



Factors influencing the prevalence of stereotypical behaviour in captive cheetahs (*Acinonyx jubatus*)

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ARTICLE INFO

Article history:

Accepted 18 September 2012

Available online 31 October 2012

Keywords:

Cheetah

Stereotypical behaviour

Captivity

Information theory

ABSTRACT

The purpose of the current study was to investigate the factors which influence the prevalence of stereotypical behaviour in captive cheetahs. An information theory approach highlighted that the most optimal model was the controllable husbandry factors model with the size of enclosures, group membership, feeding regime and the ability to view other cheetahs in adjacent enclosures being the significant factors within the model which determined the occurrence of stereotypical behaviour. Increasing size of enclosure decreased this behaviour, whilst being solitary, being fed on a predictable feeding regime and having the ability to view other cheetahs in adjacent enclosures increased levels of stereotypical behaviour. These findings allow zoological institutions to focus on these factors in order to reduce the occurrence of stereotypical behaviour in captive cheetahs. Although cheetahs were used as the subject animal in this study, this type of research can be utilised for any captive species in order to understand unwanted behaviours or behaviours that zoological institutions wish to promote, so a behaviourally healthy captive population can be exhibited, reproduced and subsequently conserved.

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1. Introduction

For many captive wild species, a number of difficulties exist in captivity. These include low conception rates, high infant mortality rates, behavioural problems, disease, artificial selection and other genetic issues. This is despite the fact that these animals receive veterinary care and are free from problems such as predation, starvation and drought (Clubb and Mason, 2007). These issues negatively affect public perception of zoological institutions, animal welfare and may also affect reintroduction attempts in the future. The issue of stereotypical behaviour is arguably the most well known and widely researched topic within the captive setting. The zoo scientific community was among

the first to focus attention on captivity-induced stereotypical behaviours in relation to the factors which promote their occurrence, as well as methods to eradicate them (Swaigood and Shepherdson, 2005).

Stereotypical behaviour has previously been defined as repetitive, unvarying and apparently functionless behaviour (Mason, 1991). Mason et al. (2007) highlighted three non-mutually exclusive reasons why captive animals perform stereotypical behaviours. These can be condensed into two main causes, namely frustration-induced stereotypical behaviours and malfunction-induced stereotypical behaviours. The former behaviours are driven directly by motivational frustration, fear or physical discomfort whilst the latter behaviours are products of central nervous system abnormality (Mason et al., 2007). There are many different types of stereotypical behaviours. Holzapfel (1939) was one of the first researchers to describe some of the behaviour patterns that develop into repetitive movements in zoo animals and the situations in which this

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behaviour is elicited (Carlstead, 1998). Examples of stereotypical behaviours include pacing, body-rocking, repetitive jumping, fur plucking and self-biting. Different taxa also show differences in the type of stereotypical behaviour displayed. Analyses by Mason et al. (2007) revealed that carnivores favour locomotory stereotypical behaviours, such as pacing, whilst ungulates, and to a lesser extent, primates, favour oral forms of stereotypical behaviours. The origin of stereotypical behaviours is complex and a variety of functional reasons may be responsible for development of these behaviours. In most zoo animals, stereotypical activity arises from a primary behaviour pattern, that, over time, the animal has become motivated to perform (Holzapfel, 1939). Furthermore, these behaviours often develop from thwarted attempts to perform specific motivated behaviours, suggesting frustration, which as mentioned earlier is one of the causes of stereotypical behaviour (Mason et al., 2007).

The captive environment is characterised by relatively high population densities, limited space, low predation pressure, readily available food at regular intervals and physical barriers preventing dispersal and immigration (Newberry, 1993). Many, if not all, of these aspects of captivity may prevent captive animals carrying out certain behaviours effectively, therefore leading to the development of stereotypical behaviours. A survey by Mason and Latham (2004) highlighted that 68% of environments that cause stereotypical behaviours are associated with diminished welfare and their advice is that 'stereotypies should always be taken seriously as a warning sign of potential suffering'. However, a 'scar' from previous suboptimal environments may result in the prevalence of stereotypical behaviour even if current conditions are optimal. Also rather paradoxically, if stereotypical behaviour is a means of coping, are those animals which show these behaviours in suboptimal environments better off than the animals that do not? (Swaisgood and Shepherdson, 2005). The 'coping hypothesis' suggests that the performance of stereotypical behaviour may result in a reduction in the physiological measures of stress. Pomerantz et al. (2012) observed that self-directed stereotypies in rhesus macaques (*Macaca mulatta*) were negatively correlated with an increase in faecal corticoids following a stress challenge. Cross and Rogers (2006) observed a decrease in cortisol levels in common marmosets (*Callithrix jacchus*) when a snake-model stimulus that elicited mobbing calls was presented to them. In contrast, Gusset (2005) highlighted that pacing behaviour did not help two margays (*Leopardus wiedii*) to cope by reducing physiological stress levels. Numerous other studies, on pandas (*Ailuropoda melanoleuca*) (Liu et al., 2006), western lowland gorillas (*Gorilla gorilla gorilla*) (Clark et al., 2012) and clouded leopards (*Neofelis nebulosa*) (Wielebnowski et al., 2002a) have highlighted that an increase in stereotypical behaviour is associated with an increase in stress hormones. Tackling the causal factors of stereotypical behaviour via environmental enrichment and husbandry practices can help to minimise stress and the need for coping mechanisms in captive animals.

Environmental enrichment is widely used in order to decrease stereotypical behaviours in captivity. A

meta-analysis by Swaisgood and Shepherdson (2006) revealed that environmental enrichment works well, with carnivores, primates and other species, showing a reduction in stereotypical behaviours of between 50% and 60%. However, environmental enrichment is now widely regarded to be an essential part of the daily routine in the majority of zoological institutions worldwide. It also rarely totally eradicates stereotypical behaviour. Therefore, it is important to determine what factors promote its prevalence for all species within the captive setting. Bashaw et al. (2001) reported that sub-species, birth history, size of indoor enclosure, environmental change and type of food were all predictors of pacing behaviour in giraffes (*Giraffa camelopardalis*) and okapis (*Okapi johnstoni*). Mallapur and Chellam (2002) highlighted that enclosure type, feeding regime and the presence of visitors influenced the behaviour of captive leopards (*Panthera pardus*). Temporally predictable feeding schedules have also been linked to stereotypical behaviour in some carnivores (Carlstead, 1998). Forthman-Quick (1984) suggested that the tendency for wide ranging carnivores, such as the wolf (*Canis lupus*), to develop stereotypical pacing lies in the fact that they range widely in the wild and are frustrated by the lack of ability to do so in captivity. Robinson (1998) stated how inter-zoo comparisons between different habitats of the same species are potentially fruitful areas of research. Inter-zoo research allows for comparisons of levels of stereotypical behaviour between zoological institutions which differ substantially for a range of variables. These variables include amongst others, enclosure size, visitor numbers, feeding regime, social housing, enclosure furniture and vehicle disturbance.

The overall objective of this research was to collect data on the levels of stereotypical behaviour in cheetahs (*Acinonyx jubatus*) in a multi-institutional study, in order to identify the factors within the captive setting which determine its occurrence. Physiological measures of stress were not included in this research due to the very large samples size of cheetahs across the nine institutions and the associated feasibility issues in relation to assay numbers and resources available in each institution for sample collection. The aims of this research were to (1) provide a study to be used as a template for future researchers in order to examine levels of stereotypical behaviour in a wide range of species within the captive setting and, (2) highlight which factors relating to captive husbandry and management influence the occurrence of stereotypical behaviour through an information theory approach, and (3) discuss how these can be altered and manipulated in order to reduce the prevalence of stereotypical behaviour in cheetahs. The authors hypothesise that a range of factors influence the prevalence of this type of behaviour, some reducing its occurrence and others increasing its occurrence.

2. Methods

2.1. Study sites and animals

One hundred and twelve cheetahs maintained in 88 enclosures were the subjects of this study. Data were

Table 1
List of covariates.

Covariate	Abbreviations	Continuous/categorical
Enclosure size Measured in m ²	Size	Continuous
Visual barriers Visual barrier defined as an object/area/vegetation where a cheetah can be fully concealed.	Visual	Continuous (1–10 scale, 10 being many visual barriers)
Presence of raised areas Classified as platforms, high mounds, logs and low tree branches. Roofs of shelters not included	Raised	Categorical (1 = not present, 2 = present)
Visitor numbers	Visitors	Continuous
Feeding predictability Predictable feeding is feeding that occurred within the same hour daily	Feeding	Categorical (1 = predictable, 2 = unpredictable)
Ability to view cheetahs in adjacent 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 Number of times cheetahs were moved between different enclosures.	Enclosure	Continuous
Vehicle disturbance Number of times any vehicle passed enclosure.	Vehicle	Continuous
Diet diversity	Diet	Continuous
Age	Age	Continuous

collected on cheetahs maintained 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 (formerly De Wildt) in South Africa. Institutions had been selected based on the number of cheetahs they maintained, as well as their differences in the factors examined during the study (Table 1). The minimum temperatures during data collection periods ranged from 3 to 9 °C whilst maximum temperatures ranged from 18 to 26 °C. 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. This resulted in a narrow average temperature range (10–16 °C) across the nine institutions during data collection periods. Fifty seven cheetahs were male and fifty five were female. Ages ranged from one year to fifteen years of age. Of these, forty five were solitary and sixty seven were maintained in groups. Table 2 highlights how the cheetahs were maintained in groups. Throughout the study, no cheetahs were on contraceptives, were involved in breeding introductions or were pregnant. During the study, 102 cheetahs belonged to the southern subspecies (*Acinonyx jubatus jubatus*) and ten belonged to the northern subspecies of cheetah (*Acinonyx jubatus soemmeringii*).

2.2. Data collection

Data were collected on stereotypical behaviour using instantaneous scan sampling with a five minute inter-scan interval. Pacing was defined as repetitive locomotory movement along a given route (up/down fence line, around enclosure or object in enclosure) uninterrupted by other behaviours. At Africa Alive, Banham Zoo, Colchester Zoo,

Chester Zoo, ZSL Whipsnade, Toronto Zoo and Fota Wildlife Park, data were collected between 08:00 h and 18:00 h. Data collection during the winter months in Africa Alive, Banham Zoo, Colchester Zoo and Fota Wildlife Park was shortened to between 08:00 h and 17:00 h due to closing times of the zoo, cheetahs being put in their night

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

dens, and the fact that no researchers were permitted to remain on zoo grounds after closing hours. Behaviour data were collected between November 2008 and October 2010. Data were collected between 07:00 h and 17:00 h at the Ann van Dyk Cheetah Centre and at the Cheetah Conservation Fund. Each day was divided into a number of two hour periods (e.g.: 08:00–10:00 h, 10:00 h–12:00 h, 12:00 h–14:00 h, 14:00–16:00 h, 16:00–18:00 h), consisting of eight fifteen minute 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 point 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 one 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. Data were collected for all individuals within each enclosure. For enclosures with more than one individual, data were combined to create a single data point for behaviour within a given enclosure in order to obtain one data point for each enclosure and its associated factors.

2.3. Data analysis

Before applying any statistical models, data exploration following the protocol described in [Zuur et al. \(2010\)](#) was carried out. The presence of outliers in the response and continuous covariates was investigated with Cleveland

dotplots. Collinearity (relationships between covariates) was assessed with variance inflation factors (VIF). 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](#). Temperature was not included as a covariate due to the narrow average temperature range which occurred across the institutions during data collection periods. The data collection procedure which was carried out across a large range of temperatures for each institution negated the requirement for this to be included as a covariate. The total number of times stereotypical behaviour was observed for each enclosure was modelled using a generalised 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 stereotypical behaviour 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 stereotypical behaviour is observed for observation j in zoo i). To model this probability we used the logistic link function of the form: $\text{Logit}(\pi_{ij}) = \text{Covariates} + a_i + \varepsilon_{ij}$ $a_i \sim N(0, \sigma_{zoo}^2)$ and $\varepsilon_{ij} \sim N(0, \sigma^2)$

The random intercept a_i introduces a correlation structure between all observations 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
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 + Size:Other + Group:Enrichment + Size:Sex + Sex:Age	All zoo factor model with selected interactions
M3	Sex + Age + Sex:Age	Sex/Age model
M4	Visitors + Sex + Age + Vehicle	Not easily controllable husbandry factors
M5	Visitors + Sex + Age + Vehicle + Visitors: Vehicle + Sex:Age + Sex:Visitors + Age:Visitors	Not easily controllable husbandry factors with selected interactions
M6	Size + Other + Oc + Feeding + Group + Enclosure + Enrichment + Raised + Size:Oc + Size:Other + Size:Group + Group:Feeding + Group:Enrichment	Controllable husbandry factors with selected interactions
M7	Size + Other + Oc + Feeding + Group + Enclosure + Enrichment + Raised	Controllable husbandry factor model
M8	Size + Oc + Other + Feeding + Group + Sex + Age + Enclosure	Ranging model
M9	Size + Oc + Other + Feeding + Group + Sex + Age + Enclosure + Size:Sex + Size:Age + Oc:Other + Size:Feeding + Group:Sex	Ranging model with selected interactions
M10	Vehicle + Visitors + Oc + Enclosure + Vehicle: Visitors + Vehicle:Oc + Oc:Visitors	Possible stress sources model
M11	Enrichment + Raised + Group + Sex + Age + Enrichment: Raised + Enrichment:Sex + Enrichment:Age + Enrichment:Group	Enrichment model with interactions

†: indicates an interaction.

Table 4
Comparison of alternative models.

Model	df	AIC	AIC differences	Akaike weights (w)
M1	15	322.099	2.217	0.129
M2	20	326.044	6.162	0.018
M3	6	346.634	26.752	0.000
M4	7	344.551	24.669	0.000
M5	11	344.634	24.760	0.000
M6	16	321.483	1.601	0.175
M7	11	319.882	0	0.390
M8	11	321.471	1.588	0.176
M9	16	322.390	2.508	0.111
M10	10	346.516	26.634	0.000
M11	12	334.651	14.769	0.000

Table 3 shows the 11 models that were applied. All 11 models were decided upon *a priori*. The package lme4 (Bates and Maechler, 2011) in the software R version 2.12.0 was used to estimate the parameters of the GLMMs. The alpha level for statistical significance was taken to be <0.01.

3. Results

Two forms of stereotypical behaviour were observed during this study, pacing and repetitive fence licking (only observed on one occasion in one cheetah). Therefore, from this point on, stereotypical behaviour refers to pacing behaviour. Stereotypical behaviour was observed in 85 of 88 enclosures. The mean proportion (\pm SD) of the activity budget occupied with this behaviour was 0.108 (\pm 0.088). The highest proportion of stereotypical behaviour observed was 0.375. The use of an information theory approach, utilising 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 stereotypical behaviour in captivity (Table 3).

Table 5
Estimated parameters and *p* values for each covariate for the five most optimal models.

	M7	M8	M6	M1	M9
Size	−0.446 (0.005)	−0.315 (0.007)	0.380 (0.306)	−0.349 (0.008)	−0.371 (0.057)
Raised	0.097 (0.703)	–	0.137 (0.58)	0.125 (0.637)	–
Visitors	–	–	–	−0.04 (0.722)	–
Feeding	−0.825 (0.0006)	−0.902 (0.0002)	−0.692 (0.016)	−0.679 (0.005)	−0.875 (0.0002)
Oc	0.955 (0.00007)	1.06 (0.00005)	0.772 (0.001)	0.967 (0.0001)	1.422 (0.005)
Other	0.491 (0.032)	0.39 (0.097)	0.344 (0.166)	0.251 (0.309)	1.005 (0.074)
Enrichment	0.414 (0.067)	–	0.242 (0.430)	0.142 (0.59)	–
Group	−0.786 (0.0003)	−0.777 (0.0005)	−1.02 (0.001)	−0.865 (0.00008)	−0.357 (0.257)
Sex	–	0.026 (0.894)	–	0.055 (0.783)	0.458 (0.093)
Enclosure	−0.115 (0.289)	−0.080 (0.48)	−0.061 (0.602)	−0.080 (0.468)	−0.020 (0.87)
Vehicle	–	–	–	0.244 (0.05)	–
Age	–	−0.143 (0.188)	–	−0.145 (0.171)	−0.167 (0.119)
Size: Oc	–	–	−0.397 (0.166)	–	–
Size: Other	–	–	−0.459 (0.052)	–	–
Group: Enrichment	–	–	0.230 (0.61)	–	–
Size: Sex	–	–	–	–	0.398 (0.07)
Size: Group	–	–	−0.408 (0.09)	–	–
Group: Feeding	–	–	0.039 (0.929)	–	–
Size: Age	–	–	–	–	0.145 (0.205)
Oc: Other	–	–	–	–	−0.617 (0.327)
Size: Feeding	–	–	–	–	−0.467 (0.049)
Group: Sex	–	–	–	–	−0.885 (0.039)

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. All models were overdispersed as can be inferred from the estimated values of σ^2 with values of around 0 signifying no overdispersion. Application of initial models without the observation level random effects resulted in overdispersed 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 M7, M8, M6, M1 and M9 are 0.390, 0.176, 0.175, 0.129 and 0.111 respectively. A value of 1 signified the perfect model. Therefore, this means that if sampling would take place a large number of times, then in 39% of the cases, model M7 (Controllable husbandry factors model) is the most optimal model, and in 17.6%, 17.5%, 12.9% and 11.1% of cases, models M8 (Ranging model), M6 (Controllable husbandry factors with selected interactions), M1 (All zoo factor model) and M9 (Ranging model with selected interactions) respectively are the most optimal models. The covariates of enclosure size (size), predictability of feeding (feeding), the ability to view other cheetahs (oc) and group membership (group) are significantly different to 0 at the 1% level in models M7, M8 and M1. The covariates, oc and group and feeding and group are significantly different to 0 at the 1% level in models M6 and M9 respectively (Table 5).

Fig. 1 shows a visual representation of the most optimal model (M7). The probability of observing stereotypical behaviour decreases as enclosure size increases. Stereotypical behaviour was higher in solitary cheetahs, cheetahs fed on a predictable feeding routine and when cheetahs had the ability to view other cheetahs (Fig. 1).

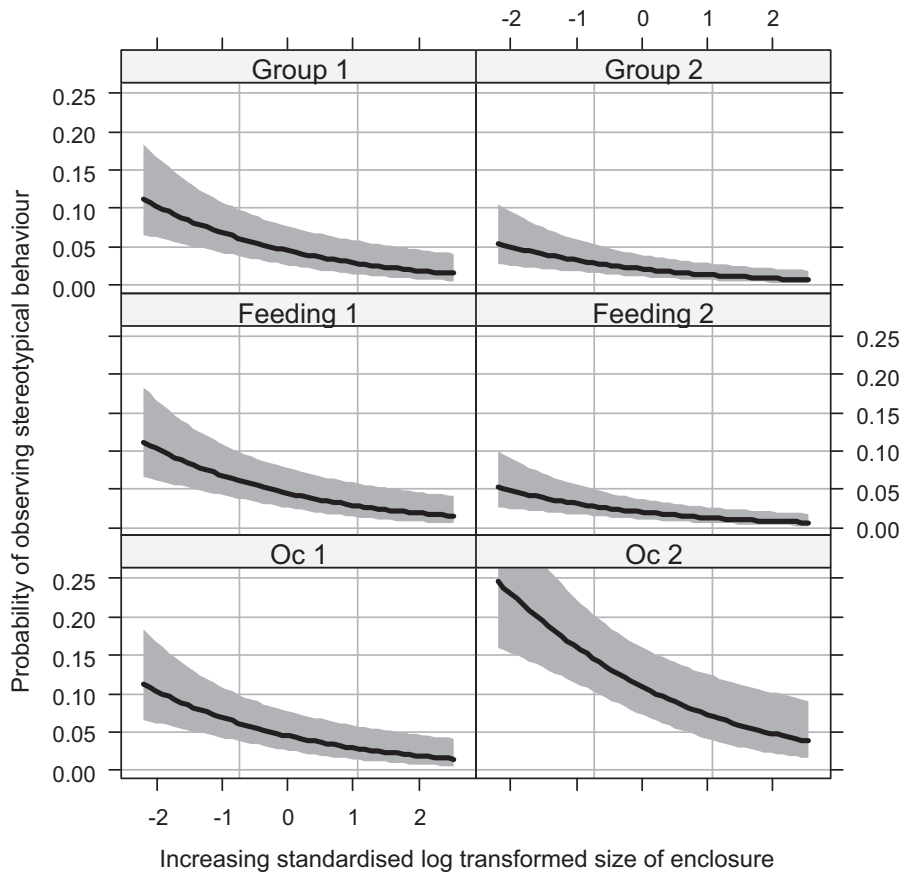


Fig. 1. Visual representation of optimal model, M7 showing the effects that the ability to view other cheetahs, feeding predictability and group membership have on the probability of observing stereotypical behaviour (Group 1 = solitary, Group 2 = in a group, Feeding 1 = predictable feeding, Feeding 2 = unpredictable feeding, Oc 1 = cannot view other cheetahs in adjacent enclosures, Oc 2 = can view other cheetahs in adjacent enclosures).

4. Discussion

The management of zoo animals requires attention to many facets of biology including behavioural requirements, social interactions, habitat characteristics, reproduction and genetics. Swaisgood (2007) outlined ten theories, proposed in order to explain good and bad welfare in captivity. These ten theories can also be utilised to design and provide enclosures which provide opportunities for animals to perform natural species-typical behaviours and minimise the performance of abnormal and stereotypical behaviours. Included in the ten theories are ethological needs, information gathering, mimicry of nature, aspects of control/choice, minimisation of boredom, sensory stimulation, reduction of stress, coping, environmental channelling where outlets for appropriate behavioural patterns are provided and finally perseveration (Swaisgood, 2007). Behaviour is a reaction of animals to their environment (Carlstead, 1996), and as Seidensticker and Doherty (1996) pointed out, a good way to understand a captive animal is to observe what the animal does in their exhibit space. The current research revealed how environmental variability within the captive setting influences the prevalence of stereotypical behaviour in cheetahs.

Increasing enclosure size resulted in a decrease in levels of stereotypical behaviour. This is in contrast to the findings of Lyons et al. (1997) who reported that size of enclosure did not affect pacing behaviour. In the present study, smaller enclosures were associated with fewer visual barriers, raised areas and proximity to other enclosures containing cheetahs. In the Serengeti, an average territory size for male cheetahs is 37 km² whilst females range over areas as large as 830 km² (Caro, 1994). In contrast, on Namibian farmlands, both cheetah sexes have very large home ranges (average 1642 km²) (Marker, 2002). Clubb and Mason (2007) have highlighted how home range size and daily travel distances significantly predicted levels of stereotypical behaviour. Wild animals ranging over large areas experience substantial sensory stimulation in the form of novel odours, sights and sounds. In captivity, smaller less complex enclosures do not provide the necessary stimulation in relation to information gathering and minimisation of boredom. Smaller enclosures also provide fewer refuges from the stressors present within the captive environment and may subsequently result in elevated levels of stress related stereotypical behaviour. Carlstead et al. (1993) observed a decrease in both levels of pacing and cortisol in leopard cats (*Prionailurus bengalensis*) when hiding places were provided within their enclosures. Larger, more

complex environments therefore can contribute to a lower level of stereotypical behaviours for captive cheetahs.

In the present study, the most optimal model highlighted that solitary cheetahs were observed to perform higher levels of stereotypical behaviour compared to those maintained in groups. Mellen et al. (1998) also observed less pacing in small felids kept in groups of three compared to when the felids were solitary. It is possible that because solitary cheetahs lack the opportunity to perform certain affiliative and other social behaviours compared to those maintained in groups, stereotypical behaviour takes up a greater percentage of their daily activity budget. De Rouck et al. (2005) highlighted that pair-housed tigers (*Panthera tigris*) performed a wider variety of behaviours, particularly social interactions, compared to singly housed tigers. Although these groupings may be considered unnatural for these species, cheetahs can be maintained in compatible groups and the benefits observed in the aforementioned studies are applicable to cheetahs. Solitary cheetahs in this study were also maintained predominantly in smaller enclosures and therefore, the enclosure size effect also contributed to the observed levels of stereotypical behaviour.

A predictable feeding schedule resulted in increased levels of stereotypical behaviour. Carnivores possess a complex foraging mode consisting of various phases including stalk, chase, kill and digest, and they devote a significant amount of time to hunting behaviour in the wild (Shepherdson et al., 1993). However, within the captive setting, whilst the motivation to perform these behaviours remains, the opportunity to do so is often lacking. Stereotypical pacing behaviour is sometimes thought to derive from the motivation to express these appetitive behaviours, particularly before feeding (Mason, 1991). Food anticipatory activity (FAA) which is characterised by increased activity and arousal (Bassett and Buchanan-Smith, 2007) was often observed in the form of pacing behaviour during this study, particularly when the feeding schedule was predictable. When the feeding schedule was unpredictable, this anticipatory activity did not develop at any particular time, subsequently resulting in a decrease in the level of stereotypical pacing behaviour. Some may argue that anticipatory pre-feeding pacing is a harmless version of hunting behaviours within a captive setting, however just as Mason et al. (2007) argued for a 'zero-tolerance' policy for stereotypical behaviour, the authors also point out that all forms of pacing are artefacts of captivity and should be minimised at all times. Previous research by Kistler et al. (2009) and Jenny and Schmid (2002) with red fox (*Vulpes vulpes*) and Amur tigers (*Panthera tigris altaica*) respectively has also highlighted the behavioural benefits of provisioning captive carnivores with food unpredictably both in time and space. Quirke and O'Riordan (2011a,b) recommend the use of temporal feeding variation, as one of the easily introduced forms of enrichment for captive cheetahs in order to reduce stereotypical pacing behaviour.

The ability to view other cheetahs in adjacent enclosures resulted in increased levels of stereotypical behaviour. Forced proximity to other individuals is a common situation in captivity. Cheetahs can be maintained in compatible groups in captivity because as with lions, they have a

relatively unique social system compared to other felids (Caro, 1994; Ziegler-Meeks, 2009). However, the problem is associated with different groups or individuals which are not compatible being maintained in adjacent enclosures with no visual barriers between those enclosures. Male cheetahs have been observed to delineate territories through scent-marking and have also been observed to fight to obtain access to a territory (Caro, 1994). De Rouck et al. (2005) also pointed out that tigers without neighbouring tigers paced significantly less than those with neighbours. Increased pacing was observed along the edges of enclosures where other cheetahs in adjacent enclosures could be observed. Lyons et al. (1997) observed that edges of enclosures were used specifically for pacing. Frustration-induced pacing behaviour may have resulted from the inability to perform appropriate behaviours in the given situation, namely, affiliation or aggression directed towards to the other individual. Alternatively, repetitive patrolling of territory boundaries as a result of visual contact with unknown males may have contributed to the increased levels of stereotypical pacing. Wielebnowski et al. (2002b) highlighted how maintaining incompatible females together in captivity resulted in agonistic behaviour (as well as suppressed ovarian cyclicity). Females are predominantly solitary in the wild but, as with males, are often maintained in compatible groups in captivity. Increased stress when in close proximity to other enclosures containing either groups of incompatible females or an individual, may have promoted increased levels of stereotypical behaviour. The inability to perform appropriate social interactions with neighbouring males may have also contributed to increased levels of stereotypical behaviour.

Increasing the size of an animal's enclosure is very rarely feasible, given the space limitations present in the majority of zoological institutions worldwide, although the effect of enclosure size should be kept in mind when designing new enclosures. However, incorporating an increased number of variable olfactory, auditory, tactile and visual cues through environmental enrichment can simulate the variability experienced in larger enclosures. Feeding cheetahs on an unpredictable schedule can be achieved relatively easily in captivity. However, care must be taken to assure that this unpredictability is not a source of stress to the animals (Bassett and Buchanan-Smith, 2007). Continued observation of the animals upon implementation of any new schedule is advised in order to ensure the appropriate behavioural changes are occurring. The maintenance of cheetahs in compatible groups can be an effective way to reduce pacing behaviour. Lyons et al. (1997) reported observing elevated levels of pacing in a male and female cheetah which previously had been kept together but had been separated. This highlights that maintaining compatible individuals in groups can be effective, however reproductive implications must be considered particularly for females (Kinoshita et al., 2011; Wielebnowski et al., 2002b; Ziegler-Meeks, 2009). Compatibility between females in relation to the prevalence of natural behaviours is important, particularly when females cannot be involved in reproduction attempts. However, reproduction is a primary goal for the cheetah population

at present and therefore, efforts should be made to house females singly whilst attempting to minimise the prevalence of stereotypical behaviours through the various means highlighted in the present study. The improvement of current enclosures or, the installation of visual barriers between enclosures containing incompatible groups or individuals, is also a viable option to reduce stereotypical behaviour in cheetahs. Alternatively, examining the possibility of creating compatible groups through the introduction of neighbouring solitary males, or indeed groups of males, may be a viable option if appropriate monitoring can occur.

5. Conclusions

As mentioned earlier, behaviour is a reaction to an animal's environment and is therefore dynamic and is not dependent on any one factor but rather influenced by a multitude of factors. The utilisation of the information theory approach is novel in relation to understanding the behaviour of captive animals. By comparing a number of models in order to predict behaviour, a more in depth view of the dynamics of certain behaviours in captivity can be obtained and also allow the complex relationship between behaviour and captive environment to be deciphered and understood in greater detail. Therefore, this allows us to focus on factors that influence both unwanted behaviours such as stereotypical behaviour, as well as behaviours which we want to promote. It is encouraging that the controllable husbandry factors model was the most optimal model. This underlines the fact that, by altering factors under our control, stereotypical behaviour in captivity can be minimised. The four next most optimal models also highlighted the importance of these factors, namely size of enclosure, ability to view other cheetahs, feeding regime predictability and group membership. Applying this information theory approach for a range of species and behaviours can provide substantial information relating to how the animals within zoological institutions react to husbandry and management practices.

Acknowledgements

The authors would like to thank the directors at Africa Alive, Banham Zoo, Chester Zoo, Colchester Zoo, Fota Wildlife Park, Whipsnade ZSL Zoo, Toronto Zoo, the Ann van Dyk Cheetah Centre and the Cheetah Conservation Fund for permitting this research to be carried out. Thanks also to all the staff at each of the institutions for their willingness to assist during this research. The authors would also like to thank the Irish Research Council for Science Engineering and Technology (IRSCET) and the National University of Ireland (NUI) for providing funding for this research.

References

- Bashaw, M.J., Tarou, L.R., Maki, T.S., Maple, T.L., 2001. A survey assessment of variables related to stereotypy in captive giraffe and okapi. *Appl. Anim. Behav. Sci.* 73, 235–247.
- Bassett, L., Buchanan-Smith, H.M., 2007. Effects of predictability on the welfare of captive animals. *Appl. Anim. Behav. Sci.* 102, 223–245.
- Bates, D., Maechler, M., 2011. *lme4: linear mixed effects models using eigen and jags*. R package version 0.999375-40. <http://CRAN.R-project.org/package=lme4>
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information Theoretic Approach*. Springer, New York.
- Carlstead, K., 1996. Effects of captivity on the behaviour of wild animals. In: Kleiman, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), *Wild Mammals in Captivity: Principles and Techniques*. University of Chicago Press, Chicago, pp. 317–333.
- Carlstead, K., 1998. Determining the causes of stereotypic behaviours in zoo carnivores. In: Shepherdson, D.J., Mellen, J.D., Hutchins, M. (Eds.), *Second Nature: Environmental Enrichment for Captive Animals*. Smithsonian Institution Press, Washington, pp. 172–183.
- Carlstead, K., Brown, J.L., Seidensticker, J., 1993. Behavioral and adrenocortical responses to environmental changes in leopard cats (*Felis bengalensis*). *Zoo Biol.* 21, 321–331.
- Caro, T.M., 1994. *Cheetahs of the Serengeti Plains: Group Living of an Asocial Species*. University of Chicago Press, Chicago.
- Clark, F.E., Fitzpatrick, M., Hartley, A., King, A.J., Lee, T., Routh, A., Walker, S.L., George, K., 2012. Relationship between behavior, adrenal activity, and environment in zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biol.* 31, 306–321.
- Clubb, R., Mason, G.J., 2007. Natural behavioural biology as a risk factor in carnivore welfare: how analysing species differences could help zoos improve enclosures. *Appl. Anim. Behav. Sci.* 102, 303–328.
- Cross, N., Rogers, L.J., 2006. Mobbing vocalizations as a coping response in the common marmoset. *Horm. Behav.* 49, 237–245.
- De Rouck, M., Kitchener, A.C., Law, G., Nelissen, M., 2005. A comparative study of the influence of social housing conditions on the behaviour of captive tigers (*Panthera tigris*). *Anim. Welf.* 14, 229–238.
- Forthman-Quick, D.L., 1984. An integrative approach to environmental enrichment. *Zoo Biol.* 3, 65–77.
- Gusset, M., 2005. Faecal glucocorticoid level is not correlated with stereotypic pacing in two captive margays (*Leopardus wiedii*). *Anim. Welf.* 14, 157–159.
- Holzappel, M., 1939. Die Entstehung einiger Bewegungstereotypien bei gehaltenen Säugern und Vögeln. *Revue Suisse de Zoologie* 46, 567–580.
- 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.
- Kinoshita, K., Ohazama, M., Ishida, R., Kusunoki, H., 2011. Daily fecal sex steroid hormonal changes and mating success in captive female cheetahs (*Acinonyx jubatus*) in Japan. *Anim. Reprod.* 125, 204–210.
- Kistler, C., Hegglin, D., Wurbel, H., König, B., 2009. Feeding enrichment in an opportunistic carnivore: the red fox. *Appl. Anim. Behav. Sci.* 116, 260–265.
- Liu, J., Chen, Y., Guo, L., Gu, B., Liu, H., Hou, A., Liu, X., Sun, L., Liu, D., 2006. Stereotypic behavior and fecal cortisol level in captive giant pandas in relation to environmental enrichment. *Zoo Biol.* 25, 445–459.
- Lyons, J., Young, R.J., Deag, J.M., 1997. The effects of physical characteristics of the environment and feeding regime on the behaviour of captive felids. *Zoo Biol.* 16, 71–83.
- Mallapur, A., Chellam, R., 2002. Environmental influences on stereotypy and the activity budget of Indian leopards (*Panthera pardus*) in four zoos in Southern India. *Zoo Biol.* 21, 585–595.
- Marker, L., 2002. *Aspects of Cheetah (Acinonyx jubatus) Biology, Ecology and Conservation Strategies on Namibian Farmlands*, PhD Thesis, University of Oxford.
- Mason, G., 1991. Stereotypies: a critical review. *Anim. Behav.* 41, 1015–1037.
- 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.
- Mason, G., Latham, N., 2004. Can't stop, won't stop: is stereotypy a reliable animal welfare indicator. *Anim. Welf.* 13, 57–69.
- Mellen, J., Hayes, M., Shepherdson, D., 1998. Captive environments for small felids. In: Shepherdson, D.J., Mellen, J.D., Hutchins, M. (Eds.), *Second Nature: Environmental Enrichment for Captive Animals*. Smithsonian Institution Press, Washington, pp. 172–183.
- Newberry, R.C., 1993. The space-time continuum, and its relevance to farm animals. *Etologia* 3, 219–234.
- Pomerantz, O., Paukner, A., Terkel, J., 2012. Some stereotypic behaviours in rhesus macaques (*Macaca mulatta*) are correlated with both perseveration and the ability to cope with acute stressors. *Behav. Brain Res.* 230, 274–280.

- Quirke, T., O'Riordan, R., 2011a. The effect of different types of enrichment on the behaviour of cheetahs (*Acinonyx jubatus*) in captivity. *Appl. Anim. Behav. Sci.* 133, 87–94.
- Quirke, T., O'Riordan, R., 2011b. The effect of a randomised enrichment treatment schedule on the behaviour of cheetahs (*Acinonyx jubatus*). *Appl. Anim. Behav. Sci.* 135, 103–109.
- Robinson, M.H., 1998. Enriching the lives of zoo animals, and their welfare: where research can be fundamental. *Anim. Welf.* 7, 151–175.
- Seidensticker, J., Doherty, J.G., 1996. Integrating animal behaviour and exhibit design. In: Kleiman, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), *Wild Mammals in Captivity: Principles and Techniques*. University of Chicago Press, Chicago, pp. 317–333.
- 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.
- Swaisgood, R.R., 2007. Current status and future directions of applied behavioural research for animal welfare and conservation. *Appl. Anim. Behav. Sci.* 102, 139–162.
- Swaisgood, R.R., Shepherdson, D.J., 2006. Environmental enrichment as a strategy for mitigating stereotypies in zoo animals: a literature review and meta-analysis. In: Mason, G., Rushen, J. (Eds.), *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare.*, 2nd ed. CAB International, Wallingford, UK, pp. 256–285.
- 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.
- Wielebnowski, N., Fletchall, N., Carlstead, K., 2002a. Noninvasive assessment of adrenal activity associated with husbandry and behavioral factors in the North American clouded leopard population. *Zoo Biol.* 21, 77–98.
- Wielebnowski, N.C., Zeigler, K., Wildt, D.E., Lukas, J., Brown, J.L., 2002b. Impact of social management on reproductive, adrenal and behavioural activity in the cheetah (*Acinonyx jubatus*). *Anim. Conserv.* 5, 291–301.
- Ziegler-Meeks, K., 2009. *Husbandry Manual for the Cheetah (Acinonyx jubatus)*, vol. 3. White Oaks Conservation Center, USA.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology With R*. Statistics for Biology and Health. Springer, New York.
- Zuur, A.F., Ieno, E.N., Elphic, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14.