. Regular checks on the pathogens present in faeces of prey animals prior to their introduction into enclosures for enrichment purposes can effectively minimise this threat.

The definition of successful enrichment in the current study was defined as a decrease in pacing behaviour and an increase in exploratory and active behaviours. The comparison of the effects of the random and sequential schedule revealed the positive and beneficial effects of the two alternative enrichment strategies. Whereas the sequential schedule showed higher levels of the active other behaviour category, the random schedule promoted higher levels of exploratory behaviour and both schedules reduced levels of pacing. The captive environment is infinitely less complex than that of the wild. Incorporating predictable sequential schedules over a period of time, even those related to enrichment, into this environment can result in increased simplicity. Also, after repeated presentations, behavioural responses towards devices and environmental changes can decrease quickly (Celli et al., 2003). The merits of utilising a random enrichment schedule were revealed through the investigation of habituation to temporal feeding variation and olfactory enrichment in the form of pacing and exploratory behaviour. Pacing during temporal feeding variation showed no evidence of the effects of habituation and in fact levels of pacing were lower on the last day of presentation, suggesting the enrichment was still effective at reducing pacing. Hare and Jarand (1998) utilised an artificial prey device for tigers which stimulated an increase in hunting behaviour, but this response reduced over a small number of trials as a result of habituation. A simple change to the device resulted in a resurgence of the response (Hare and Jarand, 1998). It is possible that the simple differences in the random nature of feeding in the current study along with spontaneous recovery and dishabituation as a result of time between temporal feeding variation days and alternative enrichments in the intervening days effectively minimised any habituation to the enrichment. Also, it raises the question whether or not cheetahs or other carnivores can habituate to such a stimulating event as feeding? The cheetahs in the current study also showed no evidence of habituation to olfactory enrichment but levels of exploratory behaviour were lower by day 8 of presentation. It may be beneficial to incorporate a number of scents into the random schedule of olfactory enrichment in order to prolong the effective period of each individual scent in terms of eliciting a behavioural response. Based on the current understanding of habituation, random schedules of enrichment have the potential to prolong the period of usefulness of the enrichments incorporated into the schedule and to introduce a greater degree of novelty into the often mundane captive environment. Future research detailing the process of habituation to enrichment provisioned on a sequential schedule will contribute greatly to the understanding of the optimal way to introduce enrichment to captive animals.

5. Conclusions

The current study revealed the behavioural benefits, in the form of increased levels of active species-typical behaviour, increased exploratory behaviour and significant

reductions in pacing behaviour, of utilising temporal feeding variation, spatial feeding variation and olfactory enrichment provisioned on a random schedule as forms of enrichment for cheetahs in captivity. Although pacing behaviour was not eliminated, it was significantly reduced. The possible advantages of pinpointing the introduction of different forms of enrichment at times of day, when particular behavioural patterns are desirable, were revealed. The use of a randomised schedule of enrichment provides a greater degree of novelty and does not allow the animals to habituate to any single form of enrichment. Overall, the authors would recommend the use of temporal feeding variation, spatial feeding variation and olfactory enrichment using prey animal faeces, introduced to cheetahs on a random schedule in order to stimulate species-typical behaviours. Zoos could benefit from first carrying out in-house research in order to determine when pacing behaviour and periods of inactivity are prevalent in cheetahs. Enrichment focused around these times will increase activity levels, reduce pacing, improve welfare and allow visitors to observe cheetahs performing natural behaviours.

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