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

Rebecca Bradford-Wright

B.A. Hons

A THESIS SUBMITTED FOR THE DEGREE DOCTOR OF PHILOSOPHY

School of Biological Sciences, Flinders University, Adelaide, Australia

February 2013

Chapter VI

Responses of Males to Female Cues in the Cheetah

Introduction

The cheetah (*Acinonyx jubatus*) has a very long history of being kept in captivity (Marker-Kraus & Grisham 1993), with records of human association dating back to ancient Sumaria (Hunter & Hamman 2003). In spite of this history, the cheetah has one of the worst breeding success rates in zoological parks (Marker 2000 and Marker & Echement 2010). Their poor record of breeding in captivity contrasts with the breeding success of wild cheetahs (Laurenson *et al.* 1992). Facilities that hold large numbers of cheetahs, and have the ability to move animals around, are having some breeding success (Bertschinger *et al.* 2008), but the majority of captive cheetahs are held in smaller suburban zoos with less than ten animals in each facility (Marker *et al.* 2007). It is in these institutions that the bulk of the cheetah's genetic diversity is kept (Marker 2000 and 2004). These are the facilities that need to breed their cheetahs in order to keep a viable and diverse population of cheetahs in captivity.

The first scientifically recorded birth of a cheetah in captivity was in 1956 (Florio & Spinelli 1967 and Marker-Kraus 1997). However, it was not until 1970 that a zoo was able to successfully rear a litter of cubs to adulthood (Rawlins 1972). During the 1980s and 1990s, success was sporadic, with little understanding of the reasons for this poor success rate. More recently, breeding has improved. However, the majority of cheetahs born in captivity over the last 15 years have come from a small number of facilities (Marker-Kraus 1997, Marker 2000, 2004, Marker *et al.* 2008 and Marker & Echement 2010). These facilities typically have ample numbers of cheetahs and/or little to no impact from public viewing (McKeown 1991, O'Donovan 1993 and Bertschinger *et al.* 2008

Due to varied management and veterinary practices, it can be difficult to undertake behavioural research at zoological parks and breeding facilities. As has been found with wild cheetahs (Caro 1994), observations of sexual interactions between male and female cheetahs in captivity are limited (Beekman *et al.* 1997). Of the interactions that are observed, it is typically those that lead to pregnancy that are reported but, even then, reports are only occasional. Information on unsuccessful breeding trials remains un-published and information on breeding is seen occasionally in zoo publications reporting single litters and events in isolation (Florio & Spinelli 1967, Manton 1970, Vallat 1971 and Bircher & Noble 1997). These reports, which flourished in the 1970s,

are typically anecdotal, as they are usually not part of a controlled experiment and not conducive to replication. At times these non-scientific reports are very vague. Results have been presented in terms of statements such as “an increase in activity and certain behaviours” and “male cheetah also displayed changes in specific behavioural frequencies” (Bircher and Noble 1997), without reporting the ‘certain behaviours’ or ‘specific behavioural frequencies’. Hence it appeared that many pregnancies result more from chance than from specific hypotheses being tested.

Hypotheses for Breeding Cheetahs in Captivity

From these initial reports, numerous problems with breeding cheetahs in captivity are noted (Schwammer 2000). However, the reports are somewhat conflicting, with some techniques for breeding cheetahs working in some facilities and very different techniques working in others. Varied attempts have been made by zoological staff to report their hypotheses on the cheetah’s inability to breed reliably in captivity. Florio and Spinelli (1967) reported that cheetahs needed to be housed with an uneven ratio of two males to one female and that ‘long views’ from their enclosure were essential to stimulate their behaviour. Manton (1970) reported that a single pair of cheetahs should be housed together until mating and maintained until just before birth. Vallat (1971) reported the exact opposite of Florio and Spinelli (1967), stating that male and female cheetahs needed to be housed together at all times with an uneven ratio of one male to two females, yet reported an associated high degree of aggression. Opposing those ideas, Rawlins (1972) reported that it was lack of privacy that was the major concern for these animals, proposing that as the cheetah is a very shy animal it must be given the opportunity for seclusion in the captive environment in order for it to reproduce. Lastly, Benzon and Smith (1974 and 1975) believed that stimulating extremely high levels of male aggression would gain female interest. The uncertainty surrounding strategies, and the resulting uncertainty of captive managers, appears to be a likely contributor to the difficulties associated with breeding cheetahs in captivity.

In the 1990s, extensive research began on cheetahs, both in the wild and in captivity. The North American population of captive cheetahs were used as a research population by the Species Survival Plan – an action group developed to try to solve the cheetah’s breeding problem (Wildt & Grisham 1993). Through this research, some consensus on what was believed to be essential elements for breeding cheetahs in

captivity was reported. These elements include isolation from other carnivores, long views from their enclosure yards (McKeown 1991), isolation of the sexes (Benzon & Smith 1975 and Wildt *et al*. 1993) and the possibility of mate choice (Caro 1994). Much of this opinion came from looking at the research on wild animals where the same problems for breeding do not exist (Laurenson 1993). While the lack of sexual interaction and resulting pregnancy in captive cheetahs had been attributed to a confusing array of factors, the emphasis had now moved to considerations of female physiology and behaviour (Laurenson *et al.* 1992 and Bertschinger *et al.* 1998).

Conflicting results emerged from the research, with some reports suggesting ovulation is induced by male aggression (Benzon & Smith 1975 and Wildt *et al*. 1993). Other reports suggested that as mating induces ovulation in the domestic cat (*Felis cattus*) something similar might operate in the cheetah (Bertschinger *et al*. 1998). Brand (1980) reported that male and female cheetahs need to be separated and then periodically reintroduced to each other, to stimulate ovulation. McKeown (1991) concurred, reporting on the importance of variety and not housing the sexes together for more than 4-5 days. Recent research shows that oestrus is cyclic and not dependent on the presence of males (Brown *et al.* 1996, and Wielebnowski & Brown 1998). This research also shows that oestrus can be tracked in some female cheetahs using changes in faecal oestradiol concentrations (Brown *et al.* 1996 and Wielebnowski & Brown 1998) and that minor changes to behaviour can be noted for some individuals (Wielebnowski & Brown 1998 and Wielebnowski 1999).

The Problems of Breeding Cheetahs in Captivity

One of the major findings of the Species Survival Plan research program was that cheetahs held in captivity display a variety of different behavioural and physiological problems than what is seen in the wild population (Laurenson 1993 and Wildt *et al.* 1993). Historically, cheetahs in captivity have been kept in unnatural holding situations. Until recent times, due to lack of knowledge of behaviour and their particular needs, many zoos and conservation parks have held female cheetahs in groups and kept male cheetahs isolated (McKeown 1991). Research from wild populations has shown that male cheetahs are often social, forming coalitions of both related and unrelated animals and holding territories in these coalitions (Caro & Collins 1986, 1987a&b and Caro 1994). This behaviour is contrasted by the females which are typically solitary, only

coming together with males to mate (Caro 1993, 1994) or socialising with cubs (Laurenson *et al.* 1992).

These differences need to be considered when housing cheetahs. It appears that zoos are often slow to incorporate research results into their practices. Therefore, the development of zoological programs, including feeding schedules, social groupings, exhibits, enclosures and animal houses, is often based on out-of-date information. Animals are housed according to what is desirable from a public viewing perspective rather than what suits the animal (McKeown 1991 and O'Donovan *et al.* 1993). Larger facilities that have placed their primary focus on breeding animals and are not dependent on public viewing, have reported greater success in breeding cheetahs, as they do not have the same constraints seen in many suburban zoos (Marker 2002).

Separation of the Sexes

A number of institutions have had one or two successful breeding attempts, but then have long periods without breeding success (Marker-Kraus 1997). The common element for many of these institutions is that the sexes have been housed separately. This separation has varied, from a single mesh fence just preventing physical contact between the sexes, to housing the sexes on different sides of a park in order to separate the animals by visual, olfactory and auditory means (Vallat 1971, Brand 1980 and McKeown 1991).

Separation of the sexes is known to be a requirement for many species, both in the wild and in captivity, for a number of reasons (Clutton-Brock 1989). Some species are purely solitary and to live socially, either with the same sex or opposite sex, is not natural (Mellen 1991). Other reasons for separation of the sexes include suppression of reproductive cycles (Wildt *et al.* 1993 and Brown & Wielebnowski 1998), synchronisation of oestrus (Say *et al.* 2001), or to provide stimulation and opportunity for mate choice (Hoefler 2007).

Reports of cheetahs mating in the wild are limited (Caro 1994 and Gottelli *et al.* 2007). However, of the information that is available, it appears that males search for females using olfactory cues, consort in their home ranges, observe and possibly guard them until they are receptive and then, if accepted by the female, they are able to mate (Caro & Collins 1987b, Laurenson *et al.* 1992, Caro 1994, Hunter 2000 and Kelly & Durant 2000). In recent research the female cheetah has been examined for promiscuity

and multiple mate choice (Gottelli *et al.* 2007). While there has been considerable research on the role played by female cheetahs in this area, male cheetahs have received comparatively little attention (Caro 1993 and Ruiz-Miranda *et al.*1998).

Aims

The aim of the current study was to stimulate interest in courtship and mating in male cheetahs by creating a semi-natural environment. Very little research has been performed on male responses to female cheetahs, particularly in captivity. Therefore this study proposed to create an environment that provided males with the opportunity to investigate multiple females, so their response to various options could be determined and behaviours observed. The male cheetahs at Monarto Zoological Park (MZP) had previously shown no interest in females and there had been no signs of courtship while housed in the same enclosures. Creating a similar social situation to what has been reported from the wild may succeed in producing interest in courtship.

One of the primary ways of investigating whether interest in courtship could be stimulated was to separate the males and females and provide a short period of isolation prior to re-initiating contact. The males and females were also prevented from observing one another during physical isolation via the construction of a visual barrier between their yards. Mate choice options were also used to attempt to stimulate interest. While running trials, both sexes were able to observe multiple potential partners. If male cheetahs were able to investigate multiple females for receptivity then it may increase the chances of stimulating interest.

Male cheetahs were also provided with an opportunity to choose between investigating the female lock-away yards, or if they were not interested in investigating the females, returning to their night-yard at any time. The choices provided made it obvious when males were disinterested in the females.

It is hypothesised that changing the social situation and environment of cheetahs to create a more natural situation for consorting would stimulate an interest in courtship behaviours. Separation of the males and females was examined to determine if males would be considerably more interested in investigating and mating when reunited with females. In the wild, male cheetahs walk through a female cheetah's home range and

find an oestrus female. While it is very difficult to replicate a similar experience in captivity, it may be a key to improving breeding success.

Methods

Animals and Facility

Animals used in this experiment included four of the five male cheetahs (Induna, Ndonda, Izipho and Nyomfoza) and all three female cheetahs (Pinda, Lula and Bopha) held at MZP. A female cheetah from Perth Zoo (Zilkaat) was brought in on breeding loan for a short time at the end of 2002 and was also included in the study.

Apparatus /Materials

Equipment used to observe cheetahs included a *Realistic*® Minisette–20 tape recorder, an *Olympus*® C-740 digital camera and a JVC GR-520 EA® video camera.

As there was no possibility of completely separating the males and females within the zoo facility, the means of separation had to be in the form of a physical and visual barrier. This barrier was erected between night yards A and B, as yard A was the largest and allowed direct access to the raceway so that animals could move into the main enclosure. Using yard A for male cheetahs meant they could be moved into the exhibit with limited visual access to the other yards in the facility.

A barrier was constructed, consisting of a corrugated iron fence, 25 metres long by 2.5 metres high. The smaller night-yards, B, C and D were also separated from one another using brush fencing and shade cloth to block visual access as much as possible. These barriers were constructed in late 2001, ready for the beginning of the data collection in 2002 (Figure 1).

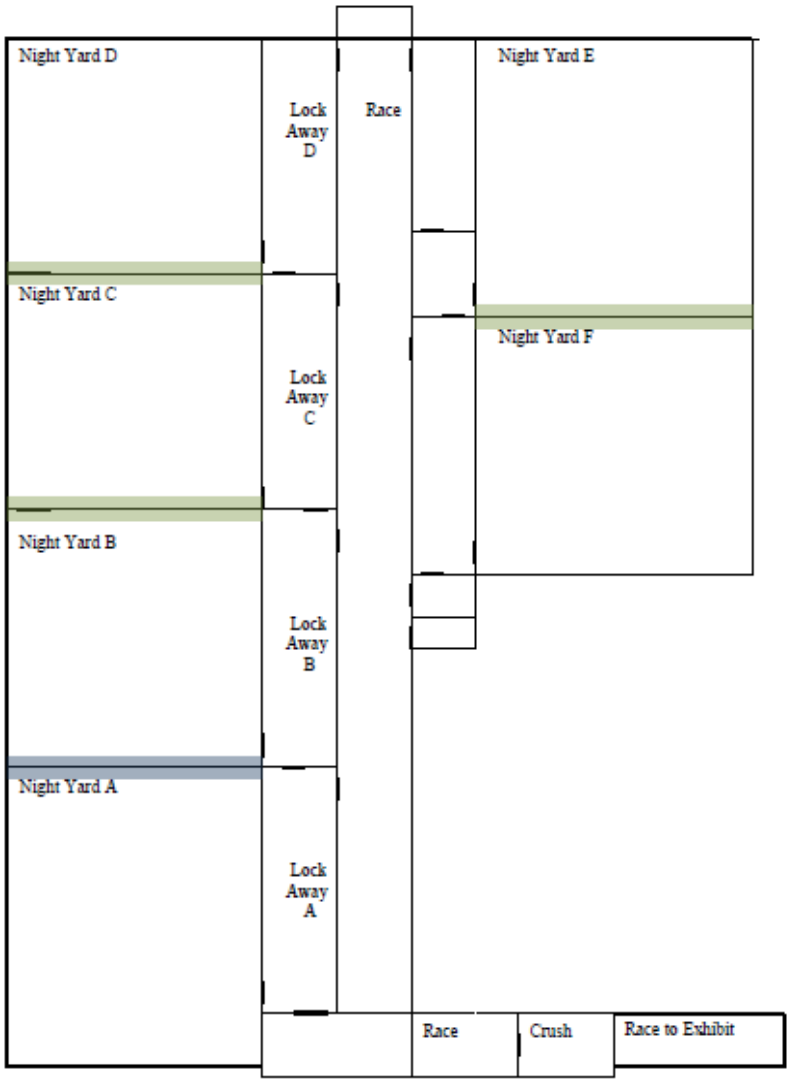


Figure 1. *Night-yard and lock-away map. (Tan indicates brush fencing and blue indicates iron fencing).*

Procedure

Males and females were totally excluded from each other for a month after the visual barriers were erected to provide some time for the separation to have an impact. Males were housed in the main exhibit during the day and in yard A overnight. Females were placed into each of the different night-yards as follows. Lula was in yard B, Pinda was in yard C and Bopha was in yard D (Figure 1) Bopha and Lula were further separated from one another by placing Pinda between them. Females were not

completely visually separated, but these yards had a lot of shrubbery providing many areas of seclusion. For the short time MZP housed the Perth female Zilkaat (November to December 2002), she was placed into yard C and Pinda was moved across the raceway into yard E. For five days prior to the beginning of trials, the males were housed and fed in their exhibit rather than returning to night yard A. This eliminated the need for them to come near the females and provided a greater separation (olfactory and auditory) just before the start of the experimental work. Females were kept in their lock-away areas overnight to maximise any deposition of scents, including fresh urine and faeces, for the males to investigate in the lock-away areas.

The key requirement from the staff at MZP was a thorough cleaning of each female lock-away after each trial. As it was important to provide fresh samples for the males to investigate each day, each yard needed to be thoroughly cleaned by rinsing the floor, washing all hard objects and changing the straw bedding.

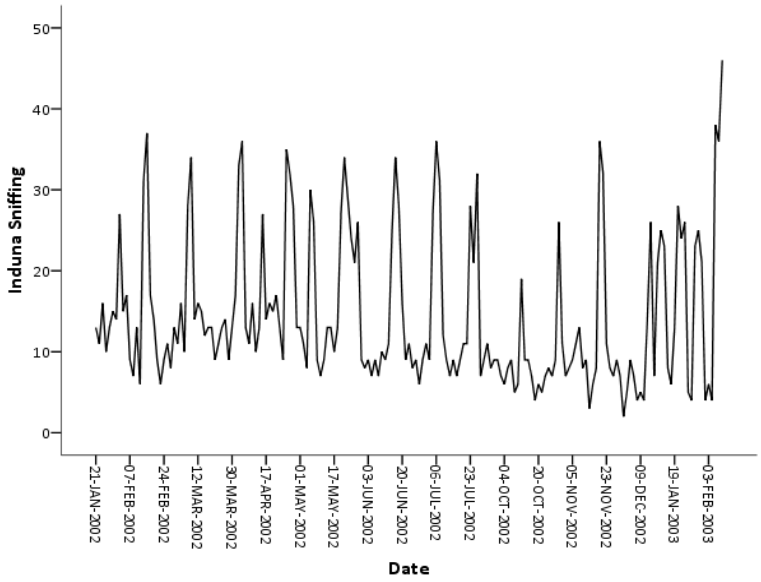
Throughout the experiment, behaviours were recorded using a small tape recorder. The method of recording was continuous (Martin and Bateson 2000). Behaviours were spoken into the recorder and then transcribed as soon as possible after the session. A video recording of each period was also produced to improve the accuracy of the results. Recording was performed from inside lock-away areas for yards E and F and also along the race so that all cheetahs were visible at any one time (Figure 1). Males were given access between 07:30 h and 10:00 h every morning. During this time, responses towards both the females and the other males, if any, were recorded.

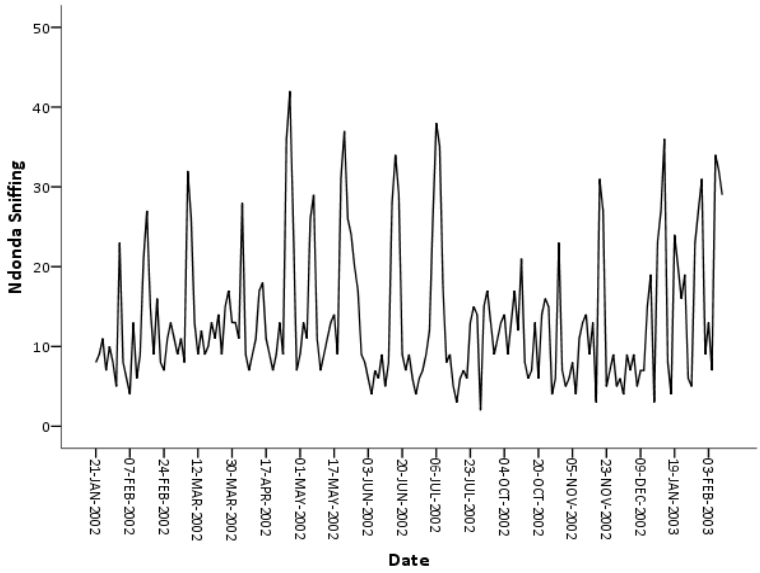
All males were to given access to the lock-away areas of the female night-yards for 30 minutes each morning. The males as a group were allowed to roam freely through the lock-away yards and their levels of interest in the females were assessed. As before, the males were not allowed to have access to the female, only being able to interact through the mesh fence. If, after 30 minutes with the females, there was no interest shown by either sex, the males were allowed back out into the main enclosure. If there was interest shown by either sex, the level of this interest was assessed and a decision made on whether the male showing the most interest was allowed access into that females' night-yard.

Results

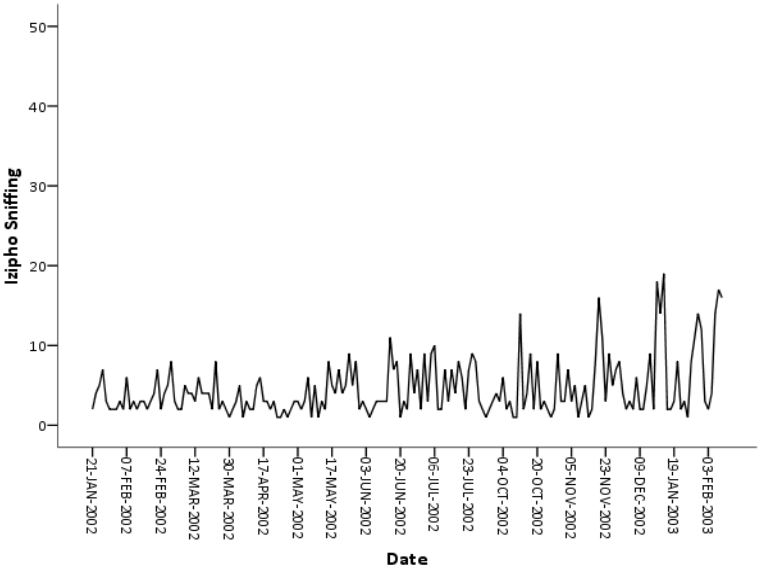
Males were examined for 185 observation periods during this study. During these observations a number of behaviours were seen to occur frequently and also fluctuate over the observation periods. Surprisingly, behaviours such as Fighting, Spraying and Grooming that had frequently been observed when examining the males, were no longer being displayed now they were investigating the females. Data were examined to determine which of the behaviours were observed in multiple males from the group. Behaviour frequencies varied within each variable as well as between individual males, therefore six key behaviours were selected for analysis from the data set. These behaviours were Sniffing, Chassé, Stutter Call, Lying, Calling and Pacing. Five of these behaviours were selected due to the frequency which they were observed and the sixth behaviour, Stutter Call, was selected as it occurred periodically but with considerable changes in frequency over time. Its occurrence also appeared to covary with the increase or absence of a number of the other key behaviours. These behaviours were explored using line graphs to compare males over the study.

a) Induna

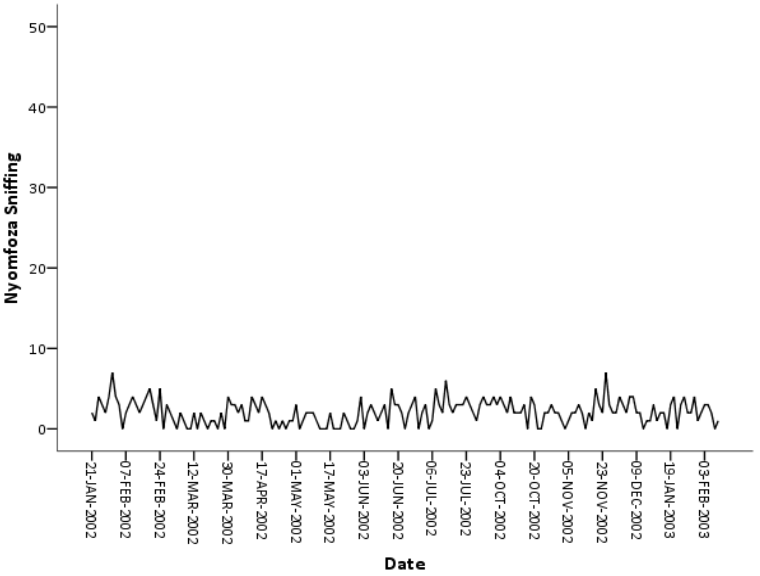




b) Ndonda



c) Izipho



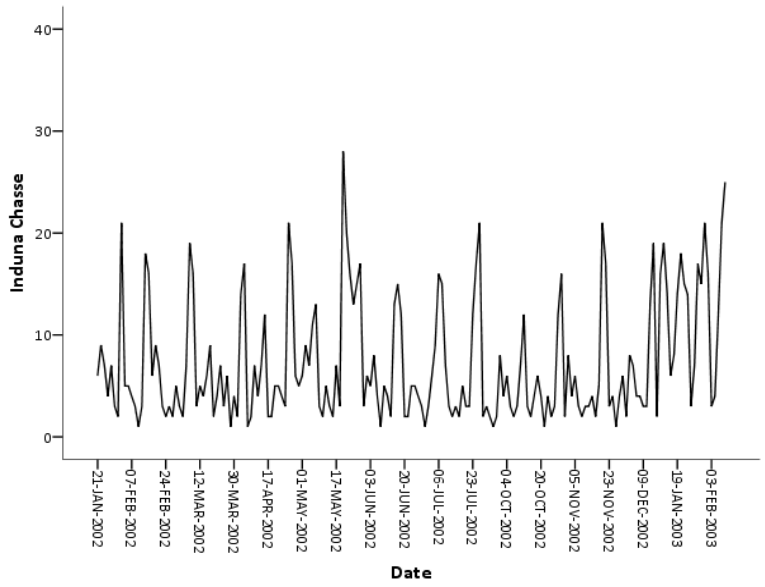
d) Nyomfoza

Figure 2. *Absolute counts for Sniffing observed for individual males over the study*.

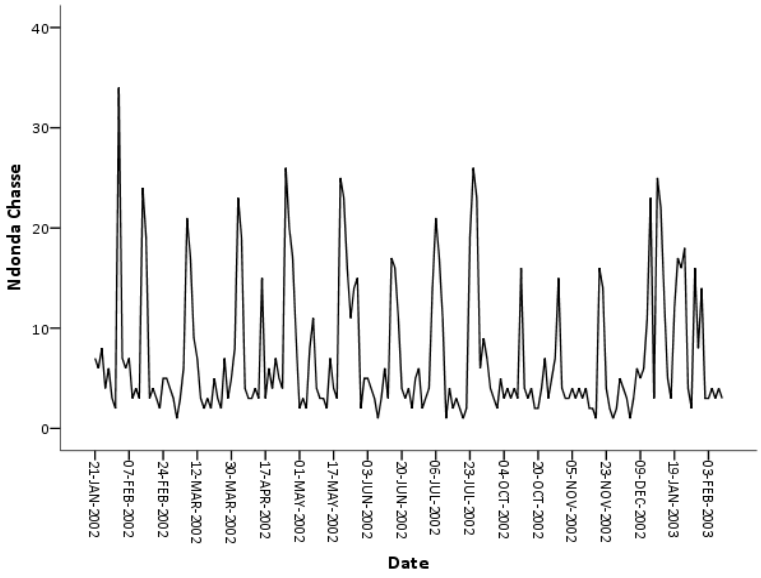
Sniffing was the key behaviour observed for males investigating the female lock-away yards (Figure 2). As females had spent their nights in these yards, it is likely these yards contained olfactory signals for the males to investigate. All males displayed this behaviour, but the variation between males ranged dramatically through the observation periods, ranging from nil occurrences for some observation periods for Nyomfoza (Figure 2d) through to 46 for Induna (Figure 2a). Nyomfoza was the only male observed to enter the lock-away area and fail to sniff in an observation period. Other male's rates of Sniffing were observed to fluctuate strongly over the study and it was evident that there appeared to be an element of cyclicity to this behaviour, particularly for Induna and Ndonda.

Figure 3 depicts the observations for all males on Chassé (see Chapter 3). This behaviour was only observed while males were watching females and it was noted as a key behaviour. Males would observe a female in her night-yard and move laterally back and forth whilst watching her. The male appeared excited and this behaviour was frequently observed in association with Sniffing, Stutter Call, Drooling and Penis Exposure. Again the observations for Chassé show an apparent cyclicity, with Induna and Ndonda showing large fluctuations over time. Izipho (Figure 3c) also showed cyclical patterns in expression of Chassé, with higher event numbers in the second part of the study but with generally lower levels of expression than Induna (Figure 3a) and Ndonda (Figure 3b).

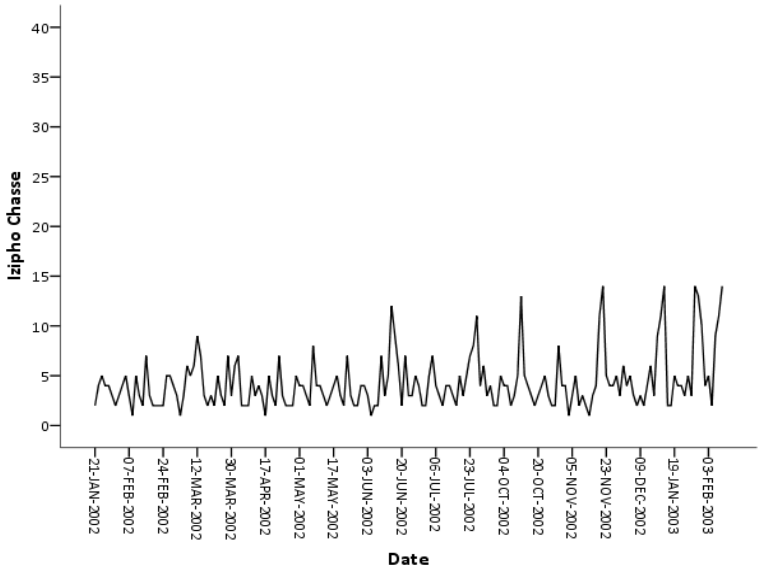
a) Induna



b) Ndonda



c) Izipho



d) Nyomfoza

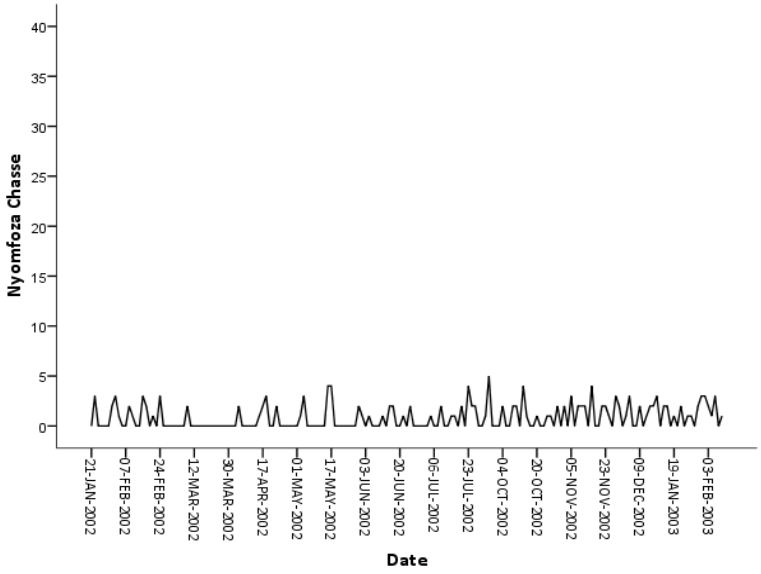


Figure 3. *Absolute counts for Chassé observed for individual males over the study.*

Correlations between all males on these behaviours were calculated. As there were a number of behaviours that appeared to fluctuate regularly, it was important to know if there was a relationship between males exhibiting those behaviours. Table 1 shows the correlations between all male pairs for Sniffing and Chassé.

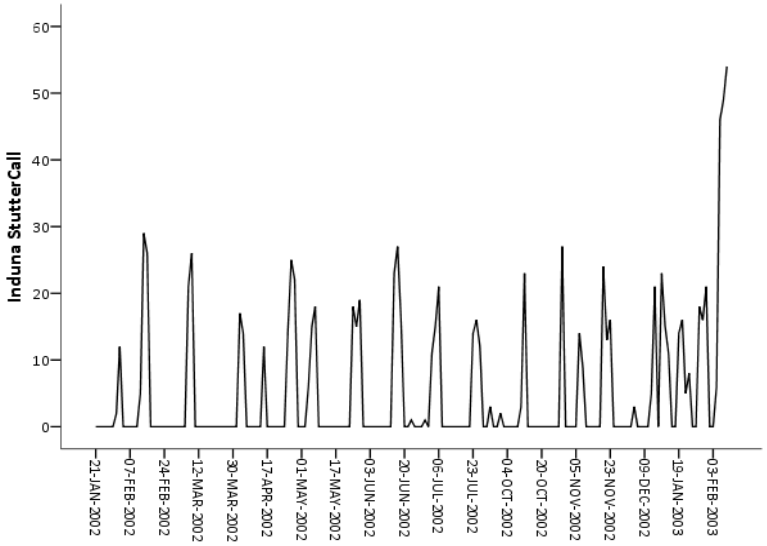
There were strong relationships evident between Induna, Ndonda and Izipho on both behaviours, with the strongest relationship between Induna and Ndonda on Sniffing. However, Nyomfoza behaviour did not correlate with the other males.

Table 1. *Correlation coefficients and associated statistical significances (in brackets) for Sniffing (values above the diagonal) and Chassé (values below the diagonal) for the male pairs in the study. Significant values are in bold type.*

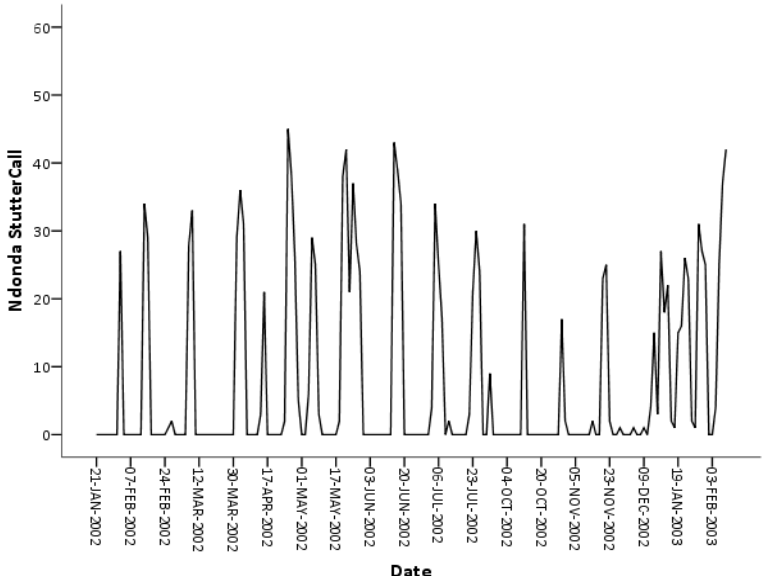
	Induna	Ndonda	Izipho	Nyomfoza
Induna	--	**0.821**	**0.452**	-0.088
		(< 0.001)	**(< 0.001)**	(0.233)
Ndonda	**0.799**	--	**0.436**	-0.094
	(< 0.001)		**(< 0.001)**	(0.204)
Izipho	**0.460**	**0.330**	--	-0.022
	(< 0.001)	**(< 0.001)**		(0.765)
Nyomfoza	0.094	0.081	0.151	--
	0.205)	(0.270)	(0.040)	

Stutter Call (see Chapter 3 for a description) has been reported as a call to convey excitement and also sexual interest (Wielebnowski & Brown 1998). This call was observed at various times during the study. It was observed to occur in short bouts, with an almost complete absence of the behaviour between the bouts. Figure 4 illustrates the incidences of Stutter Call over the study. Again there is cyclicity in this behaviour, with peaks occurring at the same time as peaks were evident in Sniffing and Chassé.

a) Induna



b) Ndonda



c) Izipho

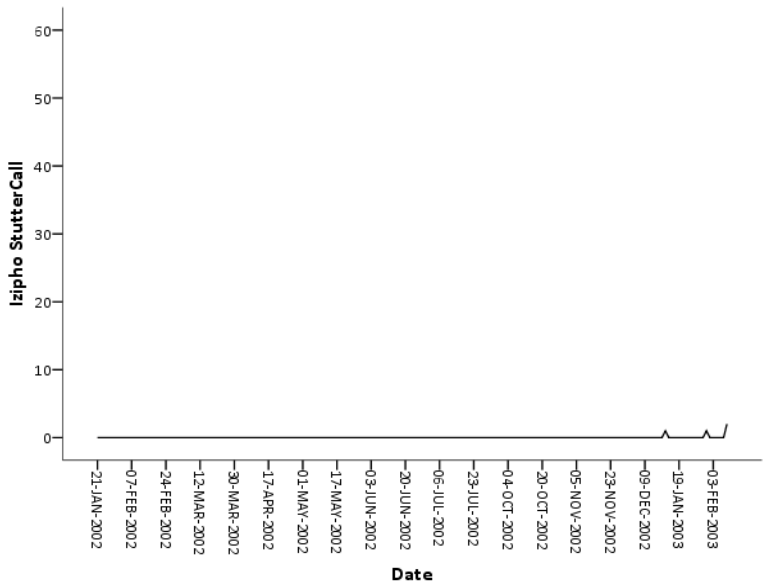
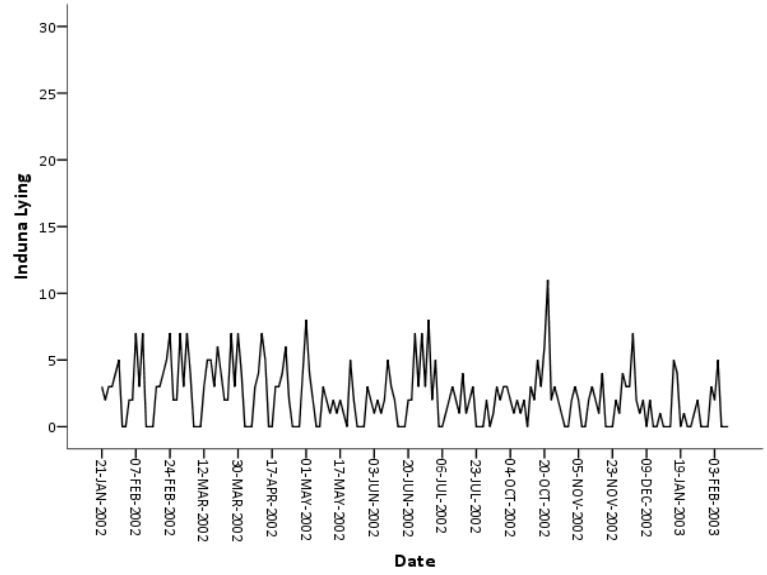


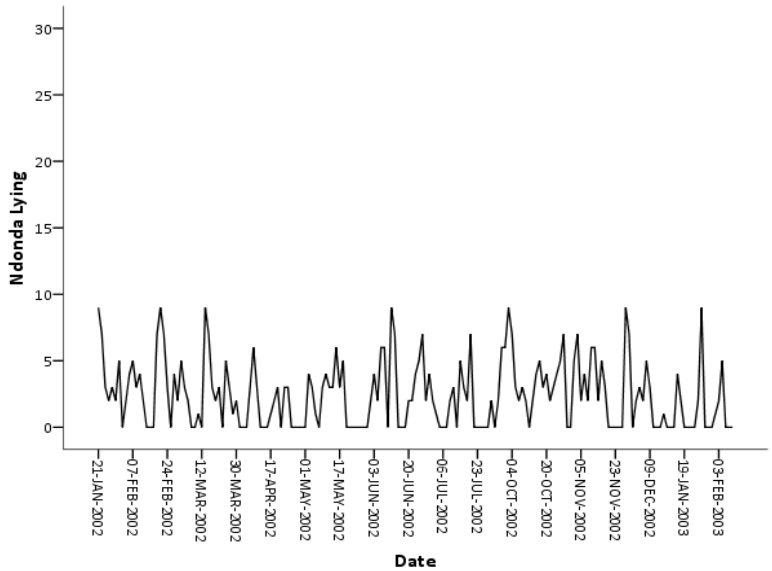
Figure 4. *Absolute counts for Stutter Call observed for individual males over the study.*

While Induna and Ndonda displayed this behaviour in bouts over the entire study period, Izipho only began to Stutter Call during late 2002, and even then counts were much lower than for Induna and Ndonda. Nyomfoza did not produce a Stutter Call throughout any of the observations.

Figure 5 graphs incidences of Lying over the observation period and it is apparent that this behaviour exhibited very different patterns than seen with the other behaviours analysed above. Lying was noted when males no longer appeared interested in looking for or observing the females behaviour or investigating their lock-away yards. Observations of this behaviour for Induna and Ndonda were relatively low and remained relatively stable over the study. Once given access to the female lock-away yards both remained relatively active. However, Nyomfoza displayed a considerably higher frequency of this behaviour than the other males. Again, the behaviour remained stable over the study. Izipho differed from other males as he showed a higher degree of variability over the study for Lying and a distinct decrease in this behaviour in the last four months of the study.

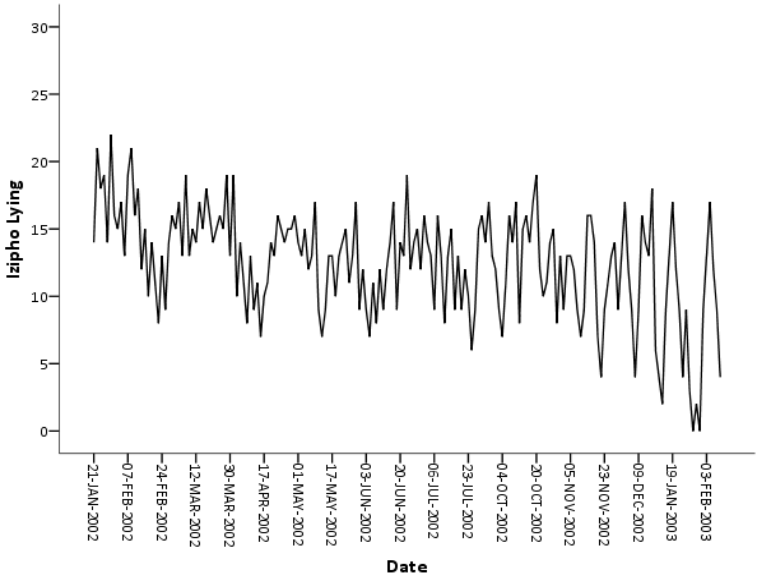


a) Induna



b) Ndonda

c) Izipho



d) Nyomfoza

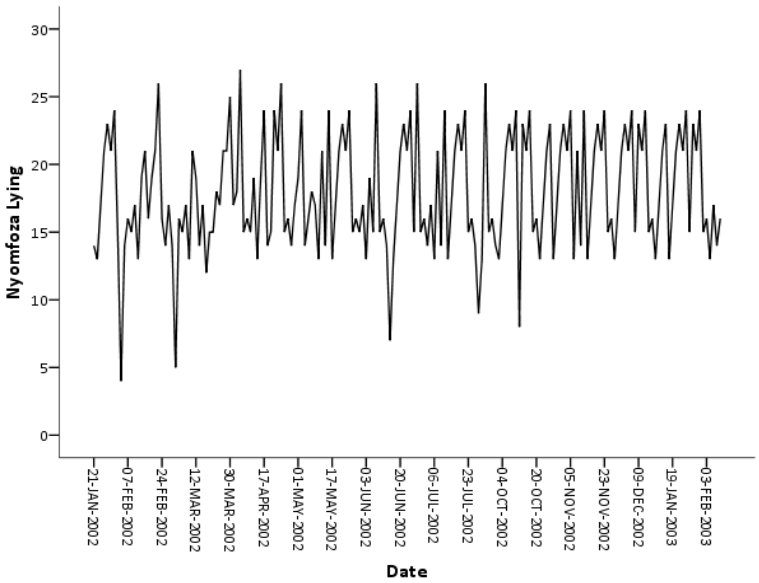


Figure 5. *Absolute counts for Lying observed for individual males over the study*.

The relationship between males was explored further using correlations for Stutter Call and Lying. Table 2 illustrates the relationships between male pairs for these behaviours. Strong correlations were found between Induna, Ndonda and Izipho for Stutter Call. Nyomfoza was omitted from this analysis as he did not produce a stutter call in the study period. The relationships between males for Lying are not as clear. There are positive correlations between Induna and Ndonda, and Induna and Izipho, for this behaviour.

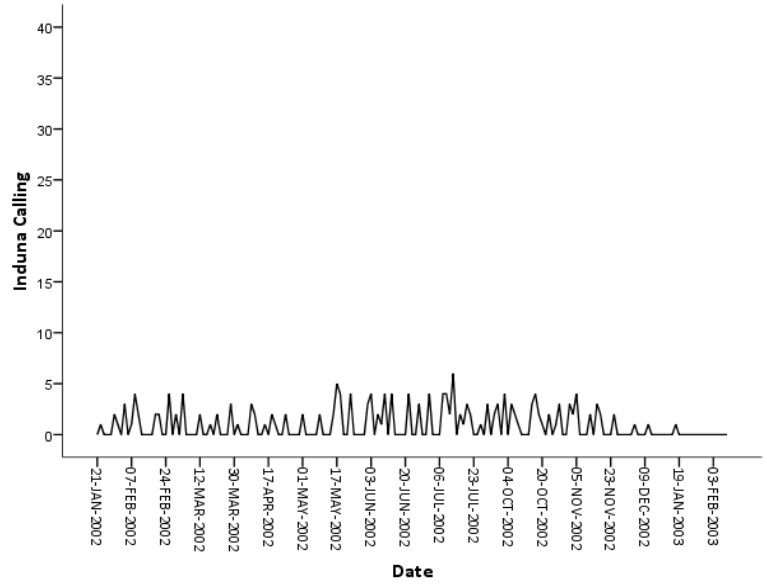
Table 2. *Correlation coefficients and associated statistical significances (in brackets) for Stutter Calling (values above the diagonal) and Lying (values below the diagonal) for the male pairs in the study. Significant values are in bold type.*

	Induna	Ndonda	Izipho	Nyomfoza
Induna	--	**0.749**	**0.387**	a
		(< 0.001)	**(< 0.001)**	
Ndonda	**0.332**	--	0.229	a
	(< 0.001)		(0.002)	
Izipho	**0.312**	0.055	--	a
	(< 0.001)	(0.456)		
Nyomfoza	-0.016	-0.064	-0.133	--
	(0.830)	(0.387)	(0.070)	

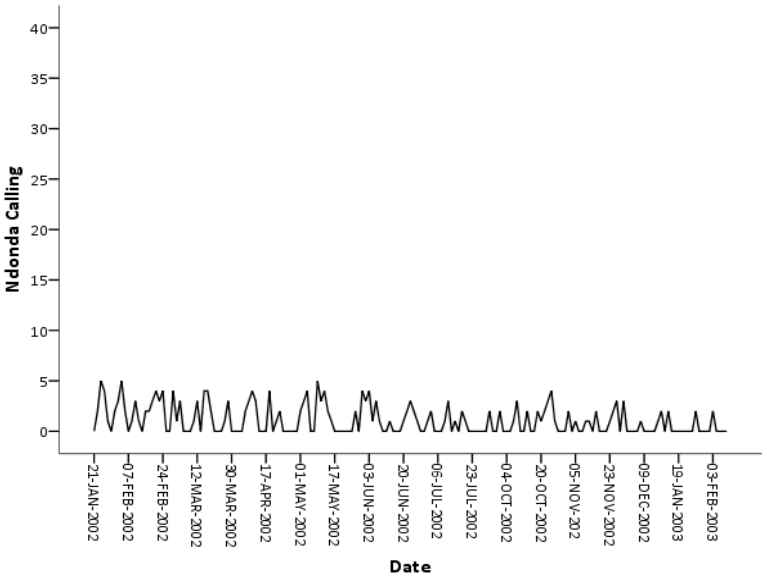
a = *could not be computed as Nyomfoza did not display this behaviour.*

Calling was observed frequently from male cheetahs during the trials and primarily consisted of the separation/distress call made by cheetahs when they are separated. Males were generally observed to make these calls when all other males were at least two metres away from them and when other males would move through the lock-away yards leading to a physical barrier between the 'Calling' male and the others. Figure 6 shows the results obtained for Calling over the study. Calling was observed from males which were generally not observing the females.

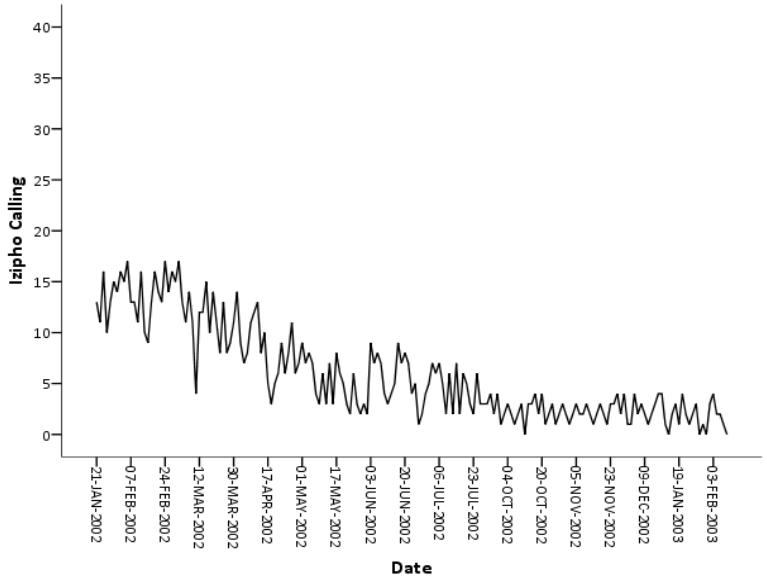
Minimal Calling was observed from Induna and Ndonda (Figures 6a & b) over the study, but this behaviour was observed frequently from Izipho (Figure 6c) during the earlier parts of the study, and throughout the study from Nyomfoza. Interestingly, over the study it was seen that Calling reduced considerably for Izipho. His rate of Calling started at a level similar to that of his brother Nyomfoza (Figure 6d), but by the end of the study his results were similar to Induna and Ndonda. Conversely, Nyomfoza's Calling was seen to increase over the study, where it was seen that the behaviour began to reduce for Izipho.



a) Induna



b) Ndonda



c) Izipho

d) Nyomfoza

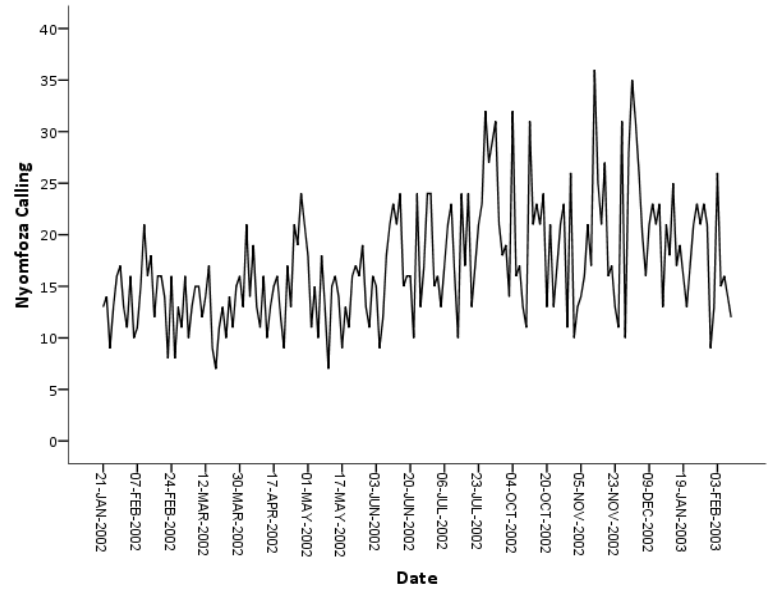
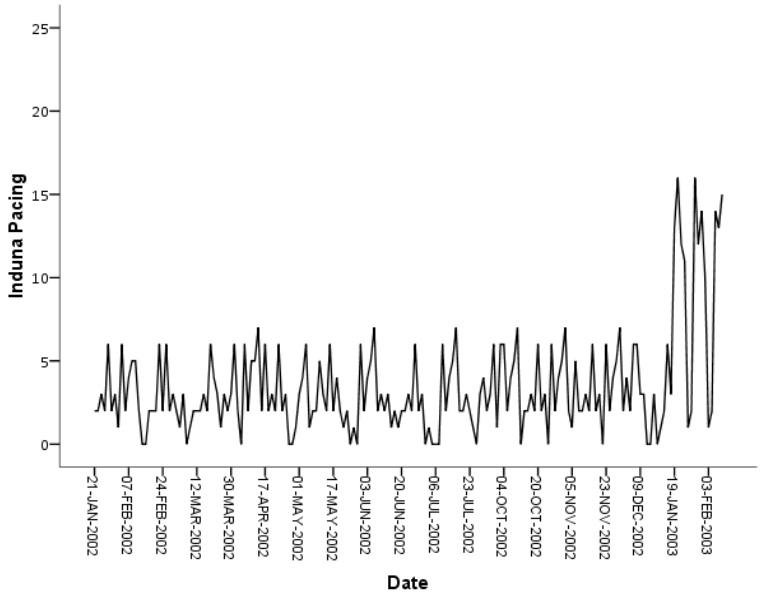


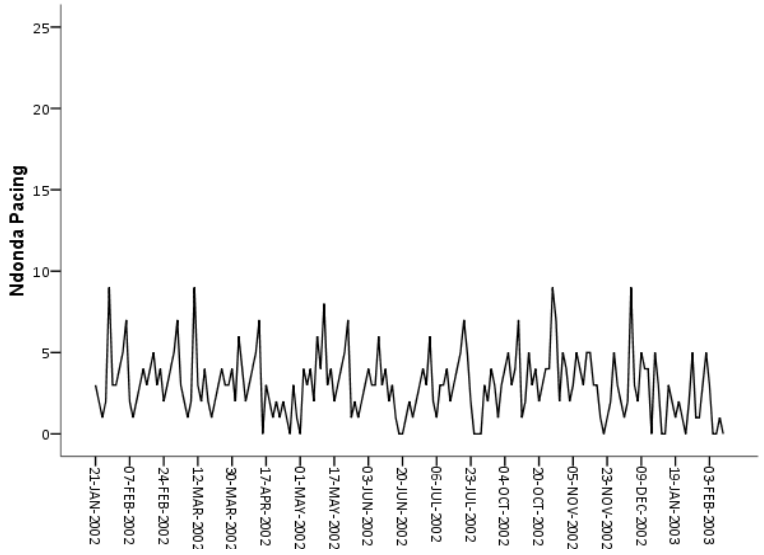
Figure 6. *Absolute counts for Calling observed for individual males over the study*.

Finally, Figure 7 depicts the behaviour of Pacing for all males over the study. This behaviour was observed frequently during the observation periods and expression rates varied between the males. Pacing was seen to fluctuate within individuals, but there was no apparent cyclicity. Results for Induna and Ndonda were lower than the other two males and remained constant over the majority of the study. However, increased Pacing was observed in Induna at the very end of the study. Again, it was evident that as the observations of Pacing increased for Nyomfoza, they reduced for Izipho.

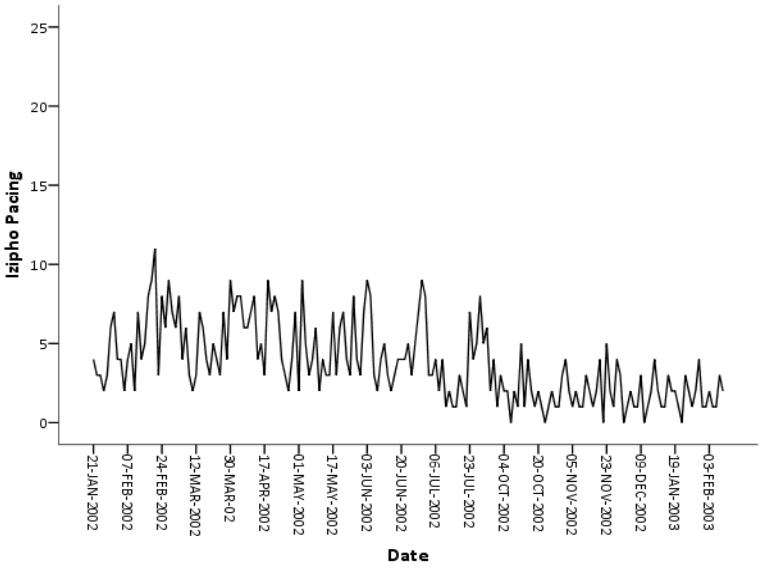
a) Induna



b) Ndonda



c) Izipho



d) Nyomfoza

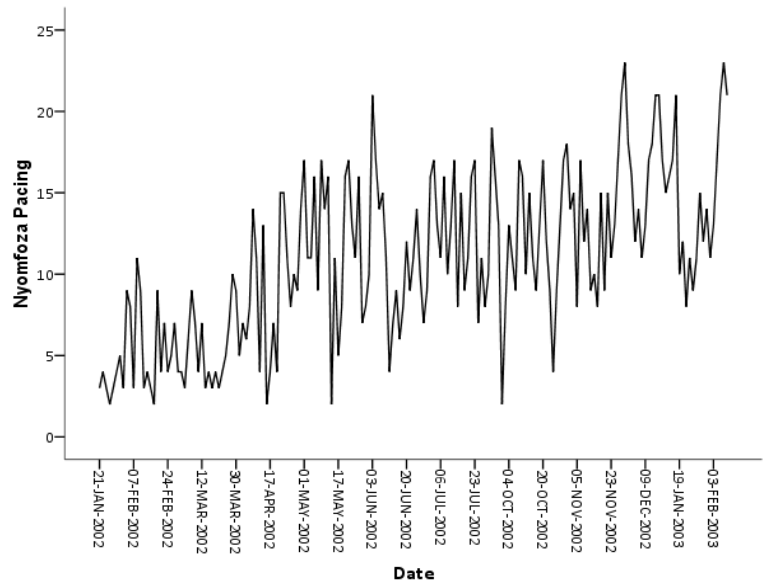


Figure 7. *Absolute counts for Pacing observed for individual males over the study.*

Finally, Table 3 examines the relationship between pairs of males for Calling and Pacing behaviour.

Table 3. *Correlation coefficients and associated statistical significances (in brackets) for Calling (values above the diagonal) and Pacing (values below the diagonal) for the male pairs in the study. Significant values are in bold type.*

	Induna	Ndonda	Izipho	Nyomfoza
Induna	--	0.093	-0.006	-0.100
		(0.208)	(0.935)	(0.176)
Ndonda	-0.076	--	**0.337**	-0.227
	(0.307)		**(< 0.001)**	(0.002)
Izipho	-0.192	-0.002	--	**-0.408**
	(0.009)	(0.981)		**(< 0.001)**
Nyomfoza	0.212	0.029	**-0.291**	--
	(0.004)	(0.694)	**(< 0.001)**	

Table 3 shows that there were fewer correlations between males for Calling and Pacing than for the previously analysed behaviours. There are strong positive correlations for both Calling and Pacing for the brothers Izipho and Nyomfoza and there is a positive correlation for Calling between Ndonda and Izipho. Ndonda and Nyomfoza showed a negative correlation on Calling and there Pacing was negatively correlated between Induna and Izipho.

Male Behaviours and Female Tail Rolling

Due to cyclicity in a number of the male behaviours above, it was important to compare the patterns of Tail Rolling expression observed in female cheetahs. As it was found that Tail Rolling was highly cyclic and likely to be a good indicator of oestrus in the female cheetah (Chapter 4), it was important to see if this potential indicator of oestrus was a driver of male behaviours such as Sniffing and Stutter Call. Male behaviours were examined to see if their expression were linked to female Tail Rolling. It was initially noted from scanning the data that female Tail Rolling patterns were observed 12 to 24 hours before males began to display interest in females. An accurate time frame was not established with certainty as there was only one male/female interaction period during the mornings. Males were not seen to show intense interest before this increase in Tail

Rolling began. Correlations were performed for male behaviours and female Tail Rolling.

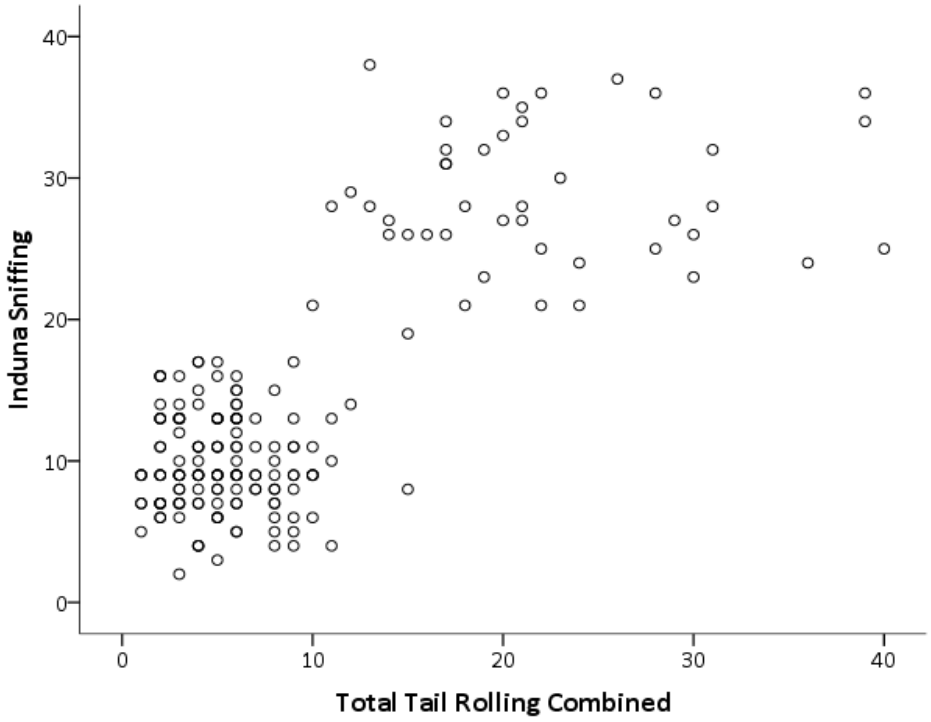


Figure 8. *Scattergram of absolute counts per observation period by Induna Sniffing versus combined (Pinda and Lula) Female Tail Rolling.*

Figure 8 shows the correlation of Induna's Sniffing events to female Tail Rolling, for Lula and Pinda combined. As Induna and Ndonda produced very similar results and patterns of Tail Rolling, Induna was used in the following analysis. It was evident that there was a positive relationship between these behaviours. These behaviours were explored further by examining Sniffing against Tail Rolling for each female separately.

Figure 9 illustrates the relationship between Induna Sniffing and Pinda Tail Rolling. The blue data points represent the Sniffing by Induna at times of Tail Rolling by Pinda. The pink data points indicate counts of Sniffing when Lula was not exhibiting Tail Rolling and may therefore be responses to Pinda in the absence of cues from Lula.

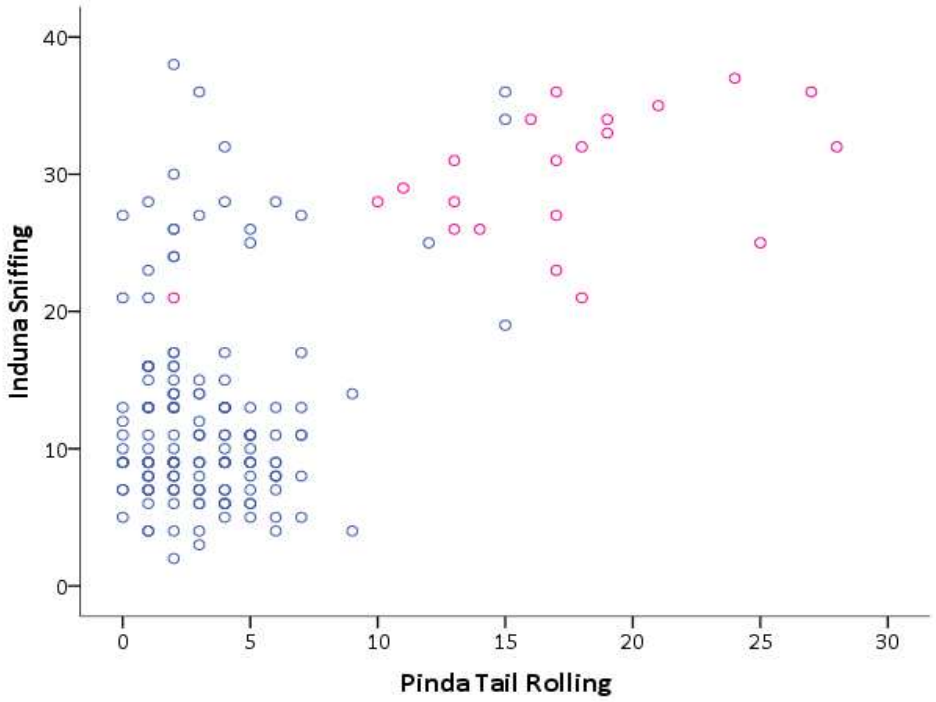


Figure 9. *Scattergram of Induna's Sniffing behaviour and Pinda's Tail Rolling. Points represent absolute counts per observation period, with blue data points representing responses to Pinda and pink data points representing responses to Pinda when Lula was not Tail Rolling.*

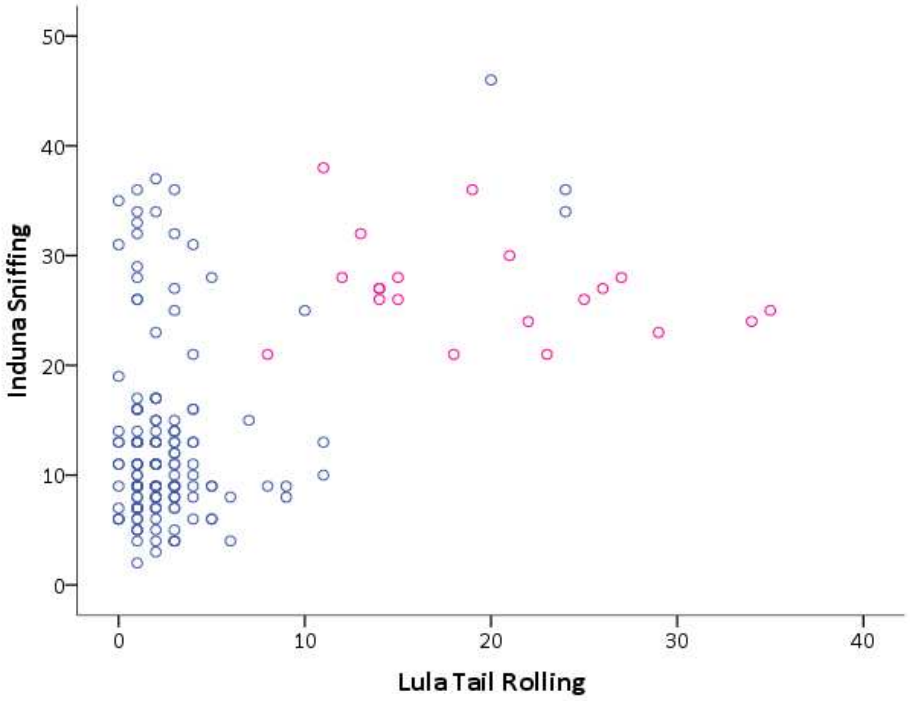


Figure 10. *Scattergram between Induna's Sniffing behaviour and Lula's Tail Rolling. Points represent absolute counts per observation period, with blue data points*

representing responses to Lula and pink data points representing responses to Lula when Pinda was not Tail Rolling.

.

Figure 10 illustrates the relationship between Induna Sniffing and Lula Tail Rolling. The blue data points represent the Sniffing by Induna at times of Tail Rolling by Lula. The pink data points represent elevated Sniffing when Pinda was not exhibiting Tail Rolling.

Izipho's behaviour was then compared to the females' Tail Rolling. It was evident that Izipho's behaviour changed dramatically over the study. At the beginning of the study Izipho showed low levels of Sniffing and Chassé, and high levels of Calling and Pacing (see Figures 2c, 3c, 6c, and 7c). However, towards the end of 2002this began to change and Izipho showed increased rates of Sniffing and Chassé, began to Stutter Call and reduced his rates of Lying and Calling (see Figures 4c and 5c).

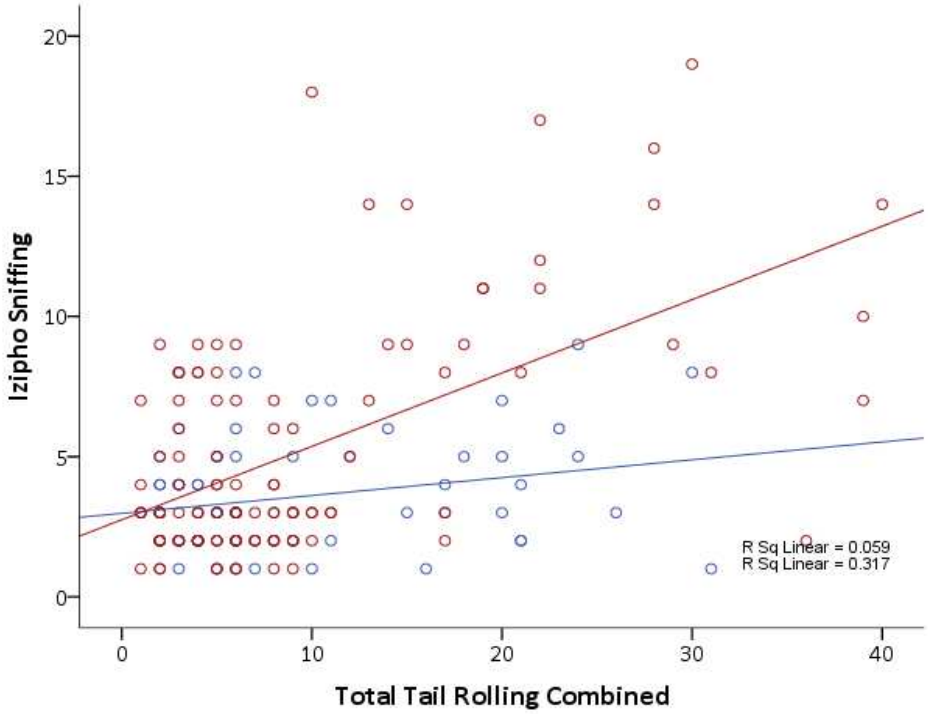


Figure 11. *Observations for Izipho Sniffing versus Tail Rolling for Pinda and Lula combined. Blue points represent the results from observation period January to May 2002 and red points represents the results from observation period June 2002 to February 2003. The* r^2 *values for the two periods are given in the lower right hand corner and the lines are best fit linear regressions fitted separately to the two time periods.*

Figure 11 shows the relationship of Izipho Sniffing to female Tail Rolling, along with r^2 values, which indicate the proportion of variation in behaviour attributable to correlation. It can be seen that there is a considerable change in his behaviour between the first and second halves of the study. Initially, Sniffing showed little correlation to female Tail Rolling behaviour ($r^2 = 0.059$), with results shown in blue remaining low. However, after June 2002 there is a strong correlation to female Tail Rolling ($r^2 = 0.317$), with results shown in red.

These results suggest that when Tail Rolling by Pinda is taken into account, the correlation between Lula's Tail Rolling and Induna and Izipho's Sniffing increases substantially. This was also the case with Stutter Call for Induna, but not for Izipho. This analysis helps to explain the results seen in the graphs above (see Figures 10 and 11) and strongly suggests that Induna and Izipho were responding separately to signals from both Lula and Pinda. It also strongly suggests that Tail Rolling behaviour, or associated signals, of both females was influencing the males' behaviours.

Table 4. *Bivariate and partial correlation coefficients between the behaviours Sniffing and Stutter Call by Induna, Izipho and Nyomfoza and Sniffing and Stutter Call by Tail Rolling for Lula. Bivariate correlation did not adjust for Pinda's Tail Rolling, whereas this was taken into account for the partial correlation. Significant values are in bold type.*

		Lula Tail Rolling (bivariate correlation)	Lula Tail Rolling Corrected for Pinda Tail Rolling (partial correlation)
Induna	Sniffing	**0.494 (< 0.001)**	**0.724 (< 0.001)**
	Stutter Call	**0.491 (< 0.001)**	**0.604 (< 0.001)**
Izipho	Sniffing	**0.249 (0.001)**	**0.421 (< 0.001)**
	Stutter Call	**0.277 (< 0.001)**	**0.250 (< 0.001)**
Nyomfoza	Sniffing	-0.077 (0.300)	-0.020 (0.788)

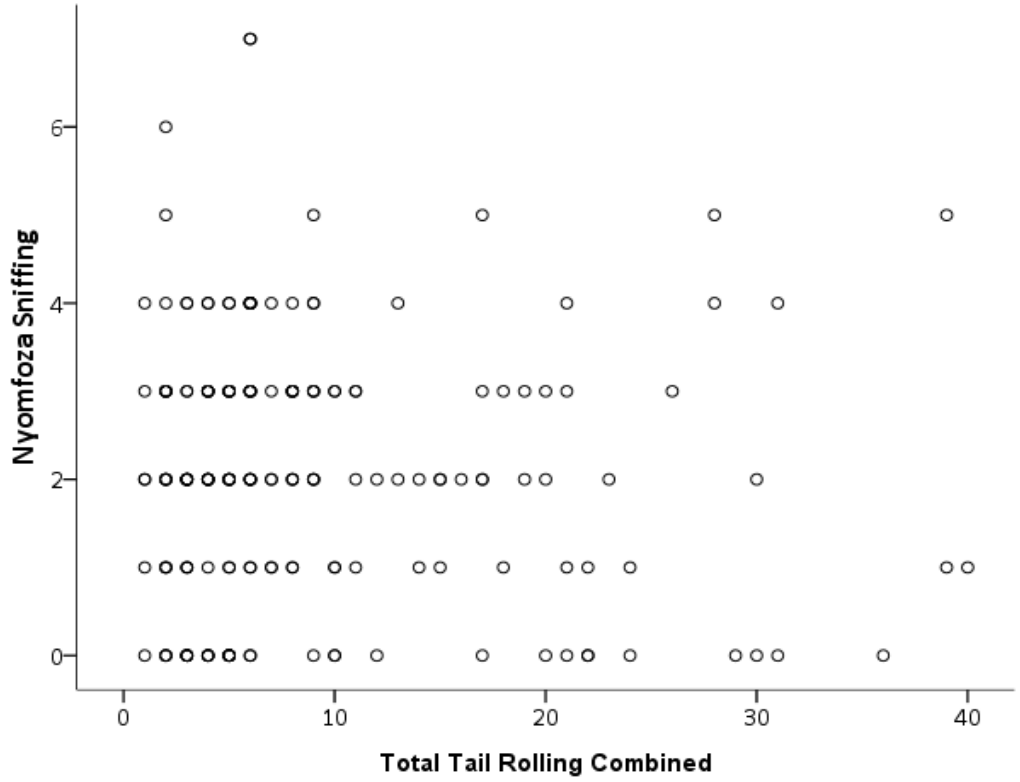


Figure 12. *Scattergram of Nyomfoza Sniffing and Female Tail Rolling (combined for Lula and Pinda).*

Figure 12 shows the relationship of Nyomfoza Sniffing to female Tail Rolling for Pinda and Lula combined. Nyomfoza displayed very different patterns of behaviour to the other males during the study. It can be seen that there is considerable variability in the data. It is evident from the graph that there is no relationship between Nyomfoza's behaviour to female Tail Rolling. This was explored further by carrying out a bivariate correlation between Nyomfoza's Sniffing and Lula's Tail rolling, as well as a partial correlation controlling for Pinda's Tail Rolling (see Table 4). It is evident that Nyomfoza's expression of Sniffing is unrelated to female Tail Rolling, contrasting strongly to the other males. The analysis of Stutter Call was not performed as Nyomfoza did not produce this call during the study.

Finally the relationship of male Pacing and Calling to female Tail Rolling (combined) was examined.

Table 5. *Correlation coefficients for males for the behaviours of Calling and Pacing and female Tail Rolling Combined, with significant correlations in bold type and exact significances indicated in brackets.*

Male	Behaviour	Correlation with Tail Rolling Combined
Induna	Calling	**-0.318 (< 0.001)**
	Pacing	0.025 (0.738)
Ndonda	Calling	**-0.281 (< 0.001)**
	Pacing	**-0.355 (< 0.001)**
Izipho	Calling	-0.137 (0.063)
	Pacing	-0.112 (0.131)
Nyomfoza	Calling	0.007 (0.920)
	Pacing	0.040 (0.587)

There are a number of strong negative relationships of male's behaviours to female Tail Rolling (Table 5). Significant correlations are highlighted in bold type, and the negative sign of these coefficients indicates that these behaviours decreased significantly when female Tail Rolling increased. It is noteworthy that significant correlations were not found for Izipho or Nyomfoza.

Female Tail Rolling and Male Introductions

As the male behaviours of Sniffing, Chassé and Stutter Call were strongly correlated with Tail Rolling behaviour observed in the females, increases in these behaviours were used as a guide to perform male/female introductions. Introductions were based on both increases in male behaviour and the absence of threat or fear responses from the female

being investigated. Introductions performed during the study period primarily involved the males Induna or Ndonda to the female Pinda.

The first instance of mating was observed on the 7th of February, 2003 between Induna and Lula. This mating occurred while both animals were displaying high levels of key behaviour components. Lula displayed 20 Tail Rolls in the hour preceding the male investigation period and Induna displayed scores of Sniffing = 46, Chassé = 25 and Stutter Call = 54. No instances of other key behaviours were recorded during the 30 minute investigation period that occurred immediately after observations on Lula. The data collection for the study ended after this mating.

Discussion

There has been much debate on the problems of cheetah breeding, with vastly different issues arising from the research on wild cheetahs (Laurenson *et al.* 1992 and Caro 1994) compared to research on captive cheetahs (Florio & Spinelli 1967, Benzon & Smith 1975 and Wielebnowski & Brown 1998). The captive environment is usually very unnatural and husbandry practices can mean that cheetahs are constrained from displaying a natural repertoire of behaviours, quite often as a result of being forced into unnatural social situations (McKeown 1991). These unnatural holding situations disrupt male and female social behaviour and may cause undue stress and impact on reproductive success (Caro 1993, 1994, Wildt *et al.* 1993, Brown & Wielebnowski 1998 and Wielebnowski & Brown 1998).

Little is known about the male cheetah in captivity, with information from wild animals being the primary source of information (Caro 1993 and 1994). Even then, reproductive behaviours of the male cheetah remain under studied, as courtship and mating is very difficult to observe in the wild cheetah (Caro 1994 and Gottelli *et al.* 2007). Aspects of male libido and mate choice need further study (Caro 1993 and Wildt *et al.* 1993). Previous reports from zoos have indicated the need for male aggression to stimulate a female's receptivity and allowing her mate choice (Florio & Spinelli 1967 and Benzon & Smith 1975). More recently, promiscuity and mate choice have been examined in populations of wild female cheetahs from the Serengeti (Gottelli *et al.* 2007). This study found that females would mate with multiple males, both within a coalition and from different coalitions, within one receptive cycle. Gottelli and colleagues proposed that this was due to multiple paternity improving the fitness of the

cubs and allowing them to 'hedge their bets' across the quality of the males. The current study aimed to explore the roles of males in mate choice by examining the behaviours that males displayed towards receptive and non-receptive females.

Key Male Behaviours

I observed the males to exhibit many behaviours during the study; six key behaviours were selected for analysis based on their frequency and also the patterns in which they occurred. Those key behaviours were Sniffing, Chassé, Stutter Call, Lying, Calling and Pacing. Behaviours such as Fighting and Spraying that had been observed in high frequencies from the male group (see Chapter 5) were observed rarely while males were investigating females. Due to the low and sporadic observations on these behaviours they were not included in the statistical analyses.

The behaviours of Sniffing, Chassé and Stutter Call were analysed for all males, and behavioural similarities between males were noted, particularly for Induna and Ndonda. Induna and Ndonda displayed the highest rates of all three behaviours, with fluctuations following very similar and cyclic patterns. Considerable increases in behaviour expression were observed for Izipho from mid-2002. Prior to this time Izipho had not displayed Stutter Call within his behavioural repertoire. Nyomfoza differed from all of the other males, showing low rates for all of these behaviours and failing to make a Stutter Call over the study.

The behaviours of Lying, Calling and Pacing exhibited very different trends. Observations of these behaviours remained low for the study for Induna and Ndonda, and were not seen when investigating female signals. Izipho showed a steady decrease in these behaviours from mid-2002. Nyomfoza displayed the opposite trend to his brother Izipho, where his expression of these behaviours increased from mid-2002 and peaked in 2003. These behaviours showed very few correlations among the pairs of males, but significant negative relationships were observed between Izipho and Nyomfoza on the behaviours of Calling and Pacing. It was evident that the behavioural patterns for these two males were moving in opposite directions.

Male Reactions to Female Tail Rolling

Due to the cyclicity in male behaviours, the behaviours of Sniffing, Chassé and Stutter Call were examined with respect to female Tail Rolling as this had been previously reported to show cyclicity and may be an indicator of oestrus (as described in Chapter 4). Increases in male Sniffing, Chassé and Stutter Call were highly correlated with elevated levels of female Tail Rolling. For the males Induna, Ndonda and Izipho, there were patterns cycling over the study that coincided with what was observed for the female Pinda. Pinda displayed a high level of cyclicity in Tail Rolling and Tail Swishing. Peaks in this behaviour were observed regularly and there was considerable evidence to suggest that this behaviour may be a cue to oestrus.

Male Sniffing/Stutter Call behaviours were analysed as they appeared to follow a similar trend to Tail Rolling behaviour observed in females. Strong correlations were found. Scores were then corrected for Tail Rolling in individual females and it was seen that the correlations to individual female Tail Rolling were strengthened when the other females' data was accounted for using partial correlation. These relationships indicate that male cheetahs are responding to the females' behaviour and males did not Stutter Call outside of the times when females were displaying elevated levels of Tail Rolling.

Nyomfoza was the only male which failed to display Stutter Call and he was also the only male which failed to show Sniffing in an observation period. This lack of Sniffing and general disinterest in investigating the female yards is very interesting. Multiple males would observe and investigate a particular females' yard without creating any increased levels of aggression. Therefore this lack of interest appears to reflect an issue particular to Nyomfoza rather than one imposed by hierarchical relationships, or threat from other males. This male did not appear to respond to female cues in any way.

Iziphos' behaviour paralleled Nyomfozas' behaviour, initially showing similar levels of disinterest at the beginning of 2002. His level of interest in investigating female olfactory signals changed considerably over the study, and by the end of 2002 Izipho was displaying high rates of behaviour similar to Induna and Ndonda.

The behaviours of Lying, Calling and Pacing did not appear to show any cyclicity during the study period. However, there were multiple patterns observed within the data. Initially, in response to Tail Rolling, it was observed that there were

strong negative correlations with Calling and Pacing for Induna and Ndonda. It was evident that when these males showed interest in investigating olfactory signals from the females, Calling and Pacing reduced significantly. This response was also suggested by the data for Izipho on Calling. The correlation was not statistically significant, but scores followed the same trend seen in the other males. Correlations were not seen for Nyomfoza, again displaying very different patterns of behaviour to the other males.

The males showed very different responses when investigating females. Induna and Ndonda showed strong similarities in their behaviours over the study. The behaviours of these males also remained very stable over the study, with trends changing little from early 2002 to 2003. As was seen in Chapter 5, Induna and Ndonda, while unrelated, have spent the longest time together. These males appear to have formed a coalition where Induna appears to be dominant and the relationship between these males on behavioural expression is relatively stable.

Izipho and Nyomfoza initially displayed very similar trends in behaviour. These trends were markedly different to those observed in Induna and Ndonda. High frequencies of consistent Lying, Calling and Pacing were observed and there was no evident cyclicity as had been seen with the other males. However, these trends diverge and Iziphos' behaviour became increasingly like the patterns observed in Induna and Ndonda. As Iziphos' behaviour began to compare to these two males, his interest in investigating the females increased. Increased Sniffing and Chassé were observed, and in December 2002 he was heard to Stutter Call for the first time. Concurrently, his Lying, Calling and Pacing behaviours were reduced.

Conversely, Nyomfozas' behaviour moved away from the trend displayed by the other males. He displayed a lack of interest in investigating the females. As the study progressed, this disinterest became more pronounced and Nyomfoza would often lie by himself while the other males would investigate the female lock-away yards. As was stated in Chapter 5, Nyomfoza experiences and number of health problems during the study period. These health problems may possibly have been a contributing factor to the distinct difference in his behaviour when compared to the other males.

Coalition Formation as a Driver of Male Behaviour Patterns

Throughout the study period it was observed that males formed coalitions and that these coalitions were affected by events occurring within the facility (as described in Chapter

5). A possible reason for the changes in Iziphos' behaviour during the trials was his acceptance into a coalition with Induna and Ndonda. As reported in Chapter 5, Izipho showed large changes in a number of behaviours to align with these males, including increased Fighting, Grooming and Lying. These changes in behaviour began during 2002. Again, there was a shift in his behaviour from mid-2002 to follow similar patterns to these males.

There is some indication that male responses to females are related to coalition membership, with the data suggesting that participation in a coalition makes males more likely to respond to female cues. The increased level of response to female olfactory signals from the males in a coalition may be directly related to their level of coalition membership. This membership may be either priming males to respond to female cues, or it may be indirectly related to other factors, such as a sick male or 'floater', displaying both lack of interest and a lack of participation in a coalition. This lack of participation was seen from Nyomfoza, being the only male in the current study that did not respond to female cues. It was noted in Chapter 5 that Nyomfoza had a number of health problems during in the study, and was excluded from the coalition. This exclusion may have contributed to his lack of interest in female cues. His status as a solitary male or 'floater' appeared to begin in mid-2002 and had been consolidated by 2003. Nyomfozas' complete lack of interest in the females is a comparison to the strong changes in the behaviour of the other males towards females. While it is not possible to determine the direct cause from the current data, it appears that being part of a coalition is important for generating interest in females.

Conclusions

Responses of male cheetah to female olfactory signals were seen to fluctuate considerably over the study. Males displayed varying responses to these cues, with differences noted between and within each male's behaviour. Key behaviours indicating male response were Sniffing, Chassé and Stutter Call. These behaviours were highly correlated to Tail Rolling in the females, suggesting that these behaviours indicate responses to the females state. The behaviours of Calling and Pacing occurred in the absence of these behaviours, suggesting they indicated a lack of interest in females.

Over the study, Induna and Ndonda responded consistently to female cues. Their behaviour was highly correlated, showing regular responses to changes in female cues.

The changes observed in Izipho's behaviour when investigating female cues appeared to be dependent on the relationship he had with other males. During the study it appeared that Izipho's behaviour, while initially similar to his brother Nyomfoza, became more like Induna and Ndonda. He initially showed low rates of Sniffing and Chassé and did not Stutter Call, while displaying high rates of Calling, Pacing and Lying. During the study these behaviours changed, with steady increases in Sniffing and Chassé, the introduction of Stutter Call and a steady decline in Calling and Pacing. These changes were noted to coincide with Izipho becoming a member of a coalition with these two males.

The behaviour of Izipho was a stark comparison to Nyomfoza, showing very different behavioural patterns over the study. While never appearing to show interest in investigating females, the increase in Calling and Pacing for Nyomfoza over the study was distinct. This increase in behaviour occured as he was slowly excluded from the coalition. The changes in Izipho's behaviour suggest that inclusion in a coalition is important for males for successful reproduction. It appears that membership of this coalition instigated his interest in investigating females

These findings are important for managing cheetah in captivity. Understanding the reasons for a coalition's response to females is important because if being part of a coalition is important for male cheetahs to respond to female olfactory signals, then holding males in groups becomes an important strategy for cheetah husbandry. It is also possible that males are primed for reacting to female cues by living in a coalition. As Izipho was gradually integrated in the coalition, we see an increase in his response to female cues. Therefore it is evident with the changes in his behaviour that his change in status is having some effect. It is also possible that females need to be able to actively choose between males and might therefore be more receptive if males occur in coalitions. Hence, while the exact driver(s) may not yet be known, keeping male cheetahs in coalitions appears to be a valuable tool for creating successful introductions for cheetahs in captivity.

References

Beekman, S.P.A., De Wit, M., Louwman, J. & Louwman, H. (1997) Breeding and Observations on the Behaviour of Cheetah (*Acinonyx jubatus*) at Wassenaar Wildlife Breeding Centre. International Zoo Yearbook, 35: 43-50.

Benzon, T.A. & Smith, R.F. (1974) Male Dominance Hierarchies and their Possible

Effects on Breeding Cheetahs. International Zoo Yearbook, 14: 147-149.

Benzon, T.A. & Smith, R.F. (1975) A Case of Programmed Cheetah (*Acinonyx jubatus*) Breeding. International Zoo Yearbook, 15: 154-157.

Bircher, J.S. & Noble, G.A. (1997) Management of Cheetah (*Acinonyx jubatus*) at Saint Louis Zoological Park. International Zoo Yearbook, 35: 51-58.

Brand, D.J. (1980) Captive Propagation at the National Zoological Gardens of South Africa, Pretoria. International Zoo Yearbook, 20: 107-112.

Bertschinger, H. J., Meltzer, D. G. A., van Dyk, A. & Strachan, A. (1998) "Breeding Of Female Cheetah in Captivity", in Proceedings of a Symposium on Cheetahs as Game Ranch Animals, Ed. Penzhorn, B. L. Wildlife Group of the South African Veterinary Association, Onderstepoort.

Bertschinger, H.J., Meltzer, D.G.A. & van Dyk, A. (2008) Captive Breeding of Cheetahs in South Africa – 30 Years of Data from the de Wildt Cheetah and Wildlife Centre. Reproduction in Domestic Animals, 43 (2): 66-73.

Brown, J.L., Wildt, D.E., Wielebnowski, N., Goodrowe, K.L., Graham, L.H., Wells, S. & Howard, J.G. (1996) Reproductive Activity in Captive Female Cheetahs (*Acinonyx jubatus*) Assessed by Faecal Steroids. Journal of Reproduction and Fertility, 106: 337-346.

Brown, J.L. & Wielebnowski, N. (1998) Influence of Social Environment on Ovarian Activity and Behavior in Captive Cheetahs. Advances in Ethology, 33: 15.

Caro, T.M. (1993) Behavioral Solutions to Breeding Cheetahs in Captivity: Insights from the Wild. Zoo Biology, 12: 19-30.

Caro, T.M. (1994) Cheetahs of the Serengeti Plains: Group Living in an Asocial Species. Chicago, University of Chicago Press.

Caro, T.M. & Collins, D.A. (1986) Male Cheetahs of the Serengeti. National Geographic Research, 2: 75-86.

Caro, T.M. & Collins, D.A. (1987a) Male Cheetah Social Organization and Territoriality. Ethology, 74: 52-64.

Caro, T.M. & Collins, D.A. (1987b) Ecological Characteristics of Territories of Male Cheetahs (*Acinonyx jubatus*). Journal of Zoology, London, 211: 89-105.

Clutton-Brock, T.H. (1989) Review Lecture: Mammalian Mating Systems. Proceedings of the Royal Society of London. Series B, Biological Sciences, 236 (1285): 339-372.

Durant, S.M., Bashir, S., Maddox, T. & Laurenson, M.K. (2007) Relating Long-Term Studies to Conservation Practice: The Case of the Serengeti Cheetah Project. Conservation Biology, 21 (3): 602-611.

Florio, P.L. & Spinelli, L. (1967) Successful Breeding of a Cheetah in a Private Zoo. International Zoo Yearbook. 7:150-152.

Gottelli, D., Wang, J., Bashir, S. & Durant, S.M. (2007) Genetic Analysis Reveals Promiscuity Among Female Cheetahs. Proceedings of the Royal Society, Biological Sciences, 274: 1993-2001.

Hoefler, C.D. (2007) Male Mate Choice and Size-assortative Pairing in a Jumping Spider, *Phidippus clarus.* Animal Behaviour, 73: 943-954.

Hunter, L. (2000) Cheetahs. Colin Baxter Photography, Grantown-on-Spey, Scotland.

Hunter , L. & Hamman, D. (2003) Cheetah, Struik Publishers, Cape Town.

Kelly, M.J. & Durant, S.M. (2000) Viability of the Serengeti Cheetah Population. Conservation Biology, 14(3): 786-797.

Laurenson, M.K., Caro, T. & Borner, M. (1992) Female Cheetah Reproduction. National Geographic Research and Exploration, 8: 64-75.

Laurenson, M K. (1993) Early Maternal Behavior of Wild Cheetahs: Implications for Captive Husbandry. Zoo Biology, 12: 31-43.

Manton, V.J.A. (1970) Breeding Cheetahs *Acinonyx jubatus* at Whipsnade Park. International Zoo Yearbook, 10: 85-86

Marker, L. (2000) 1999 International Studbook Cheetah (*Acinonyx jubatus*). Cheetah Conservation Fund, Otjiwarongo.

Marker, L. (2002) 2000/2001 International Studbook Cheetah (*Acinonyx jubatus*). Cheetah Conservation Fund, Otjiwarongo.

Marker, L. (2004) 2002 International Studbook Cheetah (*Acinonyx jubatus*). Cheetah Conservation Fund, Otjiwarongo.

Marker, L. & Echement, K. (2010) 2008 International Studbook Cheetah (*Acinonyx jubatus*).Cheetah Conservation Fund, Otjiwarongo.

Marker, L., Linn, L. & Le Quesne, S. (2008) 2006 International Studbook Cheetah (*Acinonyx jubatus*). Cheetah Conservation Fund, Otjiwarongo.

Marker, L., Schumann, B. & Wilkinson, C. (2007) 2005 International Studbook Cheetah (*Acinonyx jubatus*). Cheetah Conservation Fund, Otjiwarongo.

Marker-Kraus, L. & Grisham, J. (1993) Captive Breeding of Cheetahs in North American Zoos: 1987-1991. Zoo Biology, 12 (1): 5-18.

Marker-Kraus, L. (1997) History of the Cheetah *Acinonyx jubatus* in Zoos 1829-1994. International Zoo Yearbook, 35: 27-43.

Martin, P & Bateson, P. (2000) Measuring Behaviour: An Introductory Guide. 2nd Ed.

Cambridge University Press. Cambridge.

McKeown, S. (1991) 'The Cheetah', in Management Guidelines for Exotic Cats, Ed. Partridge, J. Association of British Wild Animal Keepers, Bristol.

Mellen, J.D. (1991) Factors Influencing Reproductive Success in Small Captive Exotic Felids (*Felis spp*): A Multiple Regression Analysis. Zoo Biology. 10: 95-110.

O'Donovan, D., Hindle, J.E., McKeown, S & O'Donovan, S. (1993) Effect of Visitors on the Behaviour of Female Cheetahs *Acinonyx jubatus* and Cubs. International Zoo Yearbook, 32: 238-244.

Rawlins, C.G.C. (1972) Cheetahs (*Acinonyx jubatus*) in Captivity. International Zoo Yearbook, 12: 119-120.

Ruiz-Miranda, C.R., Wells, S.A., Golden, R. & Seidensticker, J. (1998) Vocalizations and Other Behavioral Responses of Male Cheetahs (*Acinonyx jubatus*) During Experimental Separation and Reunion Trials. Zoo Biology, 17:1-16.

Say, L., Pontier, D & Natoli, E. (2000) Influence of Oestrus Synchronisation on Male Reproductive Success in the Domestic Cat (*Felis catus L.*). Proceedings of the Royal Society, London, 268:1049-1053.

Schwammer, H.M. (2000) "Breeding Cheetahs (*Acinonyx jubatus*) at the Vienna Zoo", In 1999 International Studbook Cheetah (*Acinonyx jubatus*). Ed. Marker, L. Cheetah Conservation Fund, Otjiwarongo.

Vallat, C. (1971) Birth of Three Cheetahs *Acinonyx jubatus* at Montpellier Zoo. International Zoo Yearbook, 11: 124-125.

Wielebnowski, N.C. (1998) "Contributions of Behavioral Studies to Captive Management and Breeding of Rare and Endangered Mammals", in Behavioral Ecology and Conservation Biology. Ed Caro, T. Oxford Uni. Press, London.

Wielebnowski, N.C. & Brown, J.L. (1998) Behavioral Correlates of Physiological Estrus in Cheetahs. Zoo Biology, 17: 193-209.

Wielebnowski, N.C. (1999) Behavioral Differences as Predictors of Breeding Status in Captive Cheetahs. Zoo Biology, 18: 335-349.

Wildt, D.E., Brown, J.L., Bush, M., Barone, M.A., Cooper, K.A., Grisham, J. & Howard, J.G. (1993) Reproductive Status of Cheetahs (*Acinonyx jubatus*) in North American Zoos: The Benefits of Physiological Surveys for Strategic Planning. Zoo Biology, 12: 45-80.

Wildt, D.E. & Grisham, J. (1993) Basic Research and the Cheetah SSP Program. Zoo Biology, 12:3-4.