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The effect of different types of enrichment on the behaviour of cheetahs (*Acinonyx jubatus*) in captivity

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ABSTRACT

Enrichment, in the form of changes to the structure and content of enclosures, in addition to changes to husbandry practice, have been used on a range of felids resulting in increased activity levels and decreased levels of pacing behaviour. It is important to determine what types of enrichment are effective for individual species in captivity. The aim of this research was to test the effect of three different enrichment treatments on the behaviour of cheetahs at Fota Wildlife Park, Ireland. The three treatments; temporal variation in feeding, spatial variation in feeding and olfactory enrichment using scimitar-horned oryx (*Oryx dammah*) faeces were chosen to provide a degree of novelty and unpredictability to the captive environment, with the goal of decreasing pacing while increasing active and exploratory behaviours. Following baseline data collection, treatments were introduced to the five cheetah enclosures according to a schedule, with each treatment being carried out for five days followed by a 14-day post-treatment (PT) period prior to the next treatment being introduced. A Friedmann ANOVA was carried out to test if the schedule of enrichment treatments had an effect on cheetah behaviour. Vigilance behaviour was observed less frequently during treatment and post-treatment phases (4.1–9.5%) compared with the baseline observations (11.1%). Exploratory behaviour fluctuated with the highest level occurring during the olfactory enrichment treatment. There was a trend for pacing to decrease during enrichment treatments. A range of behaviours were also significantly affected at different times of the day by the schedule of treatments. The results were similar to previous enrichment studies on other felids suggesting that the use of these types of enrichment can be an effective form of enrichment for cheetahs in captivity. Individual groups also reacted differently to the enrichment treatments, suggesting that enrichment can have varying effects on behaviour of captive cheetahs depending on group identity and configuration. The schedule of treatments, punctuated by the return to baseline conditions, is also cited as having an enriching effect. Due to different behaviours being affected at different times of day, the question was raised about the use of specific enrichments during periods of time when abnormal behaviour is prevalent. Research on the behavioural effects of a randomised enrichment treatment schedule, rather than a sequential one used in this study may be of benefit, in order to separate the effects of the schedule and the treatments.

1. Introduction

As of 1925 when Robert Yerkes wrote 'the greatest possibility for improvement in our provision for captive primates lies with the invention and installation of

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apparatus which can be used for play and work', an age of developing enrichment strategies for animals in captivity began, along with the idea that zoo animal enclosures should allow a captive animal to behave like its wild counterparts (Hediger, 1969). Environmental enrichment is widely used to enhance the quality of life for animals in captivity by providing stimuli necessary for psychological, physiological and behavioural wellbeing (Swaisgood and Shepherdson, 2005). Increasing the prevalence of natural active behaviours, reducing stereotypical behaviours and improving the welfare of captive animals are the primary goals of enrichment. Enrichment can take the form of changes to the structure and content of enclosures, in addition to changes in husbandry practice.

Notoriously inactive in captivity, large felids still remain one of the most popular species for zoo visitors (Margulis et al., 2003) and, like other carnivores, they have a tendency to carry out locomotory stereotypies such as pacing (Carlstead et al., 1991; Mason, 1991). The use of environmental enrichment can enhance activity levels, increase the prevalence of natural behaviours and also reduce levels of pacing. Previous environmental enrichment research on cheetahs (*Acinonyx jubatus*) has included the use of a moving bait system which stimulated greater levels of hunting and observation behaviours (Williams et al., 1996). Skibiel et al. (2007) also recorded an increase in levels of activity in cheetahs provisioned with bones and frozen fish. The three environmental enrichments for this study on cheetahs, namely; temporal feeding variation, spatial feeding variation and olfactory enrichment were chosen based on the ease of their provision, their safety and the fact that no research on their effect on cheetah behaviour has been recorded in the literature. Previous research on a number of other species in captivity has also highlighted their enriching effects. Kistler et al. (2009) successfully utilised electronic feeders and a self-service food box in a simple enrichment experiment in order to promote natural foraging behaviours in red fox (*Vulpes vulpes*) by delivering food unpredictably both in time and space. Electronically controlled feeding boxes, delivering small amounts of food at semi-random times resulted in decreased levels of stereotypical pacing in two Amur tigers (*Panthera tigris altaica*) in Zurich Zoo (Jenny and Schmid, 2002). The provisioning of leopard cats (*Felis bengalensis*) with multiple feedings of hidden food, effectively incorporating spatial feeding variation, resulted in increased exploratory behaviour, behavioural diversity and, a decrease in stereotypical pacing behaviour (Shepherdson et al., 1993). The addition of herbs, spices and scents of the dung of prey animals has been shown to increase activity levels in lions (*Panthera leo*) (Pearson, 2002; Powell, 1995). In terms of enrichment, what is suitable for one species may not be for another, hence the importance of determining what types of enrichment are effective for individual species.

The cheetah is a diurnal, cursorial predator which is markedly different in anatomy and behaviour when compared to other members of the Felidae family. Cheetahs have a relatively unique social organisation when compared to other felids (Caro, 1994). Females are solitary except for when they have dependent cubs or when they remain with siblings for a period of time after independence from their mother, whereas males can be solitary or form coalitions containing sibling and non-sibling members (Caro, 1994).

The objective of this research was to test the behavioural effect of providing captive cheetahs with temporal feeding variation, spatial feeding variation and olfactory enrichment, on a sequential schedule, punctuated by post-enrichment periods where no enrichment was provided, in order to assess their usefulness as environmental enrichment for captive cheetahs. The effect of the enrichment schedule on the behaviour of captive cheetahs at different times of day was also examined. The activity budget of the cheetahs in each enclosure was examined particularly in relation to levels of pacing throughout the enrichment schedule. The definition of successful environmental enrichment used in this study is a decrease in levels of pacing behaviour and an increase in active and exploratory behaviours. The main hypothesis for this research is that levels of pacing, active and exploratory behaviours will all be affected by the schedule of enrichment treatments. This research is part of a range of experiments testing different schedules of enrichment for cheetahs, also examining overall behavioural patterns of cheetahs in captivity.

2. Methods

2.1. Study site

This research was carried out at Fota Wildlife Park (51.8992°N, 8.2982°W), Carrigtwohill Co. Cork, Ireland between November 2008 and March 2009.

2.2. Animals and enclosures

During this study, 12 cheetahs, 10 female and 2 male were kept in five enclosures (A–E), ranging in size from 420 m^2 to 3500 m^2, containing between one and five individuals (Table 1). Each of these enclosures contains grass, tall trees, numerous small shrubs and bushes as well as wooden sheds for shelter. During this study, female cheetahs kept in the same enclosure were either siblings or with their mother and did not partition the enclosure and subsequently, the area of enrichment, in response to being housed together. The enclosures also face a large grassland paddock which holds a range of fauna including zebra (*Equus burchelli*), scimitar-horned oryx (*Oryx dammah*), giraffe (*Giraffa camelopardalis*), ostrich (*Struthio camelus*), emu (*Dromaius novaehollandiae*) and wallabies (*Macropus rufogriseus*), all of which are visible to the cheetahs sporadically during the day and at different times of the year. The cheetahs in enclosures A–E are fed at a regular time once daily, six days a week on whole dead rabbits or chickens.

2.3. Enrichment

This experiment involved the introduction of three enrichment treatments to the cheetahs in enclosures A–E:

Temporal feeding variation (T1): During this treatment, feeding time was altered from the regular schedule

Table 1
Cheetahs observed in the study.

Enclosure	Composition	Age	Relationship
A	Three adult females	2 years	Siblings
B	One adult female, four cubs (one male, three female)	9 years, 7 months × 4	Mother and cubs
C	One adult hand-reared male	3 years	–
D	Two adult hand reared females	6 years	Siblings
E	One adult female	8 years	–

(around 16:00 h) to a random time between 12:00 and 14:00 h for all enclosures.
Spatial feeding variation (T2): The position where food was presented to cheetahs was altered from the back of the enclosure to the front of the enclosure. Feeding time was returned to the regular feeding time of 16:00 h.
Olfactory enrichment (T3): Freshly collected scimitar-horned oryx (*O. dammah*) faeces were placed in a number of locations within cheetah enclosure each morning during this enrichment. Feeding time was at the regular feeding time of 16:00 h.

2.4. Procedure

Six behaviours were recorded during this study; locomotion, vigilance, other, exploratory, inactive and pacing (Table 2). Prior to commencement of the enrichment treatment experiments in enclosures A–E, baseline behaviour data were collected for 20 days during November 2008. Treatments were introduced to cheetah enclosures A–E for five days followed by a 14-day post-treatment (PT) period, where baseline conditions were once again in place prior to the next treatment. A longer post-treatment period was used to avoid cumulative effects of provisioning multiple treatments (Skibiel et al., 2007). Temporal feeding variation was employed in each enclosure first, followed by spatial feeding variation and finally olfactory enrichment. Instantaneous scan sampling with an inter-scan interval of 5 min was used during this study. A random number generator was used to select the start time of sampling, based on the day (08:00–18:00 h) being divided into 40 15 min periods. Random number tables determined the order in which data were collected from the five enclosures (A–E). A sampling interval of 2 h and 25 min was used daily with 30 scan samples being carried out per enclosure. A total of 150 scan samples were carried out per enclosure per phase of the study. For enclosures with more than one cheetah, scan samples were carried out on all individuals and data were pooled to create data for that enclosure in order to accurately record the behaviour being carried out in that enclosure. Each enclosure was treated as a single data point during data analysis ($n = 5$). The 150 scan samples per enclosure were also divided between five time periods based on when they were collected. The five time periods were 08:00–10:00 h, 10:00–12:00 h, 12:00–14:00 h, 14:00–16:00 h and 16:00–18:00 h with 30 scan samples per time period per enclosure per phase of study.

2.5. Data analysis

The overall frequencies for each behaviour observed during each phase of study, for each enclosure, were expressed as proportions of the total number of scan samples carried out during each phase in each enclosure. This resulted in data which highlighted the proportion of scan samples in which each behavioural category was observed during each phase of study for enclosures (A–E). A Friedmann ANOVA was conducted for each behaviour (e.g., locomotion, vigilance, pacing, etc.) to determine whether the cheetahs' behaviour at Fota Wildlife Park was influenced by the schedule of enrichment treatments. Secondly, the proportion of scan samples in which each behaviour was observed during each individual time period was also calculated for enclosures (A–E). A Friedmann ANOVA was conducted for each behaviour in each of the five time periods using enclosures (A–E) as replicates in order to determine whether each of the six behaviours were influenced differently by the schedule of enrichment treatments in the five time periods, i.e., Did the schedule enrichment treatments significantly affect pacing behaviour during 8:00–10:00 h, 14:00–16:00 h, etc.? If the Friedmann's tests were significant, a Wilcoxon signed rank test was performed to determine significant pair-wise relationships, corrected for multiple comparisons with a Bonferroni correction. Significance level after the Bonferroni correction was $\alpha = 0.01$. Finally, using the overall frequency counts for each behaviour category for each enclosure, *G*-tests were carried out on the activity budgets of the cheetahs in each enclosure in order to determine if the schedule of enrichment treatment had an effect on the activity budgets of the individual cheetah groups.

3. Results

3.1. Cheetah behaviour at Fota Wildlife Park during enrichment treatments

The schedule of enrichment treatments utilised in this study had a significant effect on the levels of vigilance ($\chi^2 = 13.534$, d.f. = 6, $p = 0.04$) and exploratory ($\chi^2 = 15.908$, d.f. = 6, $p = 0.01$) behaviours of the cheetahs at Fota Wildlife Park (Table 3). Vigilance behaviour was observed less frequently during treatment and post-treatment phases (4.1–9.5%) compared with the baseline observations (11.1%) (Table 3). Multiple comparisons between different phases of the study, with an adjusted alpha level of 0.01 revealed no significant differences ($p > 0.01$ for all Wilcoxon's tests; Baseline vs. T3 ($z = -2.032$, $p = 0.04$), T3 vs. PT3 ($z = -2.023$, $p = 0.04$)). Exploratory behaviour fluctuated slightly throughout the study with the only large deviation from the baseline occurring during post-olfactory enrichment (PT3) where the mean levels of exploratory behaviour were very close to zero (0.24%) (Table 3). Multiple comparisons between different phases of the study,

Table 2
Ethogram of behaviours observed 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

with an adjusted alpha level of 0.01, revealed no significant differences ($p > 0.01$ for all Wilcoxon's tests; Baseline vs. T2 ($z = -1.841$, $p = 0.05$), T3 vs. PT3 ($z = -1.826$, $p = 0.052$)). Levels of other behaviour during treatment and post-treatment phases remained higher than the baseline period while levels of locomotion and inactive behaviour fluctuated non-significantly throughout the study (Table 3). Throughout the enrichment and post-enrichment phases, there was a trend for pacing to be decreased from baseline levels suggesting that the enrichment treatments resulted in a positive, albeit, a statistically non-significant, reduction in levels of pacing behaviour (Table 3).

3.2. Cheetah behaviours affected by enrichment treatments during different time periods during study

Between 08:00 and 10:00 h, locomotion ($\chi^2 = 14.652$, d.f. = 6, $p = 0.02$), vigilance ($\chi^2 = 12.491$, d.f. = 6, $p = 0.05$) and inactive ($\chi^2 = 13.173$, d.f = 6, $p = 0.04$) behaviours were significantly affected by the schedule of enrichment treatments (Table 4). Locomotion was higher during treatment and post-treatment phases (13.5–37.4%) compared to the baseline phase (12.6%). The opposite is the case for vigilance behaviour with the lowest level between 08:00 and 10:00 h occurring during the olfactory (T3) enrichment phase. Levels of exploratory behaviour fluctuated significantly during this time period with a high of 4% occurring during olfactory (T3) enrichment and a low of 0% occurring during the post-olfactory (PT3) enrichment phase. Multiple comparisons of different phases of the study during this time period for locomotion, vigilance and inactive behaviour with an adjusted alpha level of 0.01 revealed no significant differences ($p > 0.01$ for all Wilcoxon's tests) (Table 4). Pacing behaviour was also lower, but not statistically significantly so, during treatment and post-treatment phases (10–15.4%) when compared to baseline levels (23.5%), during 08:00–10:00 h. No behaviours were significantly affected during 10:00–12:00 h.

Between 12:00 and 14:00 h, locomotion ($\chi^2 = 12.571$, d.f. = 6, $p = 0.05$), vigilance ($\chi^2 = 16.992$, d.f. = 6, $p = 0.009$), other ($\chi^2 = 14.944$, d.f. = 6, $p = 0.02$), and inactive ($\chi^2 = 20.245$, d.f. = 6, $p = 0.003$), behaviours were significantly affected by the schedule of enrichment treatments (Table 4). Both locomotion (13.3–23.2%) and vigilance (5.7–11.3%) behaviours remained at similar levels during baseline and other phases except for a large decrease in both behaviours during the spatial change in feeding (T2) enrichment treatment where locomotion dropped to 4% and vigilance dropped to 0% during this phase. Other behaviour was observed to increase to 32.1% during the change in feeding time (T1) enrichment treatment, while levels of this behaviour remained between 2 and 8% during the other phases of the study. Multiple comparisons of different phases of the study during this time period for locomotion, vigilance and inactive behaviour, with an adjusted alpha level of 0.01, revealed no significant differences ($p > 0.01$ for all Wilcoxon's tests) (Table 4).

Between 14:00 and 16:00 h, vigilance ($\chi^2 = 14.295$, d.f. = 6, $p = 0.03$), and exploratory ($\chi^2 = 18.062$, d.f. = 6, $p = 0.006$), behaviour were significantly affected by the schedule of enrichment treatments (Table 4). Levels of vigilance behaviour were lowest during change in feeding time (T1) (2%) and olfactory (T3) (2%) treatments and highest during post-olfactory (PT3) (15.5%) and post spatial feeding variation (PT2) (15.6%) treatments. Exploratory behaviour once again fluctuated with levels during PT3, T2 and PT1 remaining below 1% with the highest level (5.4%) occurring during the baseline phase. Multiple comparisons of different phases of the study during this time period for vigilance and exploratory behaviours with an adjusted alpha level of 0.01 revealed no significant differences ($p > 0.01$ for all Wilcoxon's tests) (Table 4). Between 14:00 and 16:00 h, pacing behaviour remained at similar levels during all phases except for the change in feeding time (T1) treatment, during which, levels of pacing dropped to 0%.

Table 3
The mean (± SD) percentage of instantaneous scan samples in which cheetahs in five enclosures at Fota Wildlife Park were recorded exhibiting each behaviour during different phases of this study.

Behaviour	Baseline	T1	PT1	T2	PT2	T3	PT3	*p*
Locomotion	16.5 (6.4)	17.7 (7.7)	17.8 (3.4)	16.3 (3.9)	20.3(6.8)	21.1(7.2)	17.3(6.9)	*0.59*
Vigilance	11.1 (3.9)	9.5 (2.8)	7.5 (2.7)	6.2 (4)	8.7(2.5)	4.1(1.9)	7(3.0)	***0.04***
Other	10.9 (2.4)	16.8 (6.2)	16.2 (5.9)	19.5 (4.8)	18.5(2.9)	19(2.1)	16.3(2.5)	*0.06*
Exploratory	2.9 (2.5)	2.4 (0.7)	1.4 (0.7)	1.4 (1.7)	1.4(1.5)	3.1(4.2)	0.24(0.3)	***0.01***
Inactive	44.7 (11.4)	46.3(15.6)	48.3 (8.2)	46.5(10.7)	42.4(11.5)	44.5(10.9)	49.4(14.2)	*0.82*
Pacing	13.7 (7.8)	7.7 (6.4)	8.7 (6.4)	10.1 (6)	8.6(6.7)	8.1(7.6)	9.8(6.4)	*0.23*

T1 = Temporal feeding variation, PT1 = Post-treatment 1, T2 = Spatial feeding variation, PT2 = Post-treatment 2, T3 = Olfactory enrichment, PT3 = Post-treatment 3.

Table 4
Behaviours which were significantly affected by schedule of enrichment treatments and the corresponding time periods in which these behaviours were affected. Multiple comparisons with $p < 0.05$ are also shown.

Time period (h)	Behaviour	p	Multiple comparisons with p (<0.05)
08:00–10:00	Locomotion	0.02	Baseline vs. T2
08:00–10:00	Vigilance	0.05	Baseline vs. T3
08:00–10:00	Inactive	0.04	Baseline vs. T2
12:00–14:00	Locomotion	0.05	Baseline vs. T2
12:00–14:00	Vigilance	0.009	Baseline vs. T2, T2 vs. PT2
12:00–14:00	Other	0.02	Baseline vs. T1
12:00–14:00	Inactive	0.003	Baseline vs. T2
14:00–16:00	Vigilance	0.03	Baseline vs. T1, T1 vs. PT1, T3 vs. PT3
14:00–16:00	Exploratory	0.006	Baseline vs. T2
16:00–18:00	Other	0.001	Baseline vs. T1, Baseline vs. T2, Baseline vs. T3, T1 vs. PT1
16:00–18:00	Inactive	0.008	Baseline vs. T1, T1 vs. PT1

Between 16:00 and 18:00 h, other ($\chi^2 = 21.875$, d.f. = 6, $p = 0.001$), and inactive ($\chi^2 = 17.280$, d.f. = 6, $p = 0.008$), behaviours were significantly affected by schedule of the enrichment treatments (Table 4). Other behaviour showed a sharp decrease to 11.9% during the change in feeding time (T1) treatment but remained at levels between 35.9 and 58.7% for all other phases. Inactive behaviour showed the exact opposite trend, increasing to 56.6% during T1 and remaining relatively low between 9.5 and 20.7% during all other phases within the 16:00–18:00 h time period. Multiple comparisons of different phases of the study during this time period for other and inactive behaviour with an adjusted alpha level of 0.01 revealed no significant differences ($p > 0.01$ for all Wilcoxon's tests) (Table 4). Pacing behaviour was at its lowest, at 2.7%, during T1 between 16:00 and 18:00 h.

3.3. Effect of enrichment treatments on the activity budgets of cheetahs in each enclosure at Fota Wildlife Park

The activity budgets of the three adult females (Enclosure A) ($G = 92.8$, d.f. = 30, $p < 0.001$), the one adult female with four cubs (Enclosure B) ($G = 83.3$, d.f. = 30, $p < 0.001$) and the two adult hand-reared females (Enclosure D) ($G = 59.8$, d.f. = 30, $p < 0.001$) were significantly affected during the enrichment treatments. The activity budgets of the solitary adult hand-reared male (Enclosure C) ($G = 41.5$, d.f. = 30, $p > 0.05$) and the solitary adult female (Enclosure E) ($G = 19.9$, d.f. = 30, $p > 0.05$) were not significantly affected.

3.3.1. Three adult females (Enclosure A)

A large decrease in pacing from 21% of observations in the baseline period to between 6% and 10% during the enrichment treatment and post-treatment phases of the study suggest that the enrichment treatments had both an immediate effect on this group's behaviour while also having a prolonged effect. This group also showed pronounced fluctuations in locomotion and inactive behaviour.

3.3.2. Adult female and four cubs (Enclosure B)

This group showed high levels of inactivity throughout the study with levels of locomotion remaining stable during the study. Levels of pacing in this group, although initially very low continued to decrease during enrichment treatment phases and post-treatment phases.

3.3.3. Solitary hand-reared male (Enclosure C)

Although the G test showed that this male's behaviour was not dependent on treatment phase, an initial decrease in pacing was observed from baseline to the introduction of the change in feeding time (T1). However, levels returned to above baseline periods in the post-treatment phase. After this, levels of pacing remained lower than baseline levels but only slightly. Highest levels of exploratory behaviour (11.1%) were also observed during the olfactory enrichment treatment.

3.3.4. Two hand-reared females (Enclosure D)

A notable increase in locomotion (up to a high of 26.4%) was observed during the change in feeding time treatment (T1) with levels returning to and remaining close to baseline levels thereafter. Levels of pacing showed slight fluctuations around baseline levels while vigilance levels were consistently lower than baseline levels throughout the enrichment and post-treatment phases.

3.3.5. Solitary female (Enclosure E)

Levels of pacing during treatment and post-treatment phases were consistently slightly lower than baseline levels, again suggesting that the enrichment treatments had the positive effect of reducing levels of pacing. All other behaviours remained at similar levels throughout the study with no notable large fluctuations being observed.

4. Discussion

The findings from this study suggest that enrichment in the form of temporal feeding variation, spatial feeding variation and olfactory enrichment provisioned according to a sequential schedule has an effect on the behaviour of cheetahs in captivity. Previous research testing the efficacy of a range of enrichments for six species of felid, ranging from cheetah to jaguar (*Panthera onca*) and lion (Skibiel et al., 2007), had shown that cheetahs had the highest percentage of inactive behaviours and also showed no stereotypic behaviours. When Bond and Lindburg (1990) fed carcasses to cheetahs, they reported improved appetites, longer feeding bouts and greater possessiveness of food, effectively observing behavioural variation after a change to the husbandry routine, which as mentioned earlier can be an effective form of enrichment. The findings from the present study also highlight changes in behaviour upon

the introduction of enrichment. While inactive behaviours were the most common behaviours observed during all phases of this study, the cheetahs at Fota Wildlife Park showed stereotypic behaviour in the form of pacing, ranging from 7% to 13% of overall behaviour during different phases of the study, contrary to the findings of Skibiel et al. (2007). Although multiple pair-wise comparisons testing differences in behaviour between different phases of the study were non-significant, trends indicative of an enriching effect are clear. Increases in active behaviour in the form of the other behaviour category alongside decreasing levels of pacing are present throughout the enrichment schedule.

Vigilance behaviour represents an animal's attempt to investigate its surroundings, stimulated either by fear of being predated upon or by a desire to understand its surroundings. The cheetahs at Fota Wildlife Park primarily showed vigilance behaviour upon the sight of prey species in the adjacent paddock and upon hearing or seeing park-staff vehicles. During the enrichment treatments, vigilance behaviour was consistently below baseline levels. This was partly due to the sporadic nature at which the prey species within the paddock opposite the cheetahs would come into view of the cheetahs and also because of the changes in schedule associated with the temporal feeding variation (T1) and spatial variation in feeding (T2). During both of these phases, the time and place at which park staff would pass the cheetah enclosures changed and therefore, the times in which the cats were usually vigilant were spent on other behaviours such as locomotion, inactive and exploratory behaviours. The largest decrease in vigilance behaviour came during the olfactory enrichment treatment (T3). An increase in locomotion and exploratory behaviour, combined with this decrease in vigilance behaviour can be explained by the method in which the oryx faeces were presented to the cheetahs. The keepers would enter the enclosures and place the faeces at random points throughout the enclosures. This led the cheetahs to follow at a distance while the keepers went around inside enclosures, leading to the increase in locomotion observed during this phase. The cheetahs also spent a greater proportion of time not only inspecting the faeces but also in the areas where the keepers had visited, which in turn increased levels of exploratory behaviour within the enclosures and decreased levels of vigilance associated with the passing of park vehicles outside the enclosures.

Encouraging exploratory behaviour is important for animals in captivity. It allows them to gather information about their surroundings while also allowing them to perform natural species-specific behaviours and possibly reduce stereotypies (Mench, 1998). The use of olfactory enrichment is a relatively easy way to incorporate novelty into the often mundane captive environment. Captive black-footed cats (*Felis nigripes*) showed an increase in active behaviours and a decrease in sedentary behaviours when presented with a range of novel scents (Wells and Egli, 2004). Thomas et al. (2005) observed cheetahs performing cheek-rubbing behaviour and interacting with up to 88% of the perfume and cologne scents introduced into their enclosure. While no cheek-rubbing behaviour was observed in the present study, the cheetahs at Fota Wildlife Park interacted with the oryx faeces by sniffing them and the surrounding area where the faeces had been placed, leading to slightly increased levels of exploratory behaviour. An increase in locomotion during the T3 phase of the study, caused by a combination of the cats following the movement of keepers around the enclosures during placement of the faeces and subsequent movement of the cheetah around the enclosures following the scent of the oryx faeces, also occurred mirroring the results of Wells and Egli (2004) which showed increased activity and exploration. Upon cessation of the olfactory enrichment treatment during PT3, levels of exploratory behaviour decreased significantly alongside an increase in inactive behaviours and decrease in locomotion suggesting that the use of oryx faeces placed randomly by keepers around cheetah enclosures can increase levels of exploratory and locomotory behaviours while decreasing inactive behaviours.

Pacing is a very common stereotypy observed in carnivores (Mason et al., 2007). Felids in captivity often spend a large amount of time performing pacing behaviour prior to feeding (Shepherdson et al., 1993) which is hypothesised to develop from appetitive foraging behaviour (Mason, 1993). Feeding schedules which are temporally predictable have been linked to stereotypies in carnivores (Carlstead, 1998). Food anticipatory activity (FAA), which is characterised by increased arousal and activity, is also generally seen in animals which are fed on a regular schedule (Bassett and Buchanan-Smith, 2007). The cheetahs at Fota Wildlife Park are fed on a predictable schedule and showed a high level of arousal and activity, which was often observed as pacing behaviour around feeding time during the baseline period. Upon temporal variation of feeding (T1), pacing decreased, from 13.7% during baseline, to 7.7%, although non-significantly so. Due to the unpredictable nature of feeding time, the cheetahs did not perform pacing behaviour around the usual feeding time because they were unmotivated to perform pacing behaviour due to the fact they had already been fed. A reduction in pacing was also observed for spatial feeding variation (T2) although this was not as pronounced as for T1. The movement of feeding location (T2) did not allow the cats to focus pacing behaviour at the usual feeding location. Although non-significantly affecting pacing behaviour, there is an indication that the use of these three forms of enrichment can be employed to help to reduce pacing behaviour of cheetahs in captivity. This mirrors the findings of Shepherdson et al. (1993) and Jenny and Schmid (2002) who upon the implementation of temporally and spatially unpredictable feeding regimes for leopard cats and Amur tigers respectively observed reductions in pacing behaviour. In their studies, the effects of temporal and spatial unpredictability were confounded whereas in this study temporal and spatial unpredictability of feeding were employed separately and both individually reduced levels of pacing.

It is important to keep in mind the effect of the schedule used in this study. The post-treatment phases which effectively punctuated the enrichment treatments with another baseline period are also an integral part of the study hence, the reason they were included in the analysis. They not

only did not allow the animals to become habituated to the individual treatments but also provided a degree of novelty themselves. For example from baseline to T1, feeding time was changed and from T1 to PT1 feeding time was also changed, albeit back to the original predictable schedule, allowing lingering effects of the novelty of the temporal variation in feeding to be combined with the novelty of returning back to the original feeding time. This continued into the spatial variation in feeding and introduction of novel odours. With respect to pacing behaviour in captive cheetahs, the present study (Table 3) highlights that the use of multiple types of enrichment in sequence can help to maintain novelty and the subsequent positive behavioural changes as observed in this study. Confounding variables due to the length of the schedule including weather, reproductive status of females and changes in the age of the cubs may have also influenced behaviour. However, at no stage were the females observed rolling or rubbing, two behaviours indicative of oestrus (Wielebnowski and Brown, 1998). Temperature ranges were also narrow with average maximum temperatures reaching between 7.4 and 10 °C and minimum temperatures reaching 2.1 and 5.2 °C throughout the study. However, trends that mirror previous results in the field of environmental enrichment are clear in this study and indicate that these three forms of enrichment can have an enriching effect for cheetahs in captivity. Also, the monitoring of cheetah behaviour in captivity over a long period of time is distinctly lacking in the literature and therefore this research also offers an insight into general behaviour patterns of cheetahs in captivity over an extended period of time. Experimentation with a variety of enrichment schedules also provides wardens in zoological institution with a greater array of information and choices in the environmental enrichment they employ in their institutions.

Table 4 summarises which behaviours were significantly affected by the enrichment treatment schedule and what time periods they were affected in. The fact that different behaviours were affected during different time periods during the day highlights the importance of when specific enrichment treatments are introduced to cheetahs in captivity. This is clearly observed during the 14:00–16:00 h and 16:00–18:00 h time periods particularly for the temporal variation in feeding. Pacing behaviour was eradicated between 14:00 and 16:00 h when feeding was moved to this time period. Between 16:00 and 18:00 h, pacing was at its lowest (2.7%) during T1 also. As mentioned earlier, the motivation to perform pacing behaviour was largely absent because feeding had occurred at a time when the cheetahs were not expecting food and this lack of motivation carried into the normal feeding period because the cheetahs were largely inactive after feeding had occurred. This is highlighted by the observation that inactive behaviours were low during all phases of the study between 16:00 and 18:00 h (9.5–20%) except for T1 (57%). Temporal feeding variation therefore can be used to reduce pacing in cheetahs that occurs regularly at a particular time. However, an increase in inactive behaviours will occur in the time following feeding. This also raises the question about the possible advantages of temporally pinpointing particular enrichment treatments in order to promote natural behaviours or prevent abnormal behaviours. Three of the five groups of cheetahs at Fota Wildlife Park had their activity budgets significantly affected by the enrichment treatments. All groups reacted positively to the introduction of the enrichment treatment including increases in locomotory and exploratory behaviour and decreases in pacing behaviour and at no stage of this study did the enrichment treatments cause an increase in abnormal behaviours. Individual behavioural variation between groups and their individual reactions to the three enrichment treatments suggest that particular 'tailored' enrichment treatments might be beneficial for cheetahs and indeed other species. Research into more types of enrichment designed particularly in relation to feeding for this cursorial predator may help to further promote natural behaviour patterns and reduce pacing behaviour in captivity.

5. Conclusions

Overall, the results suggest that the use of temporal feeding variation, spatial feeding variation and olfactory enrichment using oryx faeces can be an easily introduced and effective form of enrichment for cheetahs in captivity. Vigilance, exploratory and pacing behaviour were all influenced by the different types of enrichment, (albeit sometimes non-significantly), resulting in increased natural behaviours and a concomitant reduction in pacing. Different behaviours were significantly affected at different time periods raising the question about the possible use of the introduction of enrichment at particular periods of time when abnormal behaviour is prevalent. Inter-group behavioural variation in reaction to the enrichments highlight the possible need for the development of enrichment schedules to accommodate for the inherent behavioural variation within the species. Future research on the behavioural effects of a randomised enrichment treatment schedule rather than a sequential one used in the present study may be of benefit in order to separate the effects of the schedule and the treatments.

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References

Bassett, L., Buchanan-Smith, H.M., 2007. Effects of predictability on the welfare of captive animals. Appl. Anim. Behav. Sci. 103, 223–245.

Bond, J.C., Lindburg, D.G., 1990. Carcass feeding of captive cheetahs (*Acinonyx jubatus*): the effects of a naturalistic feeding program on oral health and psychological well-being. Appl. Anim. Behav. Sci. 26, 373–382.

Carlstead, K., 1998. Determining the causes of stereotypic behaviours in zoo carnivores toward appropriate enrichment strategies. In: Shepherdson, D.J., Mellen, J.D., Hutchin, M. (Eds.), Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution Press, Washington, DC, pp. 172–181.

Carlstead, K., Seidensticker, J., Baldwin, R., 1991. Environmental enrichment for zoo bears. Zoo Biol. 10, 3–16.
Caro, T.M., 1994. Cheetahs of the Serengeti Plains: Group Living of an Asocial Species. University of Chicago Press, Chicago, 500 pp.
Hediger, H., 1969. Man and Animal in the Zoo. Routledge and Kegon Paul, London.
Jenny, S., Schmid, H., 2002. Effect of feeding boxes on the behaviour of stereotyping Amur Tigers (*Panthera tigris altaica*) in the Zurich Zoo, Zurich, Switzerland. Zoo Biol. 21, 573–584.
Kistler, C., Hegglin, D., Wurbel, H., Konig, B., 2009. Feeding enrichment in an opportunistic carnivore: the red fox. Appl. Anim. Behav. Sci. 116, 260–265.
Margulis, S.W., Hoyos, C., Anderson, M., 2003. Effect of felid activity on zoo visitor interest. Zoo Biol. 22, 587–599.
Mason, G.J., 1991. Stereotypies: a critical review. Anim. Behav. 41, 1015–1037.
Mason, G.J., 1993. Forms of stereotypic behaviour. In: Lawrence, A.B., Rushen, J. (Eds.), Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare. CAB International, Oxon, UK, pp. 7–40.
Mason, G., Clubb, R., Latham, N., Vickery, S., 2007. Why and how should we use environmental enrichment to tackle stereotypic behaviour? Appl. Anim. Behav. Sci. 102, 163–188.
Mench, J.A., 1998. Environmental enrichment and the importance of exploratory behaviour. In: Shepherdson, D.J., Mellen, J.D., Hutchin, M. (Eds.), Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution Press, Washington, DC, pp. 30–41.
Pearson, J., 2002. On a roll: novel objects and scent enrichment for Asiatic lions. Shape Enrichment 11, 7–10.
Powell, D., 1995. Preliminary evaluation of environmental enrichment techniques for African lions (*Panthera leo*). Anim. Welf. 4, 361–371.
Shepherdson, D., Carlstead, K., Mellen, J.M., Seidensticker, J., 1993. The influence of food presentation on the behaviour of small cats in confined environments. Zoo Biol. 12, 203–216.
Skibiel, A.L., Trevino, H.S., Naugher, K., 2007. Comparison of several types of enrichment for captive felids. Zoo Biol. 26, 371–381.
Swaisgood, R.R., Shepherdson, D.J., 2005. Scientific approaches to enrichment and stereotypies in zoo animals: what's been done and where should we go next? Zoo Biol. 24, 499–518.
Thomas, P., Balme, G., Hunter, L., McCabe-Parodi, J., 2005. Using scent attractants to non-invasively collect hair samples from cheetahs, leopards and lions. Anim. Keep. For. 8, 342–384.
Wells, D.L., Egli, J.M., 2004. The influence of olfactory enrichment on the behaviour of captive black-footed cats, *Felis nigripes*. App. Anim. Behav. Sci. 85, 107–119.
Wielebnowski, N.J., Brown, J.L., 1998. Behavioural correlates of physiological estrus in cheetahs. Zoo Biol. 17, 193–209.
Williams, B.G., Waran, N.K., Carruthers, J., Young, R.J., 1996. The effect of moving bait on the behaviour of captive cheetahs (*Acinonyx jubatus*). Anim. Welf. 5, 271–281.
Yerkes, R.M., 1925. Almost Human, New York, Century.