Social and Reproductive Behaviours in the Cheetah (*Acinonyx jubatus*) in A Captive Population

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Chapter III

Ethogram of Captive Cheetah Behaviour

Introduction

Behavioural studies have been undertaken on all of the larger cat species for over fifty years (Packer & Pusey 1982). Ethologists have performed intensive studies on lions (*Panthera leo*), tigers (*Panthera tigris*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*), with an increasing knowledge base being built from on-going studies and analysis (Frame & Frame 1980, Caro 1993, 1994 and Scott 1996). Historically these studies have been performed on wild subjects, with captive species usually only receiving the attention of zoo keepers and volunteer groups (Caro 1993). However, the last decade has seen a slight shift in this trend, with studies on behaviour undertaken in captive facilities (Way *et al.* 2006, Pandav *et al.* 2007, Liu *et al.* 2009 and Schneider *et al.* 2010). A frequent goal for many of these studies, both in the wild and captivity, is to examine specific behavioural attributes, such as territoriality, home range use, social behaviours or reproductive behaviours (Caro 1994, Rodden *et al.* 1996, Wielebnowski 1998, McDonnell & Poulin 2002 and Jantzen & Havenhand 2003). In order to perform these studies, detailed knowledge of the full range of an animals' behaviour is required (Watters *et al.* 2009).

This analysis can be done using an ethogram (Way *et al.* 2006 and Watters *et al.* 2009). An ethogram is intended to be a simple description of an animal's behavioural repertoire and developing a key to its use makes data entry easier (Schleidt *et al.* 1984). It is developed by comprehensive study of the subject species in its environment, either in the wild or in captivity (Rodden *et al.*1996 and Watters *et al.* 2009). A comprehensive analysis of individual behaviours, and descriptions of behaviour with a key for further recording and interpretation, means that data can be consistently collected. An ethogram is an essential tool within behavioural studies as it provides a basis for recording and analysing behavioural data (Jantzen & Havenhand 2003). By breaking down more complex behavioural patterns and minimising subjective interpretation of the purpose of the behaviour, the researcher is able to develop a comprehensive overview of the activities of the animal. This information can then be used for a number of different analyses and to advance research by having a greater understanding of the behavioural repertoire of a study species. In order to detect any changes in an animal's behaviour, it is essential to have an understanding of the animal's basic repertoire of activities as well as a general baseline regarding the frequencies of these behaviours in various contexts (Schleidt *et al.* 1984). This baseline is particularly valuable when looking at social species and the various interactions they

display (McDonnell & Poulin 2002, Langkilde *et al.* 2003, Way *et al.* 2006). Each social behaviour is typically a combination of behaviours performed together that carry a particular meaning. Each element of the behaviour must be broken down into all of its individual components in order for the ethogram to accurately describe social behaviours. However, there is an element of subjectivity when recording social behaviours and they must be interpreted cautiously (Rodden *et al.* 1996).

Ethograms can be subdivided into a number of behaviour types or categories, with each of these categories having different levels of behavioural contexts. These contexts will vary depending on the animal being studied. If it is a solitary animal, such as the leopard (*Panthera pardus*) it will only be social when coming together with conspecifics for breeding (Scott 1996). There will be very different behavioural contexts for this animal than a social species, such as the eclectus parrot (*Eclectus roratus*) that lives in flocks amongst a number of different species (Heinsohn & Legge 2003 and Heinsohn *et al.* 2007). In this species there will be behaviours exhibited in isolation, with family groups, with conspecifics and with other species it may forage with.

Ethogram for the Captive Cheetah

I have developed the following ethogram to readily define the different behaviours being produced by the cheetah in captivity. A large number of typically social and solitary behaviours were seen during the time that their basic behaviours were described. As the majority of the cheetah's behaviours can be defined as either general or social, the ethogram has been divided into two parts. Any behaviour observed in a solitary form has been included in the general section. Any behaviour that has been described in the general section, but also has a social form, is re-described and the changes in the social form are included in the social behaviours section of the ethogram. The social behaviours section also includes any behaviours requiring more than one participant either directly, or when one individual reacts to the behaviour of another.

There are many types of behaviour included in an ethogram (Schleidt *et al.* 1984). These behavioural types include those that occur in isolation and are only seen as a single event. I will refer to these behaviours as 'spike' events, which include behaviours such as calling and territory marking. There are also behaviours that, while still occurring in isolation, are exhibited over a protracted period of time. I will refer to these behaviours as 'durational' events, which include bouts of behaviours such as

playing, eating and grooming. For highly social species there are also occasions where it can be helpful to group behaviours to provide a better understanding of their context. I will refer to these behaviours as 'complex' events, which include activities such as playing, fighting and courtship. The behaviours observed within each of these 'complex' events all have their own description in isolation – it is only when they are seen in specific combination that they can be referred to as a 'complex' event. While subjectively rated, these behaviour combinations can be useful in determining social behaviours.

A previous study of captive cheetah behaviour has been performed by Wielebnowski (1999). This study focused particularly on behaviours for predicting breeding status and examined a number of behavioural 'states' that these animals can display. These 'states' refer to generalised assumptions based on the temperament of an individual animal. While being subjectively rated by the observer, these 'states' allow for further interpretation of individual behaviour and contribute to individual behavioural variation (McDougall *et al.* 2006). Therefore, in addition to the two categories of behaviour (general and social), the current ethogram includes states, some of those described by Wielebnowski (1999), as well as additional states I noted on the cheetah within this study.

Methods

Animals and Facility

The study animals were eight captive-born adult cheetahs, with ages ranging between 3.5-5.5 years at the beginning of this study. These animals were parent-reared at Hoedspruit Breeding Centre (Hoedspruit, South Africa) and maintained at Monarto Zoological Park (MZP), South Australia, Australia for the entire study. Animals were housed in same sex groups within the cheetah facility of MZP, and observed from the main exhibit yard and night yard A (see Chapter 2 -General Methods).

<u>Collection Procedure</u>

I initially recorded behaviours over a two week period between the 20th of January and 2nd of February 2001. Times were sampled over the day, with the earliest starting at 06:30 h and the latest finishing at 19:00 h. The method of recording was continuous (Martin and Bateson 2000) and each collection period lasted for one hour. All animals were sampled for a total of seven hours each, originally focusing on males and then observing females. Times were broken up during the day, with 06:30 to 10:00 considered morning, 11:00 to 15:00 being midday and 16:00 to 19:00 evening. These time periods were adapted to coincide with the animals' pre-release into the exhibit, time in the exhibit and then time in their night-yards. I observed all individuals in each condition at least once during the two week observation period.

My study initially involved recording the different behaviours exhibited by cheetahs when housed in isolation as well as in single sex groups. Various groups of male cheetahs, as well as all individuals housed separately, were studied to determine the differences in behaviour when they were housed together compared to when housed in isolation. It was important to determine their behaviours in both situations, as sociality will produce a separate repertoire of behaviour. Females were studied in isolation and as a trio, with one animal at a time being the focus of the study whilst housed in the group.

All of the various behaviours were either noted directly or recorded with a small tape recorder. When a tape recorder was used, the behaviour type was spoken into the recorder and then transcribed after the session. A letter key was developed to describe the behaviours; this was used to aid in the recording of information and reduce writing time (for example 'W' for walking). Social behaviours that resulted in direct animal contact, such as social grooming, were also noted and were marked with a 'c' on data sheets. Behaviours occurring over a protracted period of time, or durational events, such as pacing, lying down or sleeping, were recorded for each full minute of observation time after the behaviour commenced. Other behaviours were continually noted as changes were observed. For example, if a cheetah walked to a tree, rubbed its head on a branch and then laid down for five minutes and then stood up and ran to the other side of the exhibit, it would score 1 for walk, 1 for rubbing, 5 for lying, 1 for standing and 1 for running.

Initially, recordings were taken from a distance between 25 to 100 metres from the fence line, aided with the use of binoculars. At times I needed to move to different

positions along the fence line to maintain visual access. After the initial few days of recording, I found that if I was quiet and slow moving, my movement along the fence line did not seem to affect the cheetahs' behaviour, and once they initially observed me, I was almost always ignored. I found no apparent difference in activity type or frequency when I was 100 metres away versus close to the fence. Hence, my presence was not considered to have any effect on their specific behaviours.

The cheetah behaviours observed were very diverse. Many differing social interactions as well as multiple calls and movements were observed. Besides the basic behaviours, such as sitting, standing, locomotion and so on, which are straightforward, there are a variety of other behaviours that require more detailed explanation such as the various forms of spraying. Where possible, I have included photographs of behaviour and phonetic descriptions of calls.

Statistical Analysis

Differences in the behavioural repertoires of individuals can be very important in ethological studies. They can, for example, indicate husbandry problems leading to stereotypic behaviours or limitation of potential roles, but they can also show whether some members of a group are excluded from some behavioural suites (e.g. reproductive activities). Establishing the extent of behavioural repertoires can be difficult as it depends on the amount of effort that can be directed towards observation, since detecting rare behaviours will depend on the amount of observations that can be made. One way to estimate the extent of repertoire size, whilst taking limited sampling into account, is to examine 'behavioural accumulation curves' (BACs) (Colwell *et* al. 2004). When behaviours vary in the commonness of their expression, plots of the cumulative number of observed behaviours as a function of observation effort, often show a curve with a declining slope that indicates an upper asymptote. If such a curve is evident, then an equation can be fit to the curve to predict the asymptote, and therefore the true size of the behavioural repertoire – even if all behaviours have not actually been observed.

BACs can be developed by simply plotting raw data (e.g. cumulative number of behaviours versus observation effort) but this may not make full use of the available data and nor provide an indication of the potential error in BACs. Colwell et al. (2004) has developed a method to overcome these problems and this is implemented in the software program EstimateS (Colwell et al. 2004, 2006; http://viceroy.eeb.uconn.edu/EstimateS). This software uses a moment-based estimator of richness, τ (tau) (Mao et al. 2004) as a function of sampling effort (initially

developed to estimate species richness in ecological research). In this thesis, I refer to this estimator as the 'Mao τ'.

While the Mao τ provides an estimate of behavioural richness that takes sampling effort into account, I also need to predict the likely true level of richness, given that behavioural sampling is unlikely to uncover all behaviours that an animal can express. One estimator of true richness is the Michaelis-Menton parameter (see review in Colwell and Coddington 1994) and this is also implemented in the EstimateS software, which was used to analyse the data. I developed BACs using Mao τ, implemented in EstimateS, based on seven behavioural samples taken for each individual cheetah within the two-week study period.

The data recorded in the study period, comprising seven samples of 60 minutes for each individual, was used in this statistical analysis. However, continued work with the cheetahs uncovered further behaviours not seen in the initial observation period. For the accuracy of the descriptive ethogram, these behaviours, such as courtship, and the associated calls, were included in the descriptions. These behaviours were not included in estimating behavioural richness or developing the BACs.

Ethogram

General Behaviours

Locomotion

There are a number of different behaviours that come under the category of locomotion. All of these forms of behaviour are dependant on variations in gait and a brief description is provided to illustrate the differences.

Walking (W)

Walking is a slow moving gait where two paws remain on the ground as the opposing two are lifted and swung forward. These are then pushed backwards to propel the animal forward. Walking was used to move around the exhibit and yards and is the primary form of locomotion.

Trotting (T)

Trotting is a quicker movement than walking. The paws are generally raised higher and then extended forward in the movement, while maintaining the two and two moving pattern. Seen as a more energetic and bouncy movement with more vertical movement than a walking gait.

Running (R)

Running is a quick-moving and loping gait. Propulsion is different to walking as both front paws are lifted and pushed forward and then the rear legs are pushed forward to meet them. The paws can meet in the middle of the gait and at higher speeds there may be times where all four paws leave the ground. This movement is purposeful as it is almost always combined with another behavior at its conclusion, i.e. running to food or running to a fight.

Sprinting (Spr)

Sprinting is an explosion of movement where the cheetah is usually initially crouched in a stalking position. The movement is technically the same as running, but begins with the crouching pose for added power and then remains faster paced than running. There are more periods where the animal is air-borne and the spine is seen to curve in reverse to extend the stride length. This movement is always purposeful; it is usually associated with stalking and hunting. It is occasionally seen in play behavior.

Pacing (P)

Pacing is a repetitive form of movement, usually seen as walking or occasionally trotting. The animal is continually moving over the same strip of ground, such as along a fence line, but apparently without a particular goal.

Roaming (Ro)

Roaming is characterised by a cheetah wandering around the enclosure with no apparent destination. The behaviour is not repetitive as in pacing, but there does not appear to be a goal and it differs from walking due to the longer duration of the activity.

Stalking (Stk)

Stalking is a slow moving gait, as with the walk, but the cheetah is crouched. The stalk is used to approach an object or animal of interest, usually in a tentative manner. The object could be another cheetah for play, a possible food item or any object that the cheetah appears to be wary about.

Basic Behaviours

Vigilance (V)

The cheetah is alert and watchful of its surroundings during vigilance. It is usually sitting or standing and muscles tend to be taught as if in readiness to run or take some form of action.
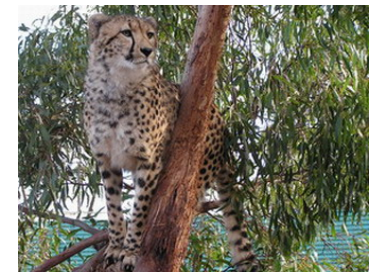

Standing (S)

When standing, the cheetah is stationary on all four paws, watching or waiting. The animal can either be relaxed or vigilant.

Sitting (St)

When sitting, the cheetah is upright with its front legs supporting its weight, while the back legs are tucked under the animal and its rump is on the ground. The cheetah is alert and able to look around and can either be relaxed or vigilant.
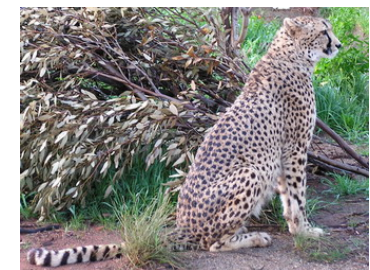
Lying (L)

The cheetah is lying flat on the ground, but with the head held upright. It may or may not have its shoulders on the ground and it is alert and able to see what is going on around it.

Sleeping (Sl)

The cheetah is lying flat on the ground with its head down when sleeping. The eyes may or may not be closed (this could not always be determined due to distance or position), and it is unable to see around itself. The animal is not vigilant.

Climbing (C)

The cheetah is using an object in its enclosure to be able to reach a greater height when climbing. Climbing can be used for better observation or in play. The animal is usually vigilant.

Grooming (G)

The cheetah is grooming itself. This usually involves directly licking an area of focus or licking the front paw and then rubbing the focus area with the wet paw. Grooming can involve one or two occurrences of licking or a continuous bout for a protracted duration. The specific action can include one or all of the following; licking, chewing, biting or gnawing at the fur.

Playing (Pl)

When playing, the cheetah manipulates an object, such as a log or food, typically with the front paws. There seems to be no proximate goal to this behaviour.

Eating (E)

The cheetah is eating something specifically fed out into the main enclosure or lock-away area. Occasionally the cheetah may eat something that has been caught in the enclosure (i.e. birds or lizards).

Drinking (D)

When drinking, the cheetah uses the tongue to lap up water or blood. Cheetahs typically drank from a designated water bowl or from accumulated water in the enclosure. Blood can accumulate on the concrete feed pads and be lapped up.

Vocalisation

Cheetahs were heard to produce a wide variety of vocalisations during observation periods. Any calls emitted by a cheetah were reported by describing the type of call and the basic phonetic sound that was made.

Meow-chirp (VM/c)

Meow-chirp is a high pitched call, of short to mid duration, that is quiet between pulses. Sounds like "mmee neeow" or "mmee oww" and usually occurs a minimum of 3 times with a 2-3 second pause between calls. This call can occur for protracted periods and does not appear to be associated with any other behaviour (unlike the distress call below).

Purr (VP)

A purr consists of repeated vibration type rumblings produced deep in the chest. Two variations were observed, with variations also among individuals. Firstly, the purring can occur rhythmically for about 0.5-2 seconds with a short pause before starting again (a bout like this can continue from 15 seconds to minutes at a time). Secondly, the purring can be a continual rumbling (a bout can continue from 5 seconds to minutes at a time). The first type sounds like "tthhhrr – tthhrr – tthhrr", while the second type sounds like "pthrrrrrrrrrrrrrrrrrr". In the protracted variation, the cheetah is able to isolate this behaviour while breathing, hence being able to continue to purr for long periods. Purrs have not been categorised separately, as different individuals appeared to show preferences for different styles of purring.

Hiss (VH)

A Hiss is different to the other calls as the noise is more like a low exhalation of air. It is typically heard as part of a threat display, and if the threat is not removed the hiss often escalates to the threat drumming or growling sounds described below. Sounds like "heeeiissss".

Growl (VG)

A Growl is a vibration type rumbling produced in the throat that is usually high pitched. This vocalisation can be soft and of short duration or considerably louder and of longer duration. It can be seen in conjunction with other threat behaviours, but it is quite often seen in isolation. Sounds like "grrrriiilllll" or "ggguuuurrrllllll".

Distress call (VN)

A distress call is usually heard when individuals are separated from each other. The call is quite often heard when related animals are moved to different pens and are unable to socialise. It is a high pitched call of short duration that is quiet between pulses. Sounds like "nyim", "nyom", "neow" or "newo", depending on the individual animal or possibly the circumstances.

Threat drumming (VD)

Threat drumming is a low pitched drumming or thudding-like noise from back of throat which is only observed in conjunction to a full threat display. Like the hiss (see above), the sound is produced by expelling air quickly. Sounds like "Ptthud".

Yelp (VY)

A yelp is a high pitch call of short duration that usually only occurs once. It is often seen in conjunction with threat or fighting behaviours. Sounds like "yip" or "yowl".

Stutter call (VSt)

Stutter calls are a drawn out cackling sound that can range from mid to high pitched. There is a considerable amount of vibration in this call, as with the purr, but the noise appears to be formulated in the throat and it does not have the deep rumbling of a purr. There are short pauses between bursts, and stutter calls are usually associated with some form of excitement, such as male-female introductions. Sounds like "kaaaahhh – kaaahhhh – kaahhh" in the mid range through to a higher-pitched "piirrrrhh – piiirrrrhhha – piirrhhhha", depending on the individual animal involved.

Scent Marking and Detection

Scratching (Sc)

The cheetah scratches an object, i.e. trees, logs or the ground, leaving visible marks with the claws.
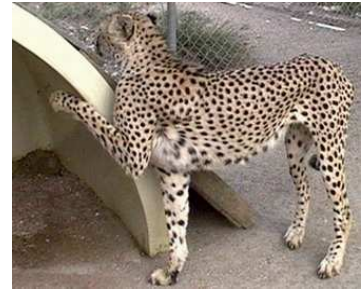
Defecation (D)

The cheetah passes faeces in a crouching position, leaving it either in a conspicuous location (on an elevated area) or on the ground.

Spraying (Sp)

Spraying is typically seen in the male, but a proximate form was occasionally observed in the female cheetah. The cheetah urinates on an object. Spraying is performed by standing upright and lifting the tail and directing the penis backwards. Urine is sprayed onto the target object in a fine mist rather than in a stream as in standard urination (see below). The female cheetah was included in this category when they targeted their urination on an elevated area or plant.
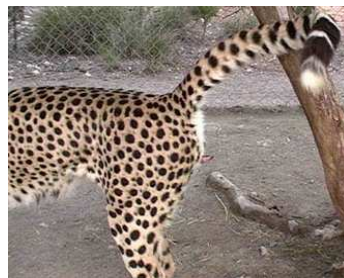
Urination (U)

The cheetah urinates on the ground by crouching slightly, scraping its feet on the ground and urinating downwards. Urine is expelled in a steady stream, unlike the fine mist seen in spraying (see above). Urination was observed in a similar manner for both male and female cheetahs.

Licking (Li)

The cheetah licks hard objects, leaves, branches or grass where another cheetah has urinated or defecated.

Lip Licking (Lli)

During lip licking, the cheetah moves its tongue over its lips repeatedly. This behaviour is often seen in conjunction with Flehmen or during times of stress.

Flehmen (Fl)

The mouth is held open during flehmen and the animal breaths lightly while slightly curling the tongue. The tongue remains in the mouth and quite often saliva builds up on the center of the tongue, occasionally running out of the mouth. There is no sign of panting or heavy breathing as if the animal was hot. The cheetah is usually seen in a standing or semi-crouched position, and appears to be tasting the air.

Sniffing (Sn)

The cheetah sniffs at leaves, branches or areas it or other cheetahs have sprayed. The cheetah sniffs at the ground (i.e. male sniffing the ground where a female had been lying).
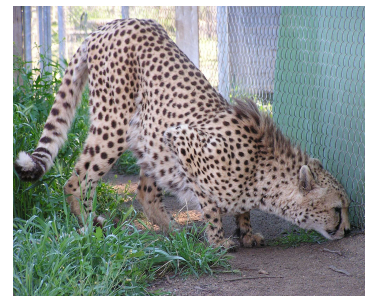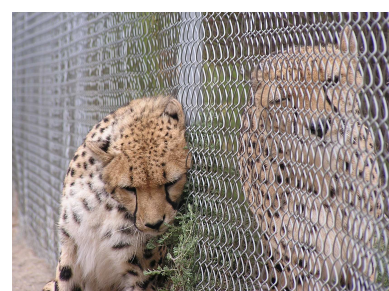
Rubbing Face (Ru F)

The cheetah rubs part of its face or head against logs, rocks, branches or fences.

Rubbing Body (Ru B)

The cheetah rubs part of its body against logs, rocks, branches or fences.

Rolling (Rl)

The cheetah rolls on the ground, rubbing its back repeatedly. Rolling is not just a single roll, where the cheetah could just be rolling over to change position.


Tail Movements

Tail Twitching (TTw)

The cheetah moves its tail back and forth rapidly from left to right. Usually it is only the lower section of the tail that is moving while the rest remains still. The movement is rapid and repeated, and often occurs in conjunction with behaviours such as sniffing, licking or flehmen.
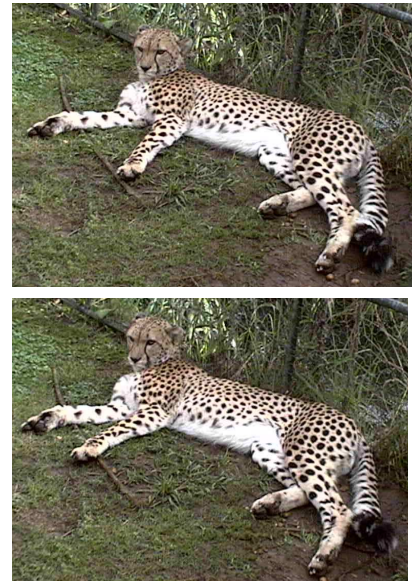

Tail Swishing (TSw)

The cheetah swishes its tail in a distinct pattern during tail swishing, and the behaviour is primarily noted in female cheetahs. The patterns were seen to vary slightly for each female. Each tail swish begins with the tail starting in the relaxed hanging position. The tail is then moved up or to the side, associated with moving the tail away from the anal-genital area (see Tail Rolling below). The tail continues through the swish movement and is returned to the relaxed hanging position. This swish behaviour may be seen once or it may be repeated. If seen repeatedly, it was not considered to be a durational event as there was normally more than 5 seconds between behaviours and it was often seen in conjunction with other behaviours such as rolling and calling.
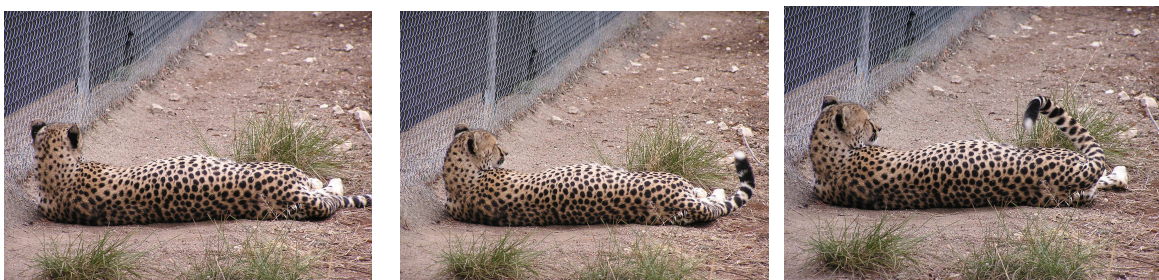
Tail Rolling (TRo)

Tail rolling is a behaviour typically seen in female cheetahs and only occasionally produced by the male. The tail is moved to the side in a rolling action and is associated with moving the tail away from the anal-genital area.
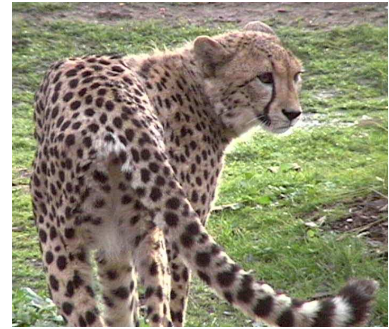
Social Behaviours

Behaviours were classified as social for a number of reasons. If a behaviour was performed by several cheetah together, such as moving around together or sleeping, it was considered social if animals were within two metres of each other. A two metre distance was chosen due to the density of the scrub in some areas of the enclosures and night-yards. If animals moved further than two metres apart there were many places where the scrub formed barriers between the individual animals. Behaviours were also considered social if they were performed to another animal, such as grooming or fighting, or in direct response to another animal's behaviour, such as spraying, scratching over another's territory markings or calling to one another. Recording of behaviour was still performed on a solitary individual, noting the individual's behaviour during the observation period. Social and solitary activities were recorded for the target animal identified. For example, if a cheetah groomed itself, then groomed another cheetah for five minutes then stood up and walked away it would be recorded as: 1 groom self, 5 groom (ID of cheetah specified), 1 stand and 1 walk.

Locomotion

The cheetah can be seen to move around the exhibit or night-yards in a group or coalition. A description of each form of locomotion is provided in the general behaviour section (see above), and the only difference in social locomotion is that more than one animal is performing the same behaviour at the same time. Hence to be walking together, all individuals must be walking in the same direction, as with trotting, running and so forth. Differences to this pattern are described below.

Pacing (P)

Two or more cheetahs are pacing together. Pacing may be in or out of unison, but must be in the same area. The gait does not need to be the same, so one cheetah can be walking as another is trotting.

Roaming (Ro)

Two or more cheetahs are roaming around the enclosure together. The roaming occurs in close proximity, but all animals need not be heading in the same direction at all times.

Basic Behaviours

Standing (St)

Two or more cheetahs are standing together. All of the animals must be standing and within two metres of each other.

Sitting (S)

Two or more cheetahs are sitting together or within two metres of each other. The behaviour is defined as sitting in larger group if two cheetahs are sitting and one or more are lying, sleeping or standing. A higher proportion of animals must be sitting.

Lying (L)

Two or more cheetahs are lying together or within two metres of each other. The behaviour is defined as lying if the greater proportion of animals are lying, or if one cheetah is lying and one or more are sleeping. However, individual animals were still recorded for their specific behaviour to determine the percentage of time spent vigilant for each animal when in a social situation.

Sleeping (Sl)

Two or more cheetahs are sleeping together and all individuals in the group are sleeping (see above for specific definition of sleeping). Social sleeping occurs when animals are within two metres of each other.

Grooming (G)

Two or more cheetahs are grooming each other. This grooming can be by only one cheetah or reciprocated by others. The level of grooming can vary, i.e. 'a' and 'c' groom 'b', but 'c' does not groom 'a' and 'b' does not groom either. The amount of grooming was detailed. The first instance of grooming was recorded and then long bouts of grooming continued to be recorded in intervals, on the minute. The amount of grooming was also recorded (one or two licks, to continual licking for the entire period).

Stamp (Stm)

The cheetah thrusts both front legs forward and slaps them on the ground in front of itself. It is usually combined with hissing, growling and threat drumming (see vocalisations above).

Slap (Slp)

A slap occurs when a cheetah lifts one of its front legs and forcefully hits an object (usually another cheetah) with it. This motion is normally from the side, such as a swipe across the body, and not downwards.

Trip (T)

A trip occurs when a cheetah lifts one of its front legs and wraps it around the leg of another cheetah while it is walking or running past, usually causing the other cheetah to stumble or fall over. The behaviour is similar in motion to a slap, but is slower, more deliberate and without the force of a slap.

Bite (B)

The cheetah mouths or bites another cheetah, pulling up the fur and skin but not breaking the skin. The action is more intense than the gnawing seen in grooming. A bite

is typically on the back of the neck or the legs and is usually performed to another cheetah as it tries to pass by.

Mounting (M)

Mounting occurs when one cheetah lifts its front legs off the ground and brings them to rest on the back of another cheetah. This behaviour is seen in mixed sex (see courtship below) and single sex pairings. Mounting typically occurs from the rear of the animal but it is occasionally seen from the side.

Rearing (Re)

One cheetah rears up or back onto its hind legs, with both front paws leaving the ground. Rearing is usually seen in response to the threatening actions of one or more cheetahs. It appears that this behaviour can be used as a threat display or a submissive gesture, and it is quite often seen in conjunction with play behaviour. Rearing typically ends with one animal grooming the other, moving away or progresses into a chase and play or fight.

Chase (Ch)

Chase occurs when one or more cheetah chase other cheetahs. There is typically only one focal animal in this behaviour but there can be many participants. The gait during chase is usually a run or sometimes a sprint. This behaviour is usually seen as a lead in or conclusion to another behaviour, such as fighting or playing.

Scent Marking and Detection

Spraying (Sp)

Spraying occurs when two or more cheetahs spray an object together or one cheetah sprays an object in response to another individual spraying. Spraying together requires the cheetahs to stand side-by-side while both targeting the same object (tree, pole, den etc.). Spraying in response to another cheetah requires one cheetah to target an object and spray and then a second cheetah to spray over the first animals' mark.

Defecating (D)

Defecating occurs when one cheetah defecates in response to another individual defecating. As seen with spraying, the faeces are left in the same position (usually an elevated mound of grass) and another cheetah responds by defecating over the top of the first deposit. Occasionally the second cheetah is seen to remove the original faeces from the position, particularly if it is in an elevated position, by pushing it aside with its paw.

Scratching (Sc)

Scratching occurs when two or more cheetahs scratch the same object together or scratch an object in response to another individual scratching, i.e. trees, logs or the ground. Scratching together requires cheetahs to stand side-by-side while both targeting the same object (tree, log or den etc.). Scratching in response to another cheetah requires one cheetah to target an object and scratch it and then a second cheetah to scratch over the first animal's mark.

Sniffing (Sn)

Sniffing occurs when a cheetah sniffs at leaves, branches or areas sprayed or marked by another cheetah. Sniffing can also include a cheetah sniffing at the ground (i.e. male sniffing the ground where a female had been lying).

Licking (Li)

Licking occurs when a cheetah licks leaves, branches or grass where a cheetah had sprayed.

Complex Behaviours

Threat (Th)

The cheetah combines hisses, threat drumming and stamps in threat behaviour. This behaviour always has a target and is usually focused at another cheetah, although occasionally it can be directed at unknown objects or people. This can be seen as a potential threat or warning of an ensuing fight.

Fight (F)

Fighting consists of two or more cheetahs fighting with each other or one targeting another. Fights include behaviours such as threats, stamping, rearing, chasing, slapping, biting, rolling, yelping, threat drumming and mounting.

Play (Pl)

Playing is characterised by one or more cheetahs playing with other cheetahs. Playing can be defined as having many similar elements to fighting behaviours, but usually with the absence of any vocalisations. It is seemingly meaningless in its function. Play usually involves chasing, tripping, mouthing (not vicious biting), slapping, jumping and rolling.

Courtship Behaviours

Tail Swishing (CTSw)

When exhibiting tail swishing, a female cheetah swishes her tail repeatedly, in a distinct way, or lifts it as a sign of interest in mating when in close proximity to a male.

Tail Rolling (CTRo)

Tail rolling occurs when a female cheetah rolls her tail away from the ano-genital region repeatedly, or lifts it as a sign of interest in mating when in close proximity to a male.

Rolling (CR)

When rolling, a female cheetah flops to her side on the ground in an exaggerated movement, in front of a male cheetah and rolls repeatedly on her back. As courtship

develops, the female may allow the male to sniff the genital area.

Lordosis (CL)

Lordosis is a position where a female is lying upright on the ground with all four legs semi- tucked under her body. With the back legs tucked under, the cheetah's rump is slightly elevated which allows a male cheetah access to mount her for sexual penetration. Lordosis is typically seen with behaviours such as tail rolling or calling.

Penis Exposure (CPE)

Penis Exposure occurs when the penis becomes unsheathed while a male cheetah is walking after, or investigating, a female or her scent markings.

Salivating (CSa)

The male cheetah begins to salivate while investigating a female's scent markings or the animal itself. This is usually seen in conjunction with stutter calling and penis exposure (see above).

Mounting (M)

Mounting occurs when a male cheetah lifts its front legs off the ground and brings them to rest on the back of a female cheetah. This behaviour can occur while the female cheetah is standing, but typically in lordosis.

Complex Courtship Behaviours

Female Courting (CFC)

A female may display a combination of tail swishing, rolling and scent marking when courting – all performed in close proximity to a male or group of males.

Male Courting (CMC)

Male courting occurs when a male displays signs of interest in a female, such as stutter call, following the female, salivation, penis exposure and sniffing. These behaviours are all directed towards the female.

Chassé (CCh)

Chassé is a lateral movement where a male moves from side to side when observing a female that he is unable to have contact with, such as through a fence. This movement can be as small as just shifting weight from one side of the body to the other or it can be full steps left or right. It is repeated frequently and appears as if he is swaying or prancing. It is usually accompanied by stutter call, drooling, penis exposure and general excitement. The male will frequently change positions along a fence line to observe the female.

Behavioural States

In conjunction to the extensive range of behaviours displayed by the cheetah, there are also a number of different states that these animals can display. These states are categories of temperament and can aid in the assessment of an individual's behaviour. While these states are very subjective, they can be important in determining behaviour as the state of the cheetah is important in captivity (Wielebnowski 1999, Feaver et al. 1986 and McDougall 2006) and can assist in the interpretation of the more complex behaviour patterns.

The following categories are 19 behavioural adjectives that describe the majority of cheetahs' temperament. Primarily based on the states developed by Wielebnowski

(1999), I have combined some of categories, such as 'Aggressive to conspecifics' and 'Aggressive to people' to simply 'Aggressive'. I have also included a number of additional categories of my own that I believe are important to understanding cheetahs' behaviour and the motivation behind a number of the complex behaviours.

Active

An active cheetah is an animal that moves frequently around the enclosure without a major motivation to do so. This movement can be walking, trotting, running or pacing and can also include purposeful behaviours such as stalking and non-purposeful behaviours such as roaming.

Passive

A passive cheetah is an animal that is content lying around the enclosure for the majority of the time, only really getting up to move when there is a reason, such as at feeding time.
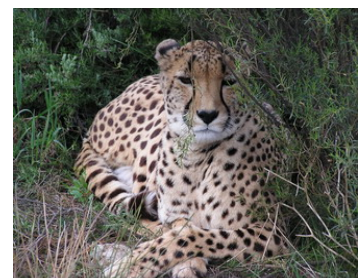
Curious

A curious cheetah investigates any changes made to the enclosure and is eager to approach and explore objects or other cheetah.

Vigilant

A vigilant cheetah is very watchful of its environment and any possible threat that may occur. The animal is usually part of a group and the level of vigilance may increase if other members of the group are lying down or sleeping. The animal also usually displays the traits for 'tense' (see below).

Dominant

A dominant cheetah shows a calm yet imposing influence over other cheetahs that are housed with him or her. The animal may be involved with marking or threat behaviours and is typically the animal that all other individuals follow within the enclosure. This animal also has priority access to resources.

Submissive

A submissive cheetah is typically quiet and content to follow a dominant animal within the enclosure. There is usually a reduction in the amount of territory marking behaviour seen in a submissive animal.

Aggressive

An aggressive cheetah frequently reacts in a hostile and threatening manner towards other cheetah and/or people. The calmness of a dominant animal is not always seen, instead aggressive behaviour is usually seen in conjunction with tense or fearful behaviours (see below).

Calm

A calm cheetah is not easily disturbed by any changes to the enclosure or the animals around them.

Social

A social cheetah initiates contact with conspecifics and chooses to spend time with them rather than in isolation.

Solitary

A solitary cheetah chooses to spend its time alone and generally moves away from conspecifics. The solitary animal tends to avoid company in all circumstances, whether it is resting in the enclosure, pacing or feeding.

Tense

A tense cheetah appears stiff and shows restraint in its movement and its posture. It appears ready to react to negative stimuli at any time.

Fearful

A fearful cheetah appears ready to retreat and hide from other cheetah or people. 'Hiss' vocalizations may or may not be present. There are also elements of 'tense' behaviour in this category.

Playful

A playful cheetah initiates and engages in play behaviour with objects or other cheetahs. This behaviour appears to have no specific immediate purpose.

Insecure

An insecure cheetah seems to scare easily and is generally fearful. The animal can be described as 'jumpy' and appears to spend most of its time with other cheetahs rather than spending time alone.

Self-assured

A self-assured cheetah is confident and moves in a seemingly well coordinated and relaxed manner. The animal is not easily 'spooked', does not show fear at new or unusual objects or people and appears to be at ease whether in the company of other cheetahs or alone.

Eccentric

An eccentric cheetah displays a high level of stereotypical behaviour, such as pacing, or exhibits unusual behaviours. Self-mutilation was not observed.

Smart

A smart cheetah shows signs of learning, and is quick to associate certain events to consequences or other events These events also appear to be remembered for long periods of time after the initial introduction.

Excitable

An excitable cheetah seems over-stimulated and over-reacts to changes around them. Small differences in the enclosure can produce a considerable increase in pacing and investigation and well as an increase in tense or fearful behaviour (see above).

Vocal

A vocal cheetah frequently and readily vocalises to other cheetahs and also at objects.

Results

Behavioural Richness in Captive Cheetahs

I used the EstimateS 8 (http://viceroy.eeb.uconn.edu/EstimateS; Colwell 2004) program to develop behaviour accumulation curves (BACs) for each of the eight cheetahs in the study group and for both sexes separately and in combination. The expected richness of behaviour, expressed as the Mao τ (Tau) parameter, was calculated for each time sample and then plotted against the sample number to create the BACs. Figure 1 shows the BACs for all eight individuals, with males depicted with open circles and females depicted with filled circles.

The steepness of the curves declines with sampling effort for the majority of individuals, with the exception of Izipho and to a lesser extent, Bopha (Figure 1). There is a considerable difference in the behavioural richness displayed by various animals. In general, female cheetahs showed lower behavioural richness over the sampling periods than males, and are all represented in the bottom portion of the graph. Four out of the five males are grouped together at the top of the graph, displaying considerably greater behavioural richness than the females as a function of sampling effort. However, one male, Nyomfoza, differed considerably from the other males, showing Mao τ scores similar to those seen for the females. Additionally, Pinda seemed to differ from the other females, with scores reaching a plateau early and then remaining stable.
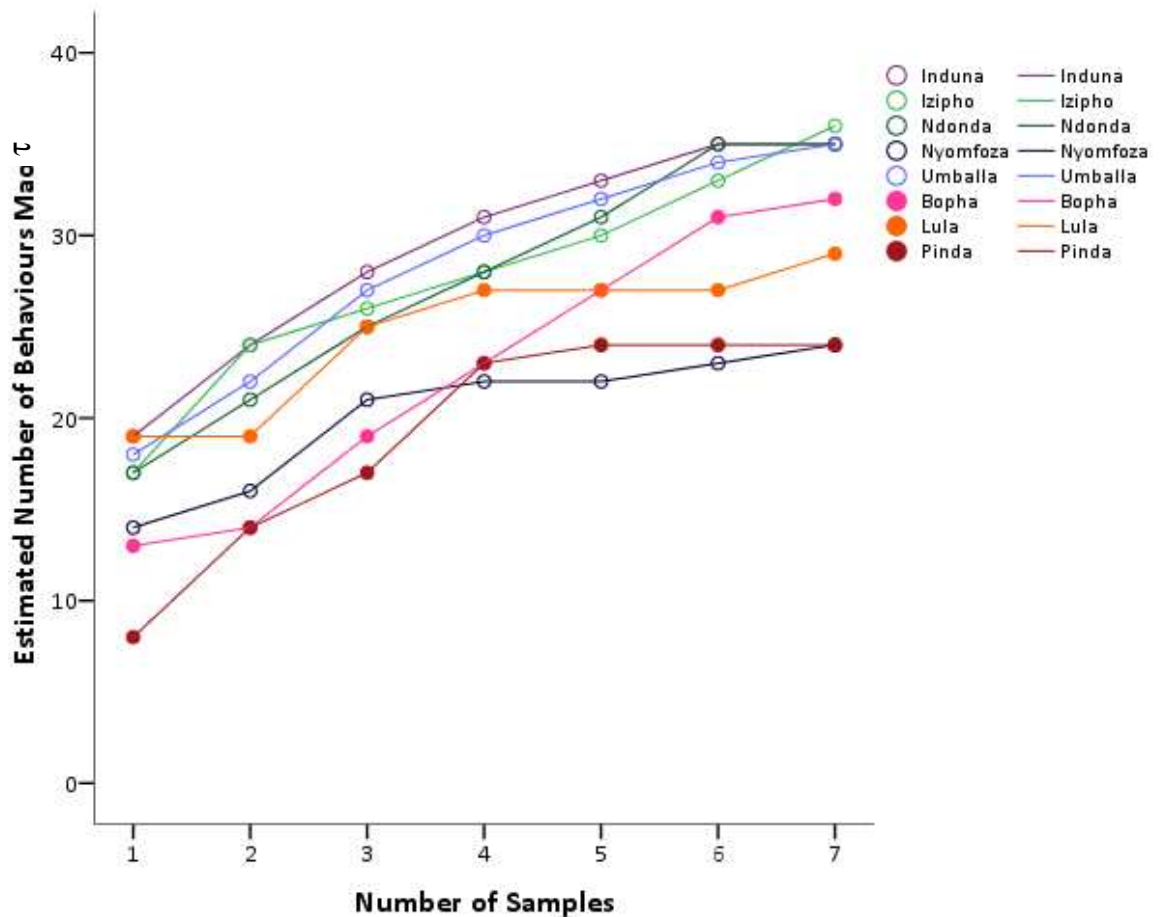
Figure 1. *Estimated cumulative number of behaviours using the Mao τ parameter for all individuals plotted as a function of the seven sampling periods. Males are represented by open circles and females are represented by filled circles.*

Table 1 illustrates the specific behaviours displayed by individual cheetahs over the observation period. There are differences between the sexes in terms of the range of displayed behaviours (Table 1). For example, females did not display Purring, Social Sleeping, Spraying, Licking, Social Sleeping, Social Standing, Social Sniffing, Fighting, Rearing, Following, Sniff Anal-Genital or Mounting. Some of these behaviours are clearly reproductive behaviours that would not be expected in females (e.g. mounting), but the others seem to be clearly linked to social interactions. Interestingly, there were no behaviours observed in females that were not also observed in at least one male.

Table 1 _Behaviours observed for each of the eight cheetahs within the two week observation period. +/- symbols indicate where the particular behaviour was observed or not for each individual. Frequencies of behaviours and complex behaviours are not shown. The presence of behaviours is highlighted, yellow for males/green for females._

	Induna	Umballa	Ndonda	Izipho	Nyomfoza	Pinda	Lula	Bopha
Walking								
Trotting								
Running								
Sprinting								
Pacing								
Roaming								
Standing								
Climbing								
Playing								
Grooming								
Sitting								
Laying								
Sleeping								
Eating								
Drinking								
Hunting								
Chirp-Meow								
Chirp-Nyim								
Purr								
Hiss								
Drum								
Scratching								
Defecation								
Spraying								
Urination								
Sniffing								
Flehmen								
Licking								
Rolling								
Rubbing								
Stalking								
Tail Twitching								
Tail Swishing								
Social Sleeping								
Social Laying								
Social Sitting								
Social Standing								
Social Pacing								
Social Grooming								
Social Sniffing								
Threat								
Fighting								
Rearing								
Chasing								
Social Playing								
Following								
Sniff Anal-Genital								
Mounting								

The BACs in Figure 1 suggest interesting patterns in terms of broad differences between males and females, but also in terms of some differences within sexes. Whilst males tended to have higher values than females as a function of sampling effort, one male, Nyomfoza, seemed to be an exception to this trend, and one female, Bopha, seemed to be quite different to the other females. Understanding how and why these differences may have arisen could be important for understanding behavioural repertoires in cheetahs, in particular with respect to pairing the sexes and mate choice. For this reason I will now discuss BACs for the two sexes and individual animals.

Male Cheetahs

Figure 2 depicts the BACs for all of male cheetahs. For this analysis, all behaviours for all males were combined within each of the seven sampling dates, so males were effectively grouped into a single sampling unit. For these data, the values of the estimated Mao τ approaches an asymptote after the seven-day sampling period. The estimated richness of behaviours, estimated over the seven days, fell short of the estimated repertoire of behaviour based on the Michaelis-Menton richness estimator (MMMeans). The Mao τ gave an estimated richness of 48 behaviours with an estimated asymptotic repertoire size (MMMeans) of 49.83.
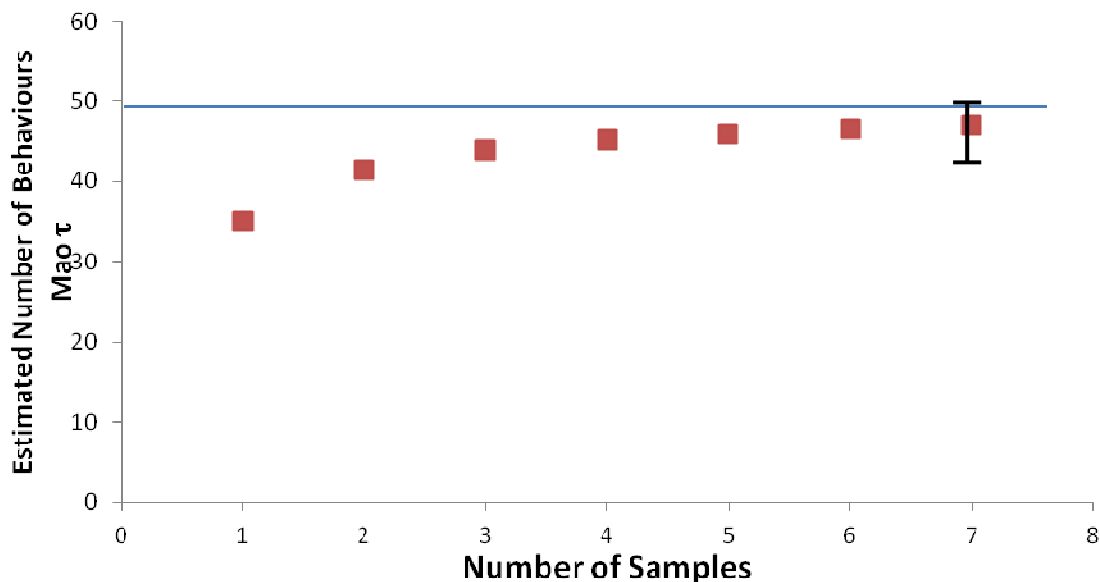

Figure 2. *Behaviour Accumulation Curve for male cheetahs combined. The estimated numbers of behaviours, as a function of sampling effort, is given as the Mao τ parameter. The 95% confidence limits for the Mao τ after sample seven are indicated by*

the error bar, and the total behavoural richness, estimated by the Michaelis-Menton richness estimator, is indicated by the horizontal blue line.

A high level of variation was seen within male cheetahs. Four of the five male cheetahs displayed a considerable amount of behaviour, accounting for all 48 behaviours between them, but one male, Nyomfoza, recorded a significantly lower BAC. Nyomfoza's behavioural suite did not include territory marking or threat/fighting/play behaviours, with many vocalisation behaviours also excluded. This lack of behaviour resulted in a Mao τ score of 24 for Nyomfoza, with a MMMeans of 25.18 (Figure 3). These values are noticeably lower than the Mao τ seen for the males combined.
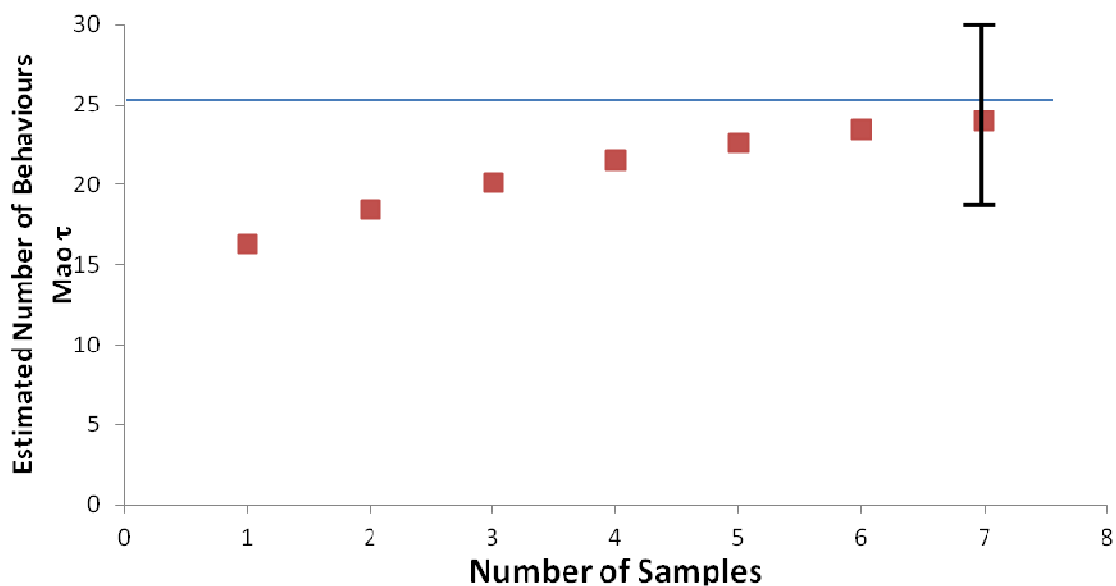

Figure 3. *Behaviour Accumulation Curve for the male cheetah Nyomfoza. The estimated number of behaviours, as a function of sampling effort, is given as the Mao τ parameter. The 95% confidence limits for the Mao τ after sample seven are indicated by the error bar, and the total behavoural richness, estimated by the Michaelis-Menton richness estimator, is indicated by the horizontal blue line.*

Izipho was similar to three other male cheetahs (Umballa, Ndonda and Induna) in his estimated number of behaviours. However, Izipho was seen to consistently display new behaviours across the observation periods. This is reflected in Figure 4 where his score for the Mao τ parameter was 35. This is considerably further away from

his estimated repetoire of 39.4 (MMMeans) which was seen for both Nyomfoza (Figure 3) and also the total for males combined (Figure 2).
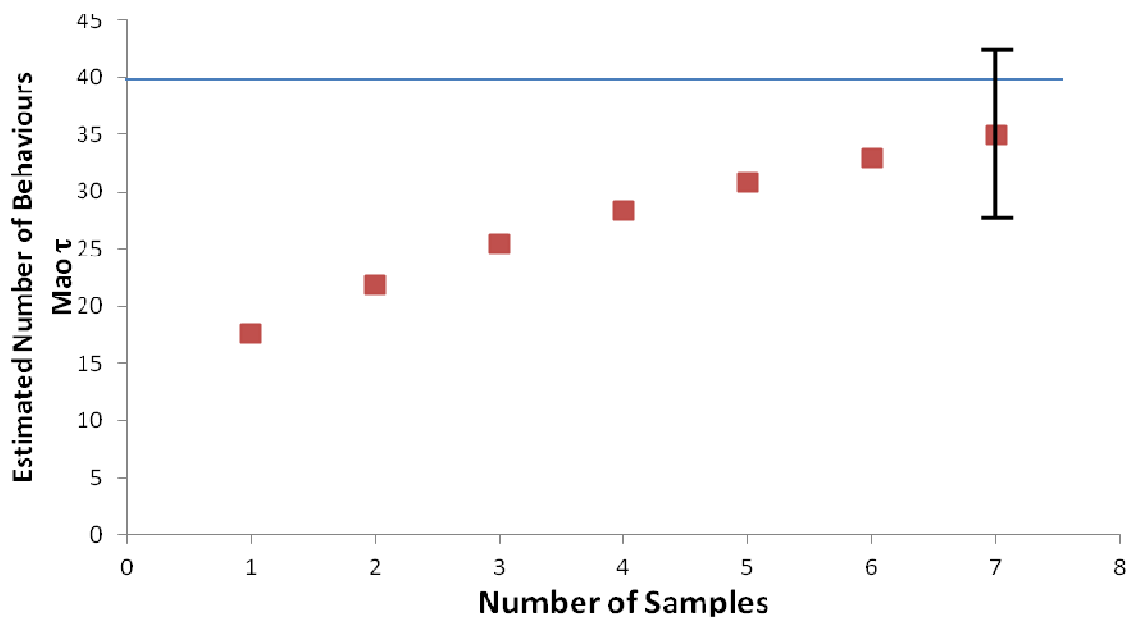

Figure 4. *Behaviour Accumulation Curve for the male cheetah Izipho. The estimated number of behaviours, as a function of sampling effort, is given as the Mao τ parameter. The 95% confidence limits for the Mao τ after sample seven are indicated by error bars, and the total behavoural richness, estimated by the Michaelis-Menton richness estimator, is indicated by the horizontal blue line.*

Female Cheetahs

Figure 5 depicts the BAC for all female cheetahs combined. As with the combined male data (Figure 1) the values of the Mao τ approaches an asymptote after the seven day sampling period. The Mao τ for females combined after seven sampling periods was 38, with an estimated asymptotic repertoire size of 40.2 (MMMeans). This discrepancy in repertoire size is due to females not displaying a number of social and reproductive behaviours, as seen in Table 1.
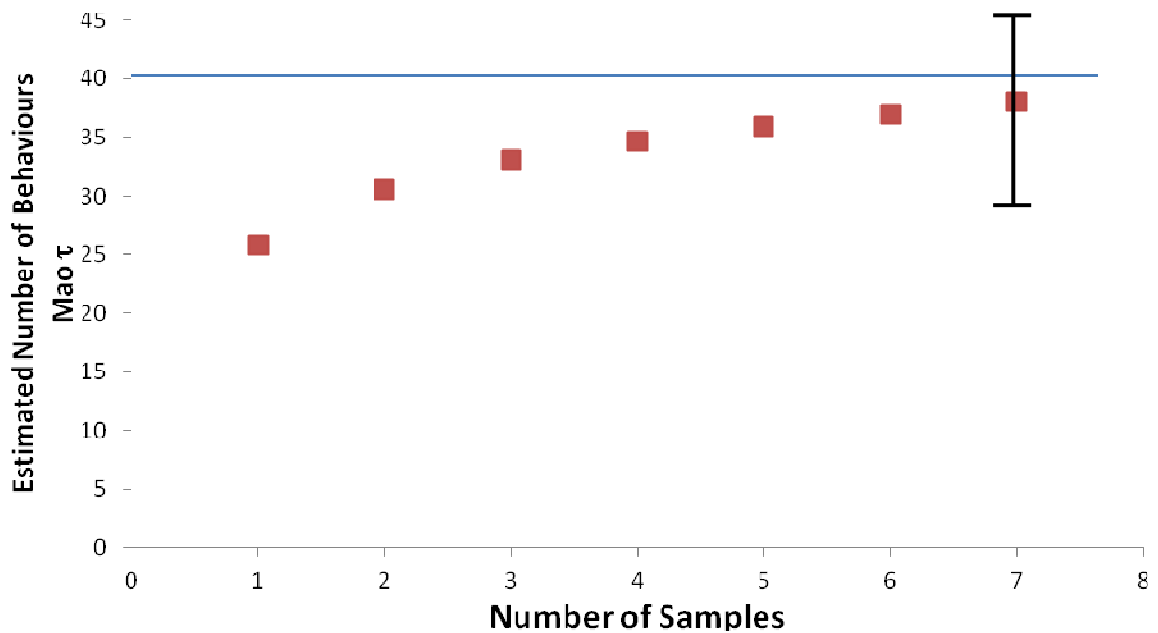
Figure 5. *Behaviour Accumulation Curve for all female cheetahs combined. The estimated numbers of behaviours, as a function of sampling effort, is given as the Mao τ parameter. The 95% confidence limits for the Mao τ after sample seven are indicated by an error bar, and the total behavoural richness, estimated by the Michaelis-Menton richness estimator, is indicated by the horizontal blue line.*

Similar to the males, the richness of behavioural repertoires varied between individual females. Bopha displayed a larger behavioural repertoire than the other females, with a Mao τ parameter of 33 (Figure 6), compared to a Mao τ parameter of 24 observed for Pinda (Figure 7) and a Mao τ of 28 observed for Lula. In fact, Bopha displayed a level of behavioural richness that was similar to the majority of male cheetahs (Figure 1), and was also seen to display a number of behaviours such as Stalking, Hunting and Sprinting that were not observed for the other female cheetahs.
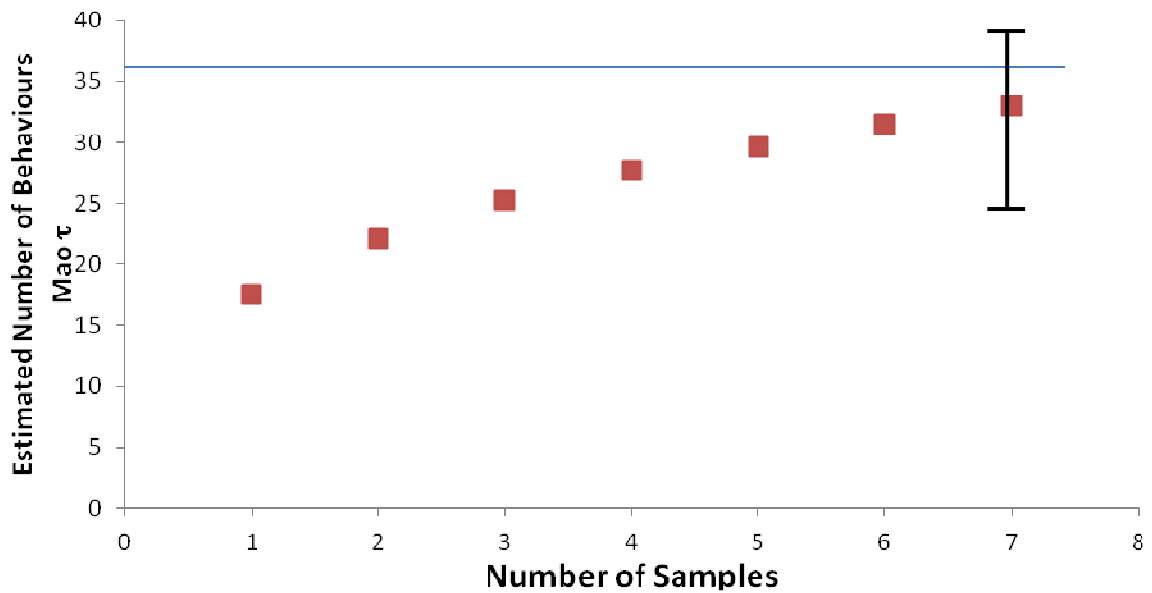
Figure 6. *Behaviour Accumulation Curve for the female Bopha. The estimated numbers of behaviours, as a function of sampling effort, is given as the Mao τ parameter. The 95% confidence limits for the Mao τ after sample seven are indicated by an error bar, and the total behavoural richness, estimated by the Michaelis-Menton richness estimator, is indicated by the horizontal blue line.*
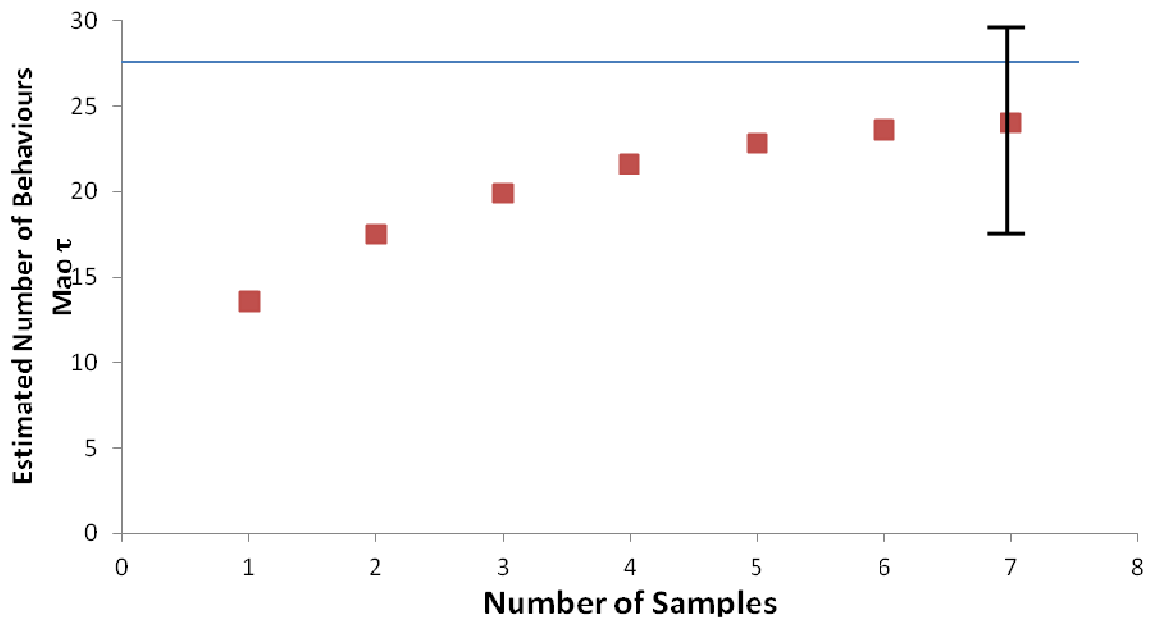

Figure 7. *Behaviour Accumulation Curve for the female Pinda. The estimated numbers of behaviours, as a function of sampling effort, is given as the Mao τ parameter. The 95% confidence limits for the Mao τ after sample seven are indicated by error bars, and*

the total behavoural richness, estimated by the Michaelis-Menton richness estimator, is indicated by the horizontal blue line.

Discussion

The Benefits of an Ethogram

A detailed ethogram is an important record of an animal's behavioural repertoire (Way *et al.* 2006). It allows for consistent results to be recorded both across the study and also with various researchers or facilities (Schleidt *et al.* 1984). This similarity in recording behaviour allows for comparisons to be made and adds to the wealth of knowledge on a species.

Observations on the Cheetah

Knowledge of the cheetah's behaviour has been acquired through extensive research on wild populations (Caro 1994, Laurenson *et al.* 1992). However, there are still considerable gaps in the knowledge of captive cheetahs' behaviour (Wielebnowski 1998). A comprehensive study of the complete behavioural repertoire of the cheetah has not previously been developed (Caro 1993).Previous research from the wild and captive environments has focused on specific elements of behaviour such as male coalition formation (Caro & Collins 1987, Caro *et al.* 1989 and Caro 1994) and interactions of mothers with cubs (Laurenson 1993). In this study, cheetahs were initially observed over a two week period in order to establish a basic repertoire of behaviour. This repertoire was then used to assess the accumulation of behaviours and determine differences between the sexes and between individuals. The full ethogram, arising from behaviours observed in this initial observation period, has been extended through continued observations of the cheetahs in various seasons and social situations.

Descriptive Ethogram

In the ethogram presented above, a total of 70 behaviours and 19 behavioural states were described for the group of cheetahs at MZP. These descriptions also include a number of behaviours not observed in the initial two week study or statistical analysis. As I performed further analysis of the cheetahs' behaviour (described in Chapters 4, 5

and 6) I observed a number of new behaviours and states. These behaviours have been included in the descriptive ethogram to give a more complete account of captive cheetahs' behaviour. These descriptions will also be used to explore variability in behavioural repertoires in subsequent chapters, which might suggest interesting trends for further research.

When I collected data for the ethogram, I found that the individual cheetah had their own behavioural repertoires. Individual distinctiveness was found by Feaver *et al.* (1986) when examining domestic cats and, more importantly for this study, by Wielebnowski (1999) and McKay (2003) when looking at the cheetah. In her paper examining behavioural differences in captive cheetahs, Wielebnowski (1999) found that ratings of temperament, such as fear of conspecifics and being tense, correlated with breeding success. This work illustrates the importance of individual differences within animal groups, as some individuals may appear better suited to captivity than others. McKay (2003) found positive correlations for breeding success with cheetahs that had a 'close and predictable relationship' (pg 188) with their keepers, suggesting appropriate management techniques play a vital role in cheetah husbandry. These kinds of differences in behaviour and temperament may impact on husbandry methods and the breeding success of many species (Boissy & Bouisson 1995).

Behavioural Richness in Captive Cheetahs

My initial two week analysis uncovered a considerable number of behaviours. In total, 48 different behaviours were observed from eight cheetahs over 56 hours of recording. For each of the individuals, their BACs had approached an asymptote over the seven samples, but their Mao τ parameters after seven days were, in most cases, only slightly smaller than the Michaelis-Menton means for the estimated repertoire of behaviour. This result suggests that the actual number of behaviours likely to occur over this sampling period is not expected to be much larger than the number of behaviours observed. This indicates that contrasts between individuals (or between sexes) based on these seven samples are likely to reflect real differences, rather than an artifact of incomplete behavioural sampling. At the same time, it was apparent from the BACs for most individuals, that behavioural repertoire richness would have continued to rise with further sampling effort. The discovery of additional behaviours that were added to the descriptive ethogram supports the finding that the full repertoire of behaviour had not

been observed. Continuing observations recorded many more behaviours, chiefly in the areas of courtship and mating, which were not witnessed within the initial two-week analysis.

Two key trends emerged from the BACs analyses. Firstly, there appeared to be a greater behavioural repertoire size in males, compared to females. Izipho is representative of the majority of males (Induna, Umballa and Ndonda) and these males were observed to have up to 10 more behaviours in their repertoire than the females. The larger repertoire size in males may be due to the social nature of male cheetahs. For male cheetahs, living in coalitions gives rise to a number of social interactions that are not generally seen in solitary females.

Table 1 illustrated the differences between the sexes, with males observed to stand and sleep together as well as show signs of communal investigation and territoriality, displaying the behaviours of Sniffing together and Spraying. Female cheetahs were not seen to perform a number of these social behaviours, and were never observed to stand or sniff objects together. Females did not display reproductive behaviours such as Sniffing Anal-genital area or Mounting, nor did they show signs of Fighting or Rearing at each other. Conversely, the behaviour of Tail Swishing was seen from all female cheetahs, yet only one male was observed to display this behaviour. These differences between the sexes can be compared to the general behaviours such as Walking, Eating, Grooming and Sleeping, which were observed from all cheetahs during the observation period.

The second trend arising from the BACs was that two individuals varied considerably in their behaviour, with one female (Bopha) and one male (Nyomfoza) showing substantially different behavioural richness than their respective cohort. Bopha appeared to be more similar to males than females in her behaviour. She displayed a higher number of observed behaviours in the study period than the other females and, in particular, showed signs of territory marking with combinations of behaviours such as Scratching, Defecation and Urination. Bopha was also observed Stalking, Hunting and Sprinting; behaviours not observed for the remaining females. Bopha's BACs is similar to that of four of the males with an observed behaviour repertoire higher than the other females (Figure 1). Conversely there was one male, Nyomfoza, which showed a reduced behavioural repertoire. This male spent most of his time during the observation period lying down or sleeping. He failed to display territory marking, threat/play or reproductive behaviours. His BACs is similar to the remaining female cheetahs, exhibiting the equal lowest score on observed behaviours for the study period. His Mao

τ parameter, and upper 95% confidence limit, was identical to those observed for the female Pinda, both displaying 24 behaviours and upper confidence limits of 30.9.

It appears that the greater behavioural repertoire of male cheetahs is linked to social living. The considerable reduction in behaviour seen for Nyomfoza, points to the need for further examination of the differences of male cheetahs' social behaviours. This raises the question: if a male is excluded from a social group does he simply show a lack of social behaviours or does his behavioural suite vary from the other males more broadly? The differences between the sexes, as well as the differences between members of each cohort, may play a role in developing husbandry practices for cheetahs. While it is known through the extensive work on wild cheetah that the male is primarily social and the female solitary (Caro 1994 & Laurenson *et al.* 1992), little research has been performed on the complete behavioural repertoire of the cheetah, particularly in captivity (Caro 1993). While Wielebnowski (1998 & 1999 and Wielebnowski & Brown 1998) has examined reproductive behaviours in captive female cheetahs, the captive behaviour of male cheetahs has not been readily studied.

Benefits and Limitations of a Captive Ethogram

The analysis of a behavioural repertoire for the cheetah in captivity is important to obtain a greater understanding of their complete behaviour. In the current study, I have shown how extensive this behavioural repertoire is for a captive population, as well as the importance of examining the sexes and individuals in their own right. The current analysis of BACs is important as they show that there are not just a reduced number of behaviours for female cheetahs, but that the repertoire consists of a different behavioural set. While there are overlaps in their general behaviour, it is important to note that there are considerable differences in the male and female cheetah's behaviour. These differences are based on sociality and reproductive behaviours and are not only isolated to the sexes, as the study also shows variability between individuals within the sexes. These variations may be important for husbandry purposes as they may provide a clue to better management techniques.

Whilst there are numerous benefits to the development of an ethogram using captive animals, there are some limitations and caution must be used when developing and applying an ethogram. The captive environment may not allow for a full repertoire of behaviour to be observed. For example, an artificial environment may have prevented the extent to which behaviours such as predation are observed. Small changes in this

artificial environment may also lead to an over-representation of other behaviours. Captivity can create a number of stereotypical behaviours such as pacing. These types of behaviours are only observed in the captive environment. Hence, there is a possibility that some behaviours are over or under represented and that some may have been excluded altogether. This limitation also holds true for the reporting of temperament. Differences between animals, especially in the areas of fearfulness and tension, may be over-represented in captivity compared to the wild. As there is no accurate way of measuring the effect captivity has on an animal's temperament, these ideas can only be applied subjectively (McDougall *et al.* 2006). Overall, the ethogram provides a greater understanding of cheetahs' behaviour in captivity as well as their repertoire in general.

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