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

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Chapter V

Male Cheetah Behaviour and the Impact of Captive Husbandry

Introduction

The social organisation of felids has received a vast amount of attention in the literature (Frame & Frame 1980, Caro & Collins 1986, 1987a&b, Laurenson 1993 and Durant 2000) and is regarded as a key element when considering their conservation. With the exception of the lion, *Panthera leo,* where females form family groups to assist in hunting and the rearing of young (Packer & Pusey 1982), the majority of cat species are solitary, with sociality being typically restricted to consorting pairs and mothers with young (Seal *et al.* 1985, Caro 1993, Laurenson *et al.*1992 and Laurenson 1993). However, for the cheetah (*Acinonyx jubatus*), sociality is seen in various forms (Caro 1994). Observations from the wild have noted consorting pairs or groups of cheetahs (Kelly *et al.* 1998 and Kelly & Durant 2000), mothers with young (Laurenson *et al.*1992), cub groups recently separated from their mothers but continuing to remain together, and groups of adult males (Caro & Collins 1987a, b and Caro 1994).

The cheetah, is unusual amongst the cat species as it shows varying levels of sociality between the sexes (Caro 1994). Extensive research has been performed *in-situ,* with studies on the cheetah performed in the Serengeti for over 30 years (Kelly *et al.* 1998). Male cheetahs in particular have been studied considerably, and are reported to live in social groups called 'coalitions'. However, unlike lions where the reasons for sociality are clear, sociality in other cat species is ambiguous, and has encouraged numerous researchers to examine the behaviour of cheetahs, with a focus on group living and the benefits of sociality (Frame & Frame 1980, Caro & Collins 1986, 1987a, b and Caro 1994).

Research on wild cheetahs has shown that male cheetahs can have complex social arrangements (Caro & Collins 1986, 1987a and Caro 1989, 1994). Many early studies looked at male behaviour in the wild, noting the various social combinations but revealing little of the structure within these male cheetah societies (Eaton 1974, Bertram 1978 and Frame & Frame 1980). Caro (1994) reported a detailed analysis of the formation of, and variation in, these groups. It had been noted previously that the males' social habit appeared reasonably common (Eaton 1974). Yet it was the research of Caro and Collins (1986, 1987a, b) that provided a good understanding of how sociality was achieved. They reported that 41% of male cheetahs lived alone, 40% lived in pairs, while the other 19% lived in trios or occasionally larger numbers. Caro (1994) referred to the solitary animals as 'floaters' and reported that they generally appeared to be in worse physical and psychological condition than group-living males.

Caro (1994) initially examined 110 animals within an extensive study of cheetahs of the Serengeti. Solitary cheetahs were usually infested with parasites and showed signs of restlessness. However, it is not known if these cheetahs were 'floaters' due to their poor physical condition, or if their condition was caused by the stress of solitary living (Caro & Collins 1987a). In contrast, coalition members were observed to be considerably healthier (Caro *et al.* 1987, 1989), with less mange, fewer ticks and softer fur. Caro and Collins (1987a) looked at the physical condition of many different individuals and the implications for behaviour. During their study on social organisation and territoriality they found that territorial males were considerably heavier (weights ranged from 40.5 kg to 48 kg), compared to non-territorial males (weights ranged from 28.5 kg to 42 kg). Caro and Collins (1987a) also found that territorial males were almost always found in coalitions, with only 4% of single males being able to secure a territory. Hence male cheetahs appear to gain considerable benefits from group living.

Hypotheses for Coalition Formation

The formation of coalitions in wild cheetah populations has received a considerable level of enquiry (Caro 1989, 1993, 1994 and Caro & Collins 1987a&b). Many different and competing hypotheses have been developed to explain why male cheetahs form coalitions, with the majority based on the role coalitions play in the ability of males to gain access to females. One major hypothesis is that brothers form co-operative groups in order to hold territories that overlap with female home ranges (Caro 1993 and 1994). This overlap provides the group with a better chance of encountering a female and mating. While the individual chance of each cheetah mating is reduced, as a group, their chances are increased. Through this co-operation, brothers still have some chance of passing on their genetic information via inclusive fitness. Caro and Collins (1986 and 1987a) and Caro (1994) concluded that coalitions could be formed from sibling groups as well as unrelated animals. Their results found that approximately 17% of the coalitions studied included at least one non-relative. These results challenge the idea that co-operative behaviour is maintained purely by kin selection acting on related animals with consequent effects on inclusive fitness, though of course a role for kin selection involving relatives is by no means excluded.

Some hypotheses to explain coalition formation in male cheetahs are based on need for space and territory acquisition (Caro & Collins 1987a&b). These hypotheses centre around the idea that the larger the territory held by a cheetah or coalition, the more access they have to resources and therefore the greater their chance of survival

(Caro 1994). Hence cheetahs might form coalitions to have a better chance of gaining and holding territories. The territories would be larger than could be held by solitary males, increasing hunting success by increasing both the number and size of kills (Caro 1994 and Durant 2000). In lion populations, the reasons behind sociality are well understood (Bertram 1978 and Packer & Pusey 1982). However, for cheetahs there does not appear to be a singular defining reason for their unusual social arrangement. It is more probable that a number of factors combine to advantage group-living males.

A further hypothesis, put forward by Benzon and Smith (1974 and 1975), is that females are stimulated by male aggression. This aggression may be found between males in a dominance hierarchy, with the female preferring to mate with the dominant male (Lorenz 1963). While little is known about the social structures within the coalitions of male cheetahs (Caro 1993), the formation of hierarchies is possible. Hence, Benzon and Smith (1974) suggested that if there is a group of males with a dominance hierarchy in place, females may be more likely to mate within this group. Presumably mating will occur with the dominant member, rather than with a subordinate or single male.

Relatedness of Cheetahs in Coalitions

Caro (1989, 1993, 1994), Caro and Collins (1986, 1987a&b) and Kelly *et al*. (1998) carried out substantial studies on the social behaviour of male cheetahs. One of the chief aims of this research was to study behavioural differences between littermates and non-littermates. Caro (1994) found that while coalitions may consist of two, three or even four cheetahs, they could also include both relatives and non-relatives. Caro (1994) compared the behaviours of three coalitions, each consisting of two related and one unrelated animal. These three trios were at different stages of formation at the commencement of study. One was in the initial stages of formation (less than 55 days old), one was reasonably well established (a minimum of 12½ months, but no more than 20 months old) and one was well established (greater than 4 years old). Caro found that in the first years of formation there were significant differences in the behaviours of different group members compared to the behaviours displayed by members of more established trios. However, these behavioural differences changed over time, with each individual's behaviour becoming more similar to that of his coalition 'brothers', usually to the point where there was no marked behavioural difference between coalition members. Caro also noted that these behavioural differences changed at varying rates.

Relatives would accept the non-relative, allowing him to lay with them much sooner than they would involve him in grooming activities.

Caro (1994) also found that in the coalitions observed, there appeared to be age constraints for the formation of a coalition involving unrelated individuals. Coalitions of unrelated males were developed between combinations of cubs and adolescents, but usually before the cubs reached 20 months of age (Caro 1994). It was suggested that cheetahs older than this would have difficulty accepting new members or banding together and hence they would remain 'floaters'. Caro (1993) argues that this age restriction may have important implications for keeping male cheetahs together in captivity.

Research on Captive Cheetahs

Research on captive cheetahs has increased over the past 20 years (Wildt *et al.* 1993, Wildt & Grisham 1993, Wielebnowski 1998, Wielebnowski & Brown 1998, Ruiz-Miranda *et al* .1998, Wielebnowski 1999, Wielebnowski *et al.* 2002 and Augustus *et al.* 2006) and has predominantly focussed on reproductive biology (Asa *et al.* 1992, Howard *et al.* 1993 and Wildt *et al.* 1993). Behavioural work has primarily focussed on female reproductive behaviour and mother-cub interactions (Laurenson 1992, Wielebnowski 1996, Wielebnowski & Brown 1998). While studies have been performed on wild male cheetahs, there is still very little known about their behaviour in captivity (Caro 1993, Wildt *et al.* 1993 and Ruiz-Miranda *et al* .1998).

In 1988, the Propagation Committee of the Cheetah Species Survival Plan (SSP) deemed that all North American cheetahs were to be considered part of a research population (Wildt & Grisham 1993). This led to the study of 128 (60 male and 68 female) cheetahs and included reproductive health, physiology and general well-being (Caro 1993, Laurenson 1993, Howard *et al.* 1993 and Wildt *et al.* 1993. While this research provided many valuable insights into the physiology of cheetahs, it did not comprehensively examine behavioural factors and needs of cheetahs in captivity.

In the limited research performed on captive cheetahs in recent times, studies have focussed on female faecal steroids and changes to behaviour (Brown & Wielebnowski 1998). Past studies of captive behaviour of cheetahs have primarily focussed on housing. Florio and Spinelli (1967, 1968) and Benzon and Smith (1974) worked with the problems that arise when housing captive cheetahs. These problems generally included issues with stereotyped behaviours, finding novel ways to introduce food and making changes to enclosures to produce more visible behaviour to the general

public/zoo patrons (McKeown 1991). The studies also included some work on the manipulation of animals, and they had some success in keeping males, both related and unrelated, together. However, facilities continue to insist on keeping male cheetahs separated or even removed from view of one another because of concerns with aggression and for the ease of management. Caro (1993) argued that there had not been enough study on captive male cheetahs, their coalition formation or their social structures. He stated that while some information gained from wild populations would be useful in husbandry practices, a complete analysis of captive populations and captive breeding programs is required. Only after a comprehensive study of captive populations will facilities such as zoos and wildlife parks be able to successfully manage and reliably breed cheetahs in the captivity.

Aims

The aim of the current study is to examine the behaviour and social interactions of a group of male cheetahs in captivity. In particular, the study will centre on behaviour when males are held together, with a focus on basic levels of acceptance of related and unrelated males and how housing impacts on sociality. These factors all have important implications for breeding programs. An additional objective of the study is to determine if males past the age of 20 months can be united into coalitions, and if so, whether they all become equal members of the group with similar social standing, or if a hierarchy develops. If a hierarchy develops then the factors on which it is based will be examined. The study will also examine whether particular males are rejected from coalitions and on what grounds.

Further, the study will investigate specific relationships amongst males, using both related and unrelated individuals, in order to identify any differences in behaviour towards one another and how these may change over time. Many factors, such as grooming, fighting and territory marking, as well as the time spent generally socialising and lying together, will be examined. As there are individuals within the study group that will be introduced to each other at ages that Caro (1993) believes to be past the age of acceptance, the relationships of pairs and trios will also be analysed to determine any obvious disparity between different groups of cheetahs.

Methods

Animals and Facility

The study group was housed at Monarto Zoological Park (MZP), South Australia and all members of the group were parent-reared at Hoedspruit Endangered Species Centre (South Africa). The study group consisted of five male cheetahs; three brothers (Umballa, Izipho and Nyomfoza), aged approximately 4 years 5 months old and two unrelated males, aged approximately 4 years 5 months (Ndonda) and 5 years 2 months old (Induna) at the start of the study 3rd of February 2001. Prior to data recording, two pairs of cheetahs were held separately; a pair of related males (Umballa and Izipho) from the existing trio of brothers (the third male, Nyomfoza was isolated due to illness but had been housed previously with his brothers) and two unrelated males (Ndonda and Induna). The unrelated males provided a valuable comparison to the related pair. The unrelated males were introduced to each other on the 13th of August 1999 with no apparent problems (Austin, T. pers. comm. 2000). The two pairs were housed in adjoining enclosures, separated by chain link fence, permitting some contact between the pairs. At the time these pairs were formed their ages ranged from 36 to 44 months old. The single male was also housed in an adjoining yard, but kept separate to avoid major interactions with the other males until he recovered.

During the study, the housing of male groups was manipulated, providing opportunities for males to be observed in pairs, trios and as a whole group. Interactions during all of these social situations were recorded to determine the levels of acceptance that males had for other males and also to allow males to pair up or avoid other males. The study group was also changed during the course of the study period due to transfers and breeding programs. Umballa was transferred out of the facility at the end of 2001 on breeding loan and was not returned to the study group during the duration of my study. Monarto Zoological Park also held five female cheetahs at various times during the study period which were housed within auditory and olfactory range of the males. However, for the majority of the study females only had limited visual contact while males moved to and from their exhibit (less than two minutes at 10:30 h and 16:30 h each day). After the first six months of the study, males and females were occasionally housed together for short periods of time for breeding purposes.

Behavioural observations, manipulations and data collection were performed periodically over a period of four years between January 2001 and November 2004.

Apparatus/Materials

Equipment used for the observation of cheetahs included, binoculars (*Bushmaster*® 8-20 × 40 mm) and in the initial stages, a *Ricoh*® camera with 35-70 mm lens for photographing of behaviour. However, for the majority of the study an *Olympus*® C-740 digital camera, 3 megapixel, 10 x optical zoom was used. A *Realistic*® Minisette-20 tape recorder was used for recording continuous behaviour.

A series of data collection tables were also used for recording the male cheetah behaviour (further details are given in Chapter 2 and see Martin & Bateson 2000). Each table was set out in two minute intervals for each hour of recording, with a key for behaviours and social interactions used to aid in recording specific behaviours (see Chapter 3). Interactions between animals from the main exhibit to the night-yards were also recorded (such as calling from the main enclosure or interactions through the wire in the back night-yards). Additional sheets for descriptions of unusual isolated events were also used to record any unique behaviour that could not be included on the data sheets.

Maps, with grid references for both the main and lock-away enclosures, were also developed. These guides made the recording of each cheetah's location easier and provided a quick reference for both areas (see Chapter 2 for illustrations of the enclosure and night-yard facilities).

Procedure

Collection of Behavioural Data

I observed the five male cheetahs for a total of 1794 hours between 2001 and 2004. Four of the five males were observed for the entire study period, with Umballa being sent to New Zealand on breeding loan at the end of 2001.

Solitary Behaviours

Initially I performed a study of solitary behaviours with seven hours of data collected for each individual male (not included in the statistical analysis here, See Chapter 3). I then collected similar data throughout the study as a parallel to the female data. Single males were observed for an hour at a time throughout the day. Recording was continuous, with all behaviours 'called' into a tape recorder (Martin & Bateson

2000). These data were then later transcribed. Frequency of behaviours, not percentage of time, was recorded. Continuous observations were carried out over 2-3 month periods (where each male was observed for a minimum of three 1-hour periods per week) rather than constantly over years as was done for the females. This data was then analysed using principal components analysis. As the focus for the males was to determine hierarchy formation and the strength of bonds over time, the collection of continuous data for the males at all times was deemed unnecessary.

Social and General Behaviours

I recorded data on social and general behaviours for each animal in both the main exhibit area and the night-yard/lock-away areas. Recording of information was in interval format (Martin & Bateson 2000) with data taken as instantaneous sampling at each two minute interval (on the minute), for one hour, beginning on the hour. Data recording began at release time each morning (approximately 9:30-10:00 h) and concluded when cheetahs were locked away at night (approximately 16:30 h). Data were collected at regular times, sampling data 3-4 days per week for all males to determine if there were any changes in the groups' social structure over time. Data were primarily collected in periods of 2-3 months, but additional periodic observations of 2-4 hours per week were also performed in between intensive data collection periods.

At each two-minute interval, the location (by grid reference) and behaviour of each individual cheetah in the enclosure was recorded. This data also included any social interactions between cheetahs that occurred, which individuals were involved and the behaviours/responses exhibited. Cheetahs were considered 'social' if they were either lying within approximately one metre of each other, or were responding to the actions of another cheetah (i.e. calling to each other). Due to time constraints, males were only observed for short times when females were pregnant or with cubs, otherwise they were observed over half days, 3-4 times per week, for two or more months at a time. Four social observation conditions were maintained during the study. These were social with males, social with females, social with minimal contact with females and social with a 30-minute observation time/introduction to females. A one-week period of isolation for each individual was also recorded.

Major contact with females consisted of a parading period during parts of the study where the males had visual access to the females for approximately 30 minutes each morning (between 7:30 h and 10:00 h) through a chain link fence. On these days, the males had their usual short period in the afternoon for visual contact (less than 2

minutes at 16:30 h) when they were brought off exhibit. At this time males were not paraded past the females, but momentary visual contact was possible as at other times. Occasionally during these periods of the study, males were introduced to females. Data on interactions between the sexes were not included in the current study (see Chapter 6).

Feeding of the cheetahs was performed primarily off-display in their night-yards, with carcass feeds occurring in the exhibit yard approximately once per month. Feeding was at approximately 16:30 h and all animals were given one fast day per week. The diet consisted of fresh carcass meat (cow, sheep, horse, chicken, rabbit, kangaroo and emu) supplemented 2-3 days per week with thiamine. On days when cheetahs were given carcass with soft fur (rabbit/kangaroo), cheetahs were given an additional supplement of Catlax® due to occasional fur blockage problems. Feeding times provided additional information on the social structure of the group and any changes that were occurring.

Generally, the cheetahs were kept off exhibit in their night-yards overnight. In order to get to the exhibit and back they had to travel through a narrow raceway that connected the two areas. As only single file movement was possible through this narrow race-way, it was used as another check for possible hierarchy order and for signs of dominance. Data were recorded while cheetahs were entering and exiting the exhibit and night-yards through the connecting race-way. Information noted included; which approached the race-way first, which entered first/last and which exited first/last, for each of these study periods as well as during additional times of observation.

Statistical Analysis

Data were explored using a series of parametric and non-parametric statistics. These statistics were performed using SPSS (Statistical Package for the Social Sciences) Version 16. Using this statistical package, tables and graphs were developed to explore trends in the behaviour of male cheetahs. For a number of the analyses, data had to be converted to scores based on a percentage of the time animals were observed. This was done to allow for the comparison between intensive observation times and times when males were sampled two to three times per week. Conversions are indicated in the relevant analyses.

Results

Primary Analysis

Multivariate behavioural analyses

Induna

The data set for each male comprised a large number of behavioural variables and an extremely large number of observational periods. Initially analyses were done using Principal Components Analysis (PCA). The entire data set (from the 3rd of February 2001 to the 29th of November 2004) was used, comprising 326 separate 1-hour observational periods. Unlike the females, this data occurred in blocks of 2-3 months and was not collected in this format during 2003. The PCA was used to extract factors with eigenvalues >1 and the initial solution was subject to Varimax rotation. The resulting four principal components are listed in Table 1 along with their eigenvalues, proportion of variation explained and cumulative variation explained.

Table 1. *Principal components extracted with eigenvalues and per cent variation explained and cumulative variation explained for Induna.*

Principal Component	Eigenvalue	Variation Explained	Cumulative Variation Explained
1	1.612	10.077	10.077
2	1.381	8.629	18.706
3	1.292	8.076	26.782
4	1.186	7.412	34.194

Behavioural variable loadings for the rotated solution are given in Table 2 where positive and negative loadings are given for each variable with the four principal components for Induna's behaviour.

Table 2. *Rotated Component Matrix for Induna. The key variables loading onto each component are shown in bold.*

Behaviours	Components			
	1	2	3	4
Fighting	**0.664**	0.019	0.224	0.105
Tail Twitches	**0.514**	-0.078	-0.138	-0.055
Rubbing Face	**0.509**	-0.049	0.226	-0.127
Activity Level	0.115	**0.584**	-0.059	0.119
Scratching	-0.267	**0.561**	0.077	0.006
Tail Swishes	0.167	0.487	-0.082	0.062
Grooming	-0.184	0.454	-0.035	-0.364
Playing	-0.120	0.236	0.082	-0.033
Lip Licking	0.262	0.087	**0.623**	-0.058
Spraying	-0.022	0.130	**0.581**	-0.333
Pacing	0.032	-0.149	0.402	0.079
Calling	0.017	-0.046	-0.378	-0.127
Defecating	-0.311	-0.229	0.359	0.102
Rubbing Body	-0.094	-0.053	0.031	**0.701**
Tail Rolling	-0.175	0.283	0.109	**0.545**
Rolling	0.368	-0.016	-0.031	0.431

The first component in Table 2 indicates high loadings from Fighting, Tail Twitches and Rubbing Face. Table 2 also shows that the two behaviours that loaded most heavily onto the second principal component were Activity Level and Scratching. The third component indicates that the behaviours of Lip Licking and Spraying are loaded most heavily. Finally, the fourth component shows Body Rubbing and Tail Rolling behaviour with a high loading, but with low loadings from all other behaviours other than spraying, which had also loaded strongly onto PC 3.

Data were not recorded as regularly for 2003 as other analysis were being performed and therefore this year has been omitted from the current analysis. Due to the periodic nature of data recording for the males, the results have been represented using scattergrams (rather than line graphs as were used for the female data) in order to make the sampling periods obvious.

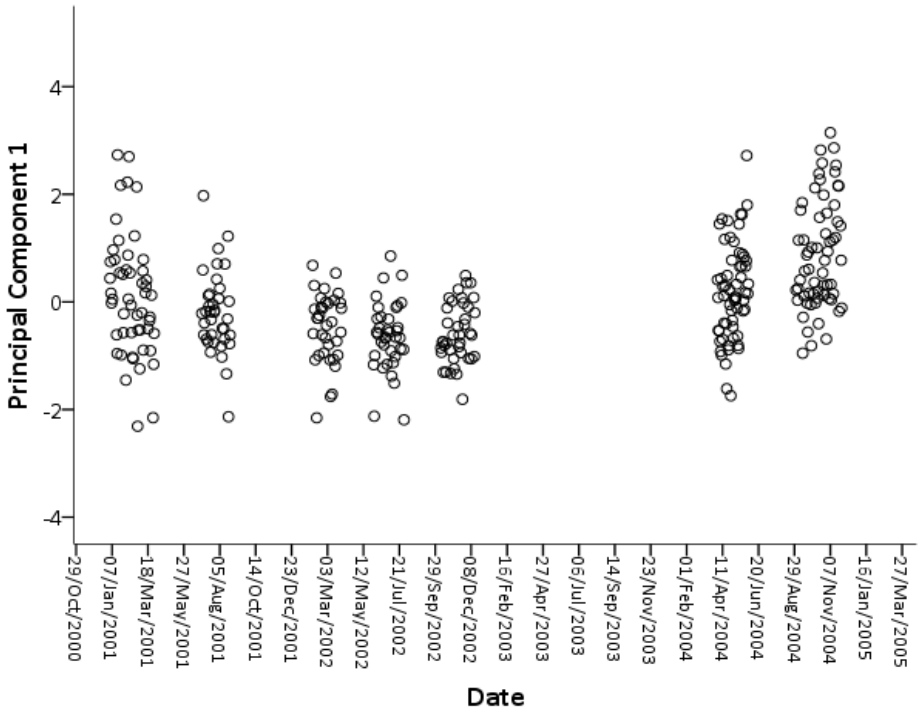


Figure 1. Principal Component 1 scores for Induna, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).

A number of behaviours loaded heavily onto each of the principal components. Figure 1 indicates variation in PC 1 over the study period for Induna. It can be observed that values for the PC declined from the initial sampling periods of January 2001 to December 2002, yet increased again considerably for the sampling periods during 2004.

PC 2 scores showed considerable variation over the study period and PC scores for individual observation periods tended to be both higher and more variable in the first year of the study. Figure 2 illustrates the PC 2 scores for Induna. The behaviours loading most strongly onto this PC were on average higher but also more variable in levels of expression earlier in the study, and that they also showed elevated, though less variable, levels in 2004.

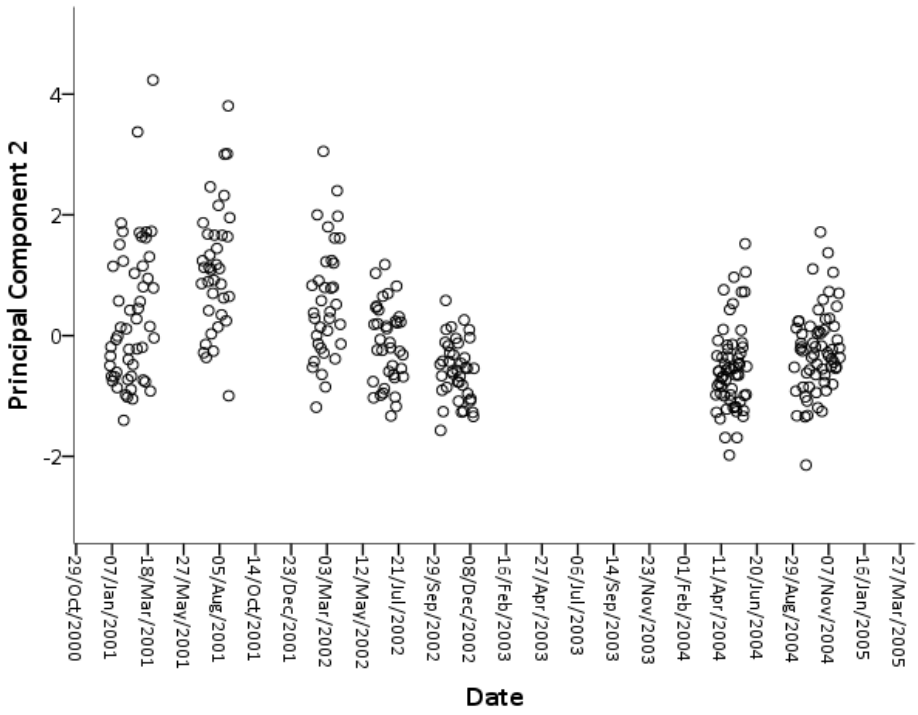


Figure 2. *Principal Component 2 scores for Induna, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

Figure 3 illustrates that PC 3 for Induna did not show similar temporal variation to PC 1 and PC 2. However, it is worth noting that there was less variation in PC 3 in late 2002 and that variation in PC1 and PC 2 was also low for this period. There is a period of lower behavioural variation at the end of 2002 that is observed throughout the first three principal components.

Figure 4 depicts variation in PC 4 during the study. Like PC 3, this principal component did not show the strong variation apparent in PC 1 and PC 2, though low levels of variation are apparent for early-mid 2002. There is an increase in variation of behaviour at the end of 2002, which is not seen in the first three components. This increase in variation continues into 2004.

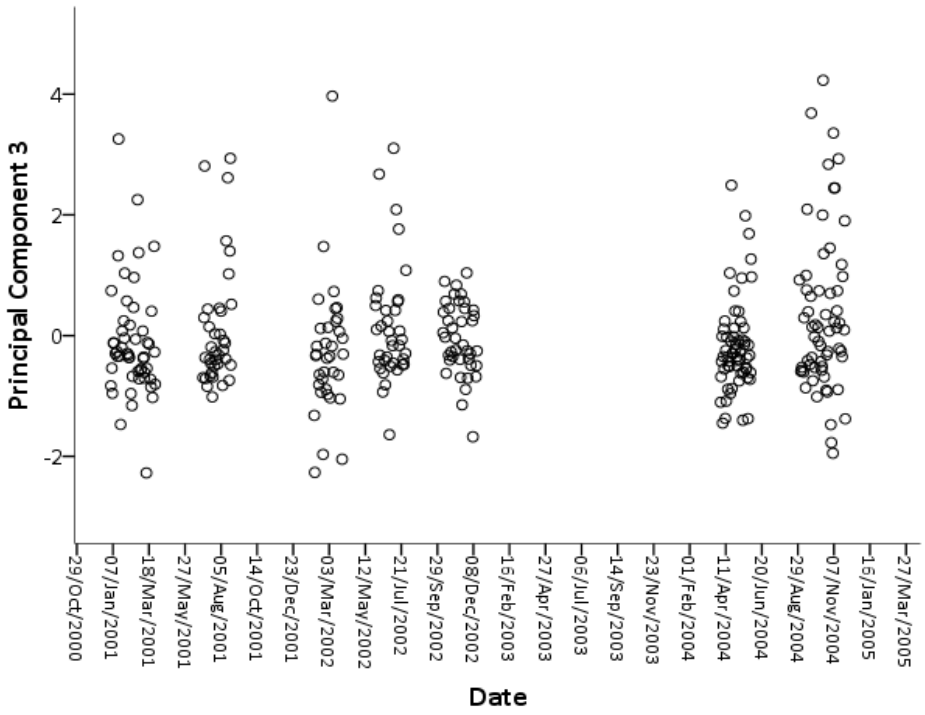


Figure 3. *Principal Component 3 scores for Induna, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

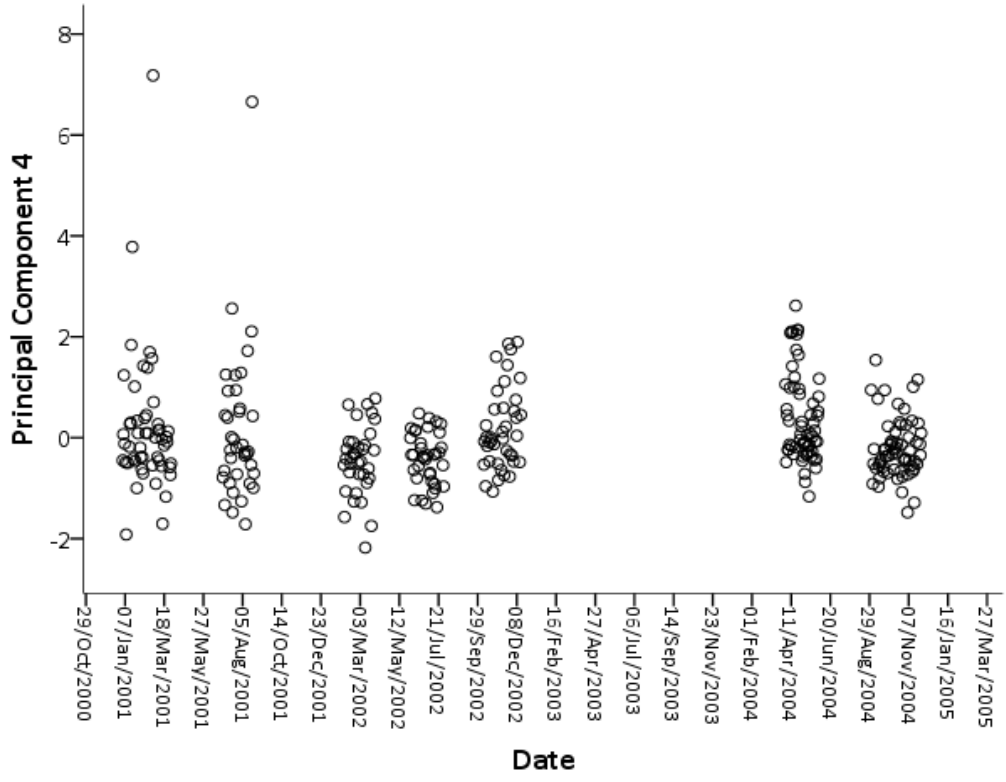


Figure 4. *Principal Component 4 scores for Induna, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

Ndonda

As with Induna, analyses of Ndonda began with Principal Components Analysis (PCA). Again the entire data set (from the 5th of February 2001 to the 29th of November 2004, excluding 2003) was used, comprising 298 separate 1 hour observational periods. The PCA was used to extract factors with eigenvalues >1 and the initial solution was subjected to Varimax rotation. The resulting four principal components are listed in Table 3 along with their eigenvalues, proportion of variation explained and cumulative variation explained.

Table 3. *Principal components extracted with eigenvalues and per cent variation explained and cumulative variation explained for Ndonda.*

Principal Component	Eigenvalue	Variation Explained	Cumulative Variation Explained
1	1.694	10.588	10.588
2	1.619	10.121	20.709
3	1.410	8.813	29.521
4	1.170	7.310	36.831

Behavioural variable loadings for the rotated solution are given in Table 4 where positive and negative loadings are given for each variable with the four principal components for Ndonda's behaviour.

Table 4. *Rotated Principal Component Matrix for Ndonda. The key variables loading onto each component are shown in bold.*

Behaviours	Components			
	1	2	3	4
Fighting	**0.711**	-0.010	0.118	0.010
Tail Twitches	0.106	**0.757**	-0.016	0.054
Rubbing Face	-0.069	0.324	0.089	0.255
Activity Level	0.030	0.150	0.262	0.053
Scratching	**0.553**	-0.342	0.052	-0.092
Tail Swishes	0.198	0.115	0.090	0.269
Grooming	-0.091	**0.639**	-0.073	-0.202
Playing	-0.147	-0.195	0.048	**0.522**
Lip Licking	**0.745**	0.219	-0.100	0.000
Spraying	0.209	-0.036	**0.589**	-0.058
Pacing	-0.068	-0.060	**0.798**	-0.081
Calling	0.044	0.376	-0.003	0.177
Defecating	0.047	-0.109	-0.028	-0.257
Rubbing Body	-0.139	0.094	0.128	**-0.523**
Tail Rolling	-0.024	0.144	-0.030	**0.562**
Rolling	0.093	0.206	-0.296	-0.146

Table 4 shows that Fighting, Scratching and Spraying were the most heavily loading behaviours on PC 1. PC 2 showed heavy loadings for Tail Twitches and Grooming. PC 3 had loadings from Spraying and Pacing with both behaviours showing high positive loadings. Lastly, PC 4 shows a relationship between Playing, Tail Rolling and Rubbing Body. Loadings for Playing and Tail Rolling were positive, whereas Rubbing Body was negative, showing that as Playing and Tail Rolling increased, Rubbing Body tended to decrease.

Figure 5 illustrates PC 1 for Ndonda over the study. It is apparent from the scattergram that the behaviours remained relatively consistent over the study rather than the more patterned fluctuations seen with Induna for PC 1.

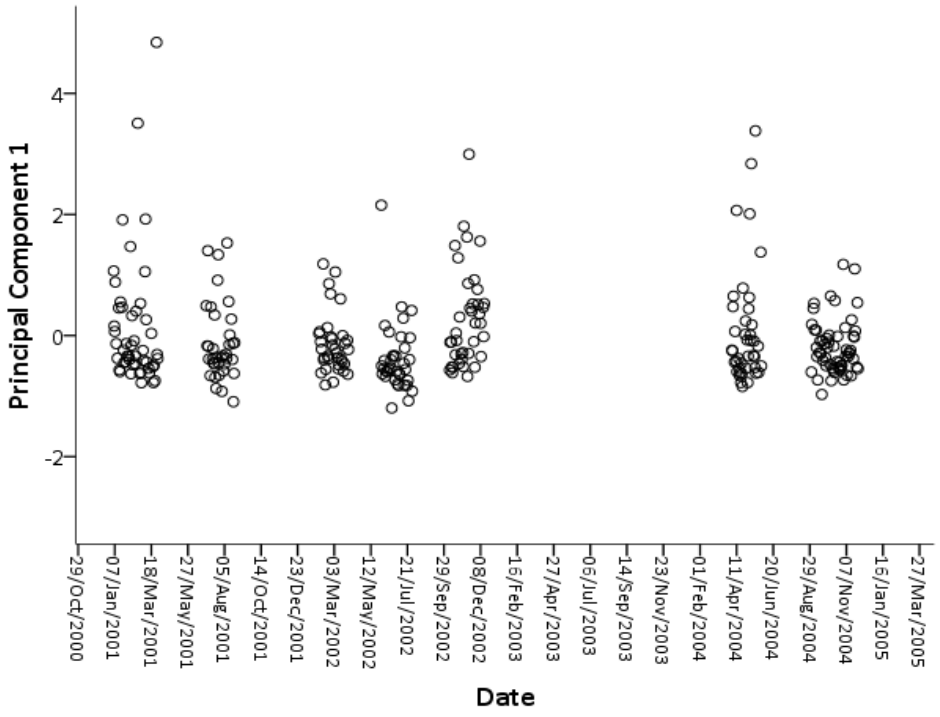


Figure 5. *Principal Component 1 scores for Ndonda, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

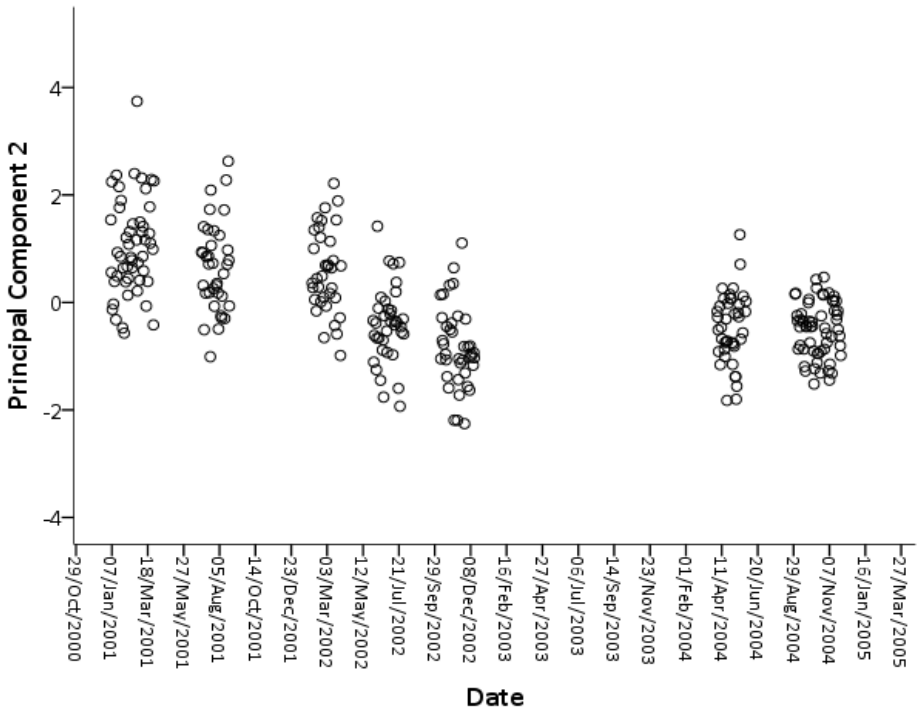


Figure 6. *Principal Component 2 scores for Ndonda, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

Figure 6 depicts this component over the sampling periods. Patterns of behaviour for PC 2 show a reduction from 2001-02 to 2004.

Figure 7 indicates the changes in PC 3 over the study for Ndonda. There is a substantial change in behaviour during early 2004, when a considerably higher level of variation in behaviour is observed. These results settle back to previously observed levels from 2001-02 by October 2004, showing less variation.

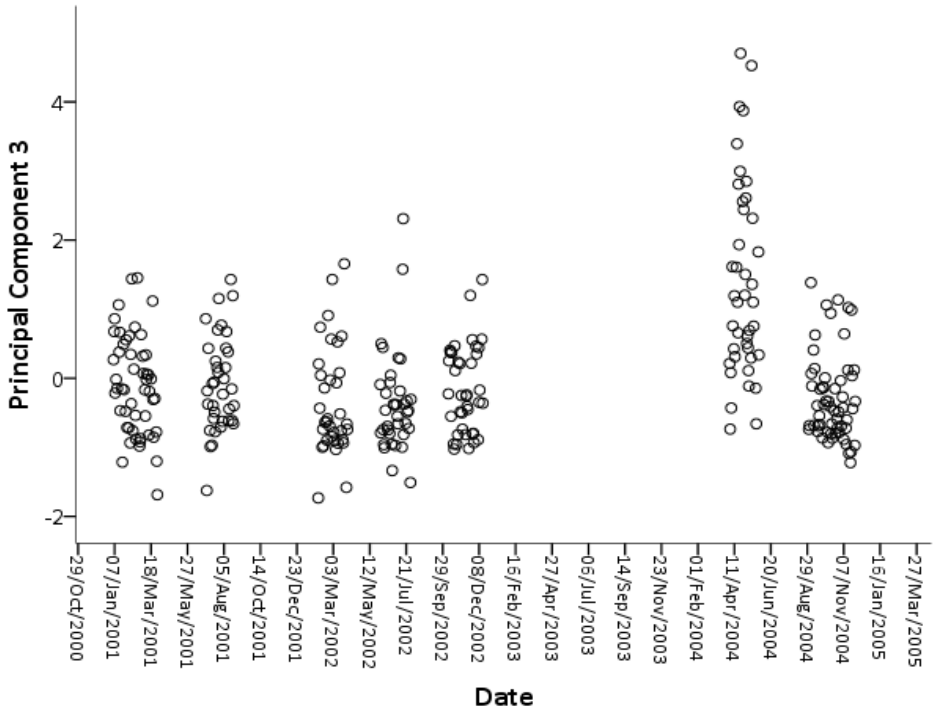


Figure 7. *Principal Component 3 scores for Ndonda, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

PC 4 for Ndonda illustrates that the relationship of behaviours changes considerably to what was observed previously in PC1 (Figure 8). This correlation of behaviour changes over the sampling periods, and the expression of the behaviours also appeared more varied in the early part of the study, clustering towards the end.

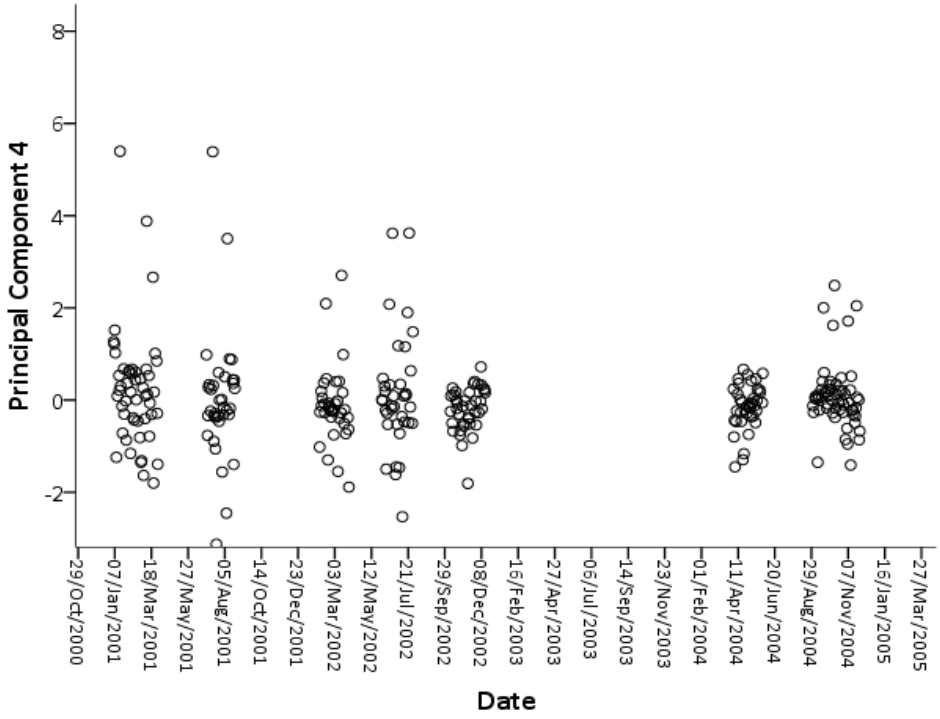


Figure 8. *Principal Component 4 scores for Ndonda, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

Izipho

Analyses of Izipho began using Principal Components Analysis (PCA). The entire data set (from the 3rd of February 2001 to the 29th of November 2004, excluding 2003) was used comprising 298 separate 1-hour observational periods. The PCA was used to extract factors with eigenvalues >1 and the initial solution was subject to Varimax rotation. The resulting four principal components are listed in Table 5 along with their eigenvalues, proportion of variation explained and cumulative variation explained.

Table 5. *Principal components extracted with eigenvalues and per cent variation explained and cumulative variation explained for Izipho.*

Principal Component	Eigenvalue	Variation Explained	Cumulative Variation Explained
1	2.878	17.990	17.990
2	1.528	9.548	27.537
3	1.256	7.848	35.385
4	1.246	7.788	43.173

Behavioural variable loadings for the rotated solution are given in Table 6 where positive and negative loadings are given for each variable with the four principal components for Izipho's behaviour.

Table 6. *Rotated Component Matrix for Izipho. The key variables loading onto each component are shown in bold.*

Behaviours	Components			
	1	2	3	4
Fighting	**0.500**	-0.082	0.057	0.078
Tail Twitches	**-0.548**	0.195	0.210	0.094
Rubbing Face	-0.036	-0.097	-0.016	**0.748**
Activity Level	-0.083	-0.024	**0.672**	-0.171
Scratching	**0.683**	-0.108	0.234	0.263
Tail Swishes	**-0.668**	-0.120	0.056	0.162
Grooming	-0.139	**0.620**	0.142	0.008
Playing	-0.184	**0.613**	0.083	-0.053
Lip Licking	0.370	-0.187	0.022	0.010
Spraying	**0.648**	-0.122	0.052	0.306
Pacing	0.000	0.081	**0.760**	0.024
Calling	**-0.518**	-0.366	0.254	-0.043
Defecating	0.124	0.054	-0.030	**0.728**
Rubbing Body	0.464	-0.365	0.098	-0.046
Tail Rolling	-0.013	**0.544**	0.025	-0.033
Rolling	0.179	0.200	0.419	0.132

Table 6 indicates that multiple behaviours had high loadings for PC 1 for Izipho, and these loadings were both positive and negative relationships. The positive relationships involved high loadings for Scratching and Spraying initially, with slightly weaker loadings for Fighting and Rubbing Body. The negative relationship involved high loadings for Tail Twitches and Tail Swishing. PC 2 shows high positive loadings for Grooming, Playing and Tail Rolling. PC 3 depicts a relationship between Activity Level and Pacing and PC 4 show high loadings for Rubbing Face and Defecating.

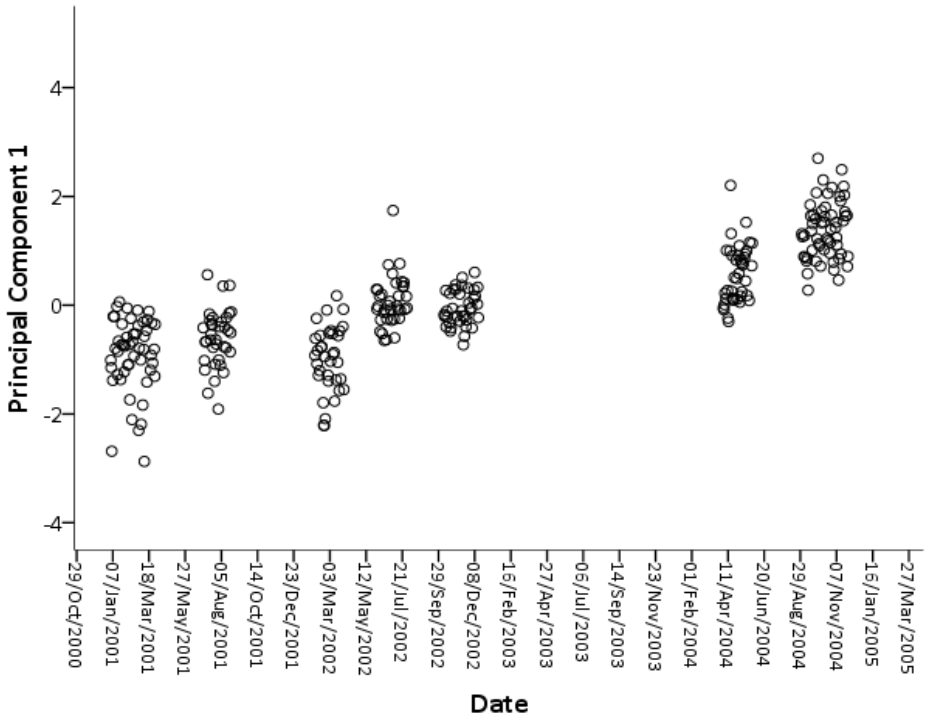


Figure 9. *Principal Component 1 scores for Izipho, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

Figure 9 illustrates variation in PC 1 scores over time for Izipho. The relationship depicted in the graph is complex. and suggests an increase in the PC scores from July 2002 in sampling periods 4 and 5, with a further and dramatic increase in 2004. To explore what behaviours underlie this variation in the PC scores, the four key behaviours loading onto PC 1were graphed against time.

Figure 10 depicts PC 2 for Izipho. It can be observed that the trend of this graph shows behavioural variation reducing towards the end of 2002.

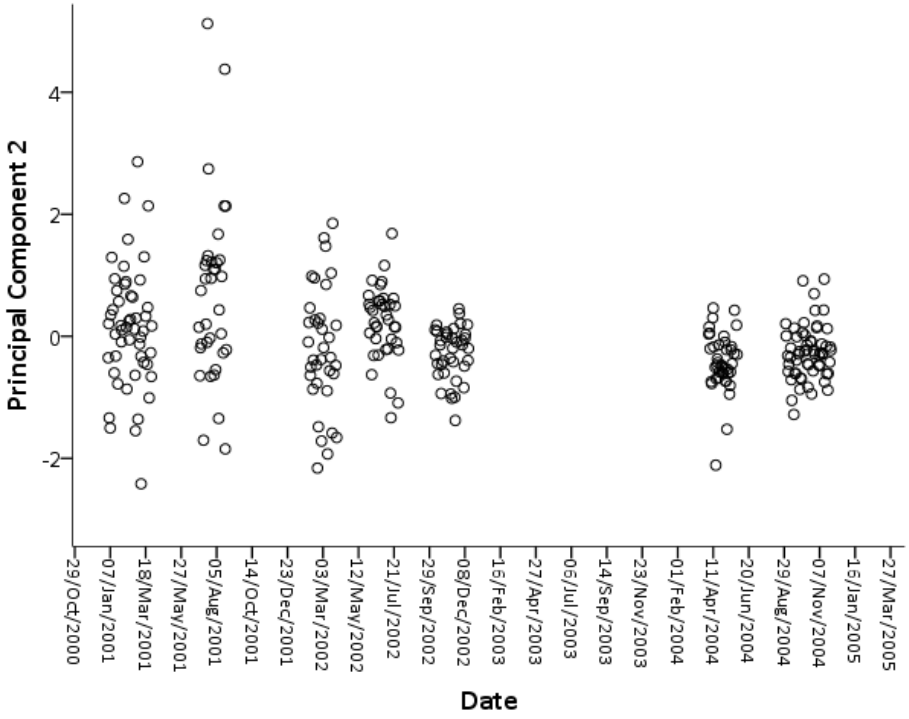


Figure 10. *Principal Component 2 scores for Izipho, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

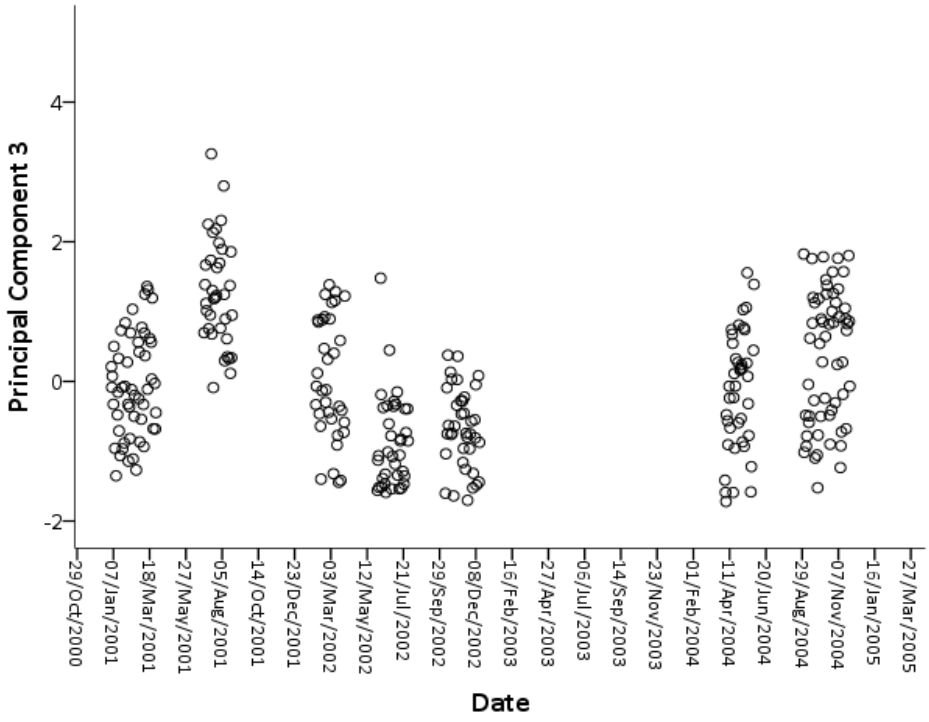


Figure 11. *Principal Component 3 scores for Izipho, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

Figure 11 shows the changes of this component over the study. With the exception of the second sampling period, the results are relatively consistent. Here it is apparent that behaviours have increased in frequency, but they return to previous levels by the next sampling period.

Lastly, Figure 12 depicts the changes in this component over the study. With the exception of sampling period 4, the remaining results are quite tightly clustered, showing little variability.

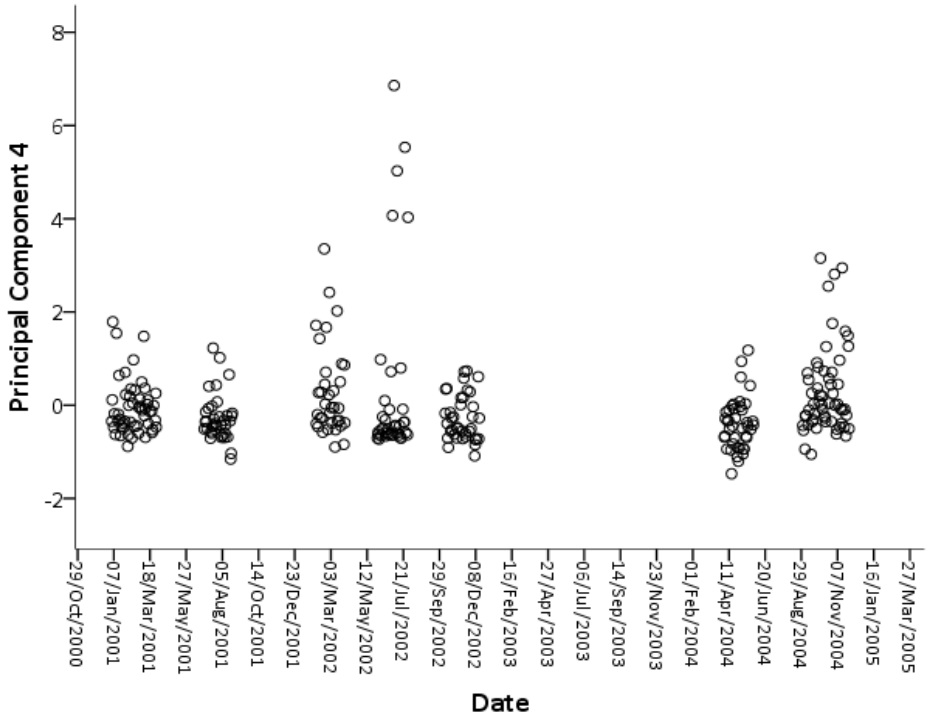


Figure 12. *Principal Component 4 scores for Izipho, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

Nyomfoza

Analyses of Nyomfoza began using Principal Components Analysis (PCA). The entire data set ranging from the 3rd of February 2001 to the 29th of November 2004 (excluding 2003) was used and comprised of 297 separate 1-hour observational periods. The PCA was used to extract factors with eigenvalues >1 followed by Varimax rotation. The resulting four principal components are listed in Table 7 along with their eigenvalues, proportion of variation explained and cumulative variation explained.

Table 7. *Principal components extracted with eigenvalues and per cent variation explained and cumulative variation explained for Nyomfoza.*

Principal Component	Eigenvalue	Variation Explained	Cumulative Variation Explained
1	2.227	17.132	17.132
2	1.354	10.415	27.547
3	1.243	9.563	37.111
4	1.082	8.324	45.435

Behavioural variable loadings for the rotated solution are given in Table 8 where positive and negative loadings are given for each variable with the four principal components for Nyomfoza's behaviour.

Table 8. *Rotated Component Matrix for Nyomfoza. The key variables loading onto each component are shown in bold. (Spraying, Scratching and Defecation have been ommitted as these behaviours were not recorded for Nyomfoza in the observation periods).*

Behaviours	Components			
	1	2	3	4
Fighting	0.061	-0.084	**0.727**	0.058
Tail Twitches	**0.604**	0.021	0.090	0.002
Rubbing Face	-0.101	0.028	-0.068	**0.869**
Activity Level	**0.605**	0.184	-0.108	0.109
Tail Swishes	0.459	-0.082	0.032	0.132
Grooming	0.446	0.073	0.490	-0.169
Playing	**0.503**	0.138	-0.064	-0.063
Lip Licking	-0.459	0.092	**0.507**	0.134
Pacing	**-0.549**	0.020	-0.022	-0.004
Calling	0.386	-0.091	0.176	**0.562**
Rubbing Body	0.042	**0.797**	-0.033	-0.081
Tail Rolling	0.048	**0.769**	0.062	0.046
Rolling	0.362	-0.137	-0.334	0.034

Table 8 shows a number of behaviours with high loadings, both positive and negative, for PC 1. The positive relationship shows high loadings for Tail Twitches, Activity Level and Playing. The negative relationship shows high loadings for Pacing. PC 2 depicts a strong relationship between Rubbing Body and Tail Rolling, with high loadings for these behaviours. Table 8 also illustrates the strong relationship between Fighting and Lip Licking for PC 3. Finally, PC 4 shows high loadings for Rubbing Face and Calling.

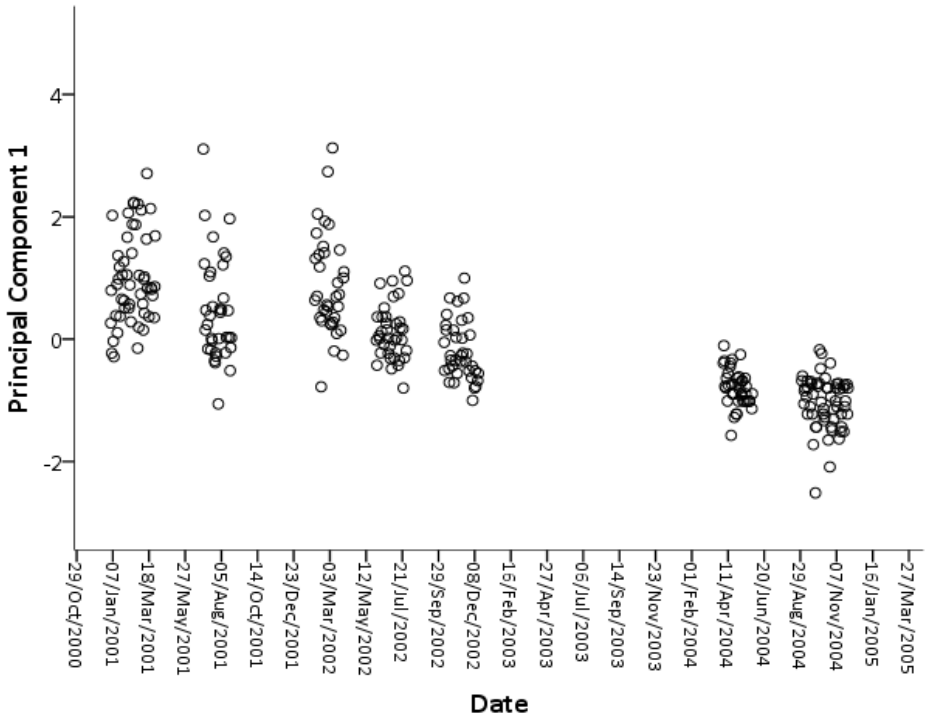


Figure 13. *Principal Component 1 scores for Nyomfoza, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

Figure 13 shows PC 1 scores against time for Nyomfoza. It can be observed that values for the PC decline from the initial sampling periods in January 2001.

The results for PC 2 for Nyomfoza in Figure 14 are very different to the results for PC1, showing low levels of behaviour with trends relatively consistent over the entire study period.

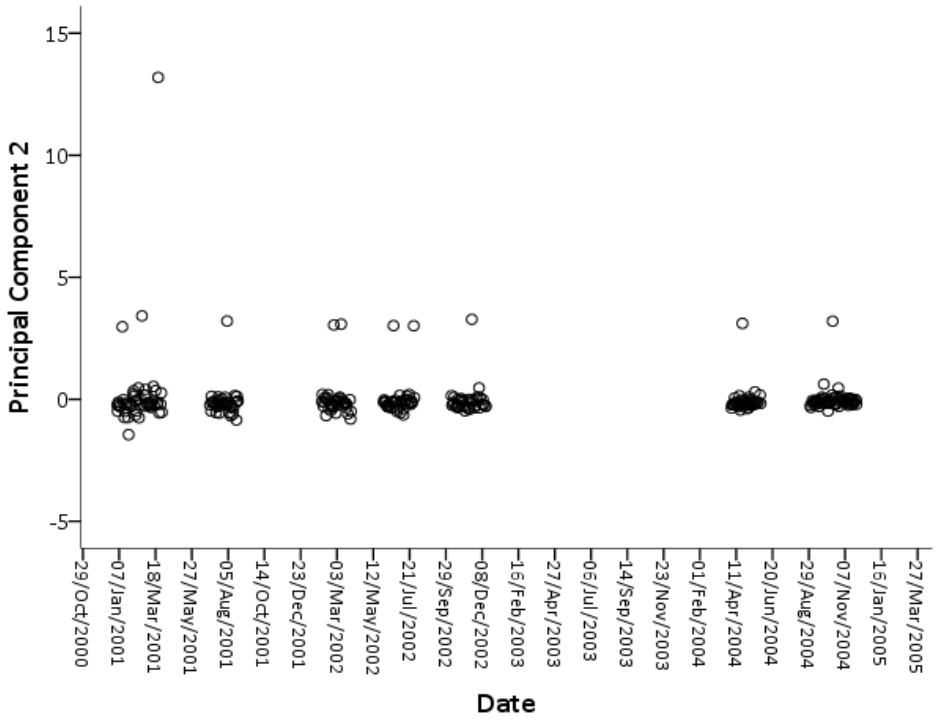


Figure 14. *Principal Component 2 scores for Nyomfoza, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

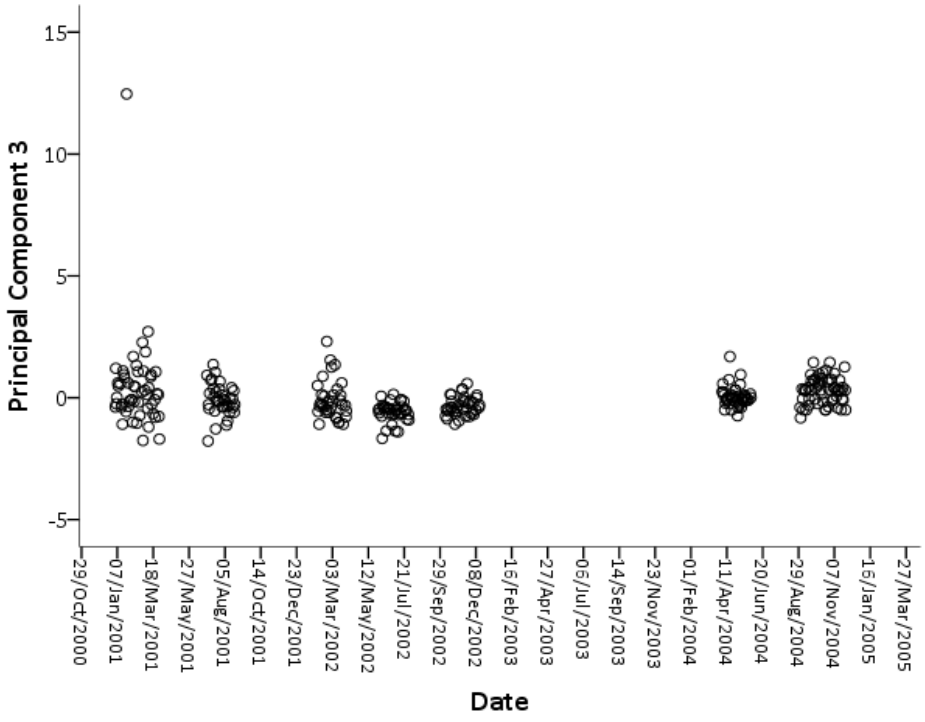


Figure 15. *Principal Component 3 scores for Nyomfoza, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

Again the results for PC3 for Nyomfoza are similar to PC2. Figure 15 depicts the low level of behaviour observed for Nyomfoza, with only sampling period 1 illustrating a higher level of behaviour.

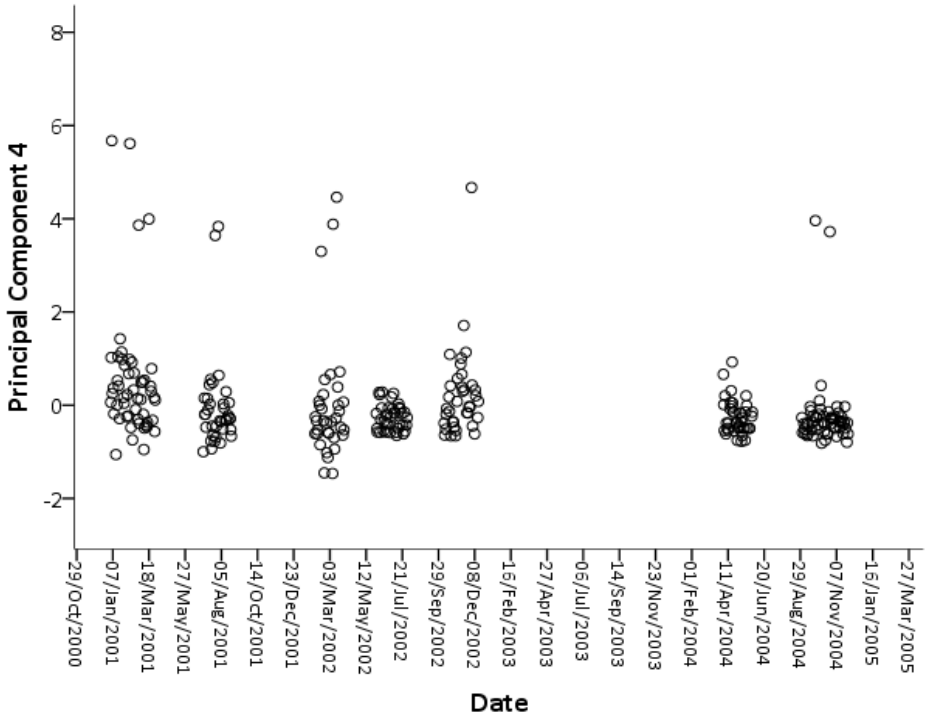


Figure 16. *Principal Component 4 scores for Nyomfoza, plotted against days (results were omitted for 2003 as they were not recorded as frequently as the other years of the recording).*

Finally, Figure 16 shows PC 4 plotted over the study period. This PC shows behaviour loaded on to this component is relatively consistent over the study, with the exception of April-June 2004, where behaviour is reduced.

Umballa

While the data set for Umballa was not as large as for the other males, a principal components analysis was included to provide consistency in how behavioural data were analysed, allowing some comparisons with the other males. The entire data set spanning from the 4th February 2001 to the 24th of August 2001 was used and comprised 88 separate 1-hour observational periods. Factors with eigenvalues >1 were obtained from the PCA and the initial solution was subject to Varimax rotation. The resulting four principal components are listed in Table 9 along with their eigenvalues, proportion of variation explained and cumulative variation explained.

Table 9. *Principal components extracted with eigenvalues and per cent variation explained and cumulative variation explained for Umballa.*

Principal Component	Eigenvalue	Variation Explained	Cumulative Variation Explained
1	1.961	12.254	12.254
2	1.861	11.633	23.886
3	1.545	9.655	33.542
4	1.395	8.720	42.262

Behavioural variable loadings for the rotated solution are given in Table 10 where positive and negative loadings are given for each variable with the four principal components for Umballa's behaviour.

Table 10. *Rotated Component Matrix for Umballa. The key variables loading onto each component are shown in bold.*

Behaviours	Components			
	1	2	3	4
Fighting	**0.579**	0.258	-0.220	0.183
Tail Twitches	-0.028	-0.125	**-0.654**	-0.326
Rubbing Face	0.144	**-0.593**	0.018	-0.013
Activity Level	0.318	0.196	0.095	**-0.620**
Scratching	-0.028	**0.535**	**0.510**	0.161
Tail Swishes	**-0.647**	0.207	0.048	0.111
Grooming	0.037	0.489	0.043	-0.081
Playing	0.011	0.017	**0.622**	-0.068
Lip Licking	0.002	**-0.653**	0.051	-0.062
Spraying	**0.619**	0.020	0.197	0.246
Pacing	0.173	0.234	-0.245	-0.308
Calling	-0.247	-0.080	-0.293	0.241
Defecating	0.073	0.096	0.038	**0.545**
Rubbing Body	0.125	0.077	-0.037	**0.632**
Tail Rolling	0.037	-0.323	**0.573**	-0.224
Rolling	**0.701**	-0.132	0.095	-0.170

Table 10 shows that the behaviours most heavily loaded for the first principal component were Fighting, Spraying, Rolling and Tail Swishing. There is a strong positive loading from these first three behaviours, with Tail Swishing having a negative loading indicating it is negatively correlated with the first three behaviours. The behaviours of Scratching, Rubbing Face and Lip Licking were most heavily loaded to PC 2. Here again there is a negative relationship, as Scratching and Rubbing Face increase, Lip Licking decreases. Table 10 illustrates the behaviours heavily loaded on to PC 3 to be Tail Twitches, Scratching, Playing and Tail Rolling. There is a positive relationship between Scratching, Playing and Tail Rolling, but as these behaviours increase Tail Twitches decreases. Finally, PC 4 shows a relationship between Body Rubbing, Defecating and Activity Level, with Activity Level decreasing as the other behaviours increase.

As Umballa was only observed over 2001, his scattergrams only display two sampling periods. Figure 17 indicates the relationship between Umballa's behaviours loaded onto PC 1. The trend of these behaviours remains quite stable over the sampling periods.

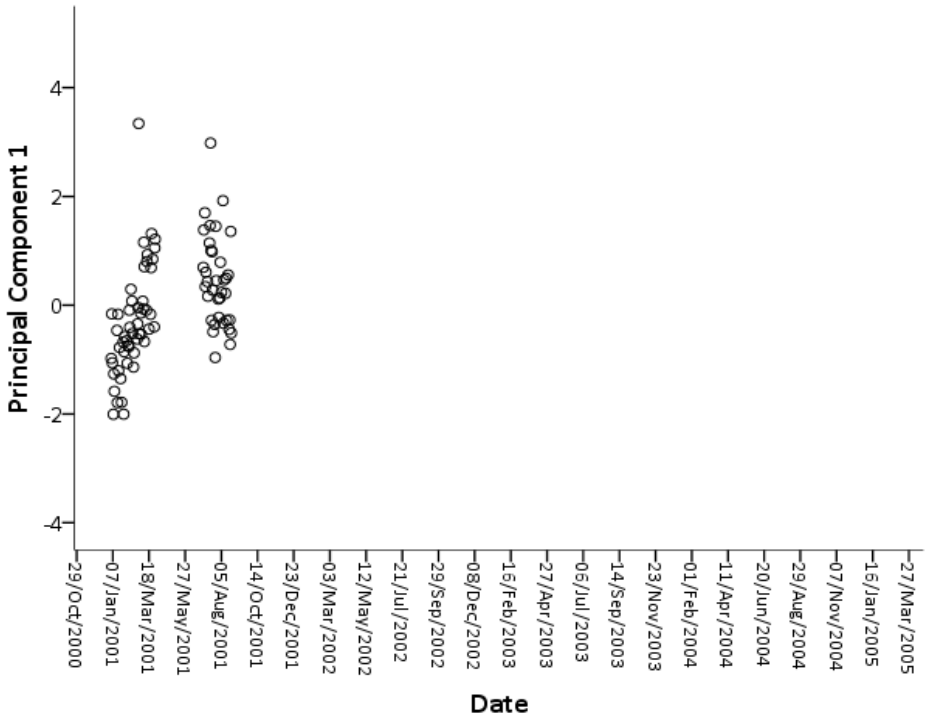


Figure 17. *Principal Component 1 scores for Umballa, plotted against days. Days are for 2001 dates only, as Umballa was sent to Orana Park, New Zealand, on breeding loan.*

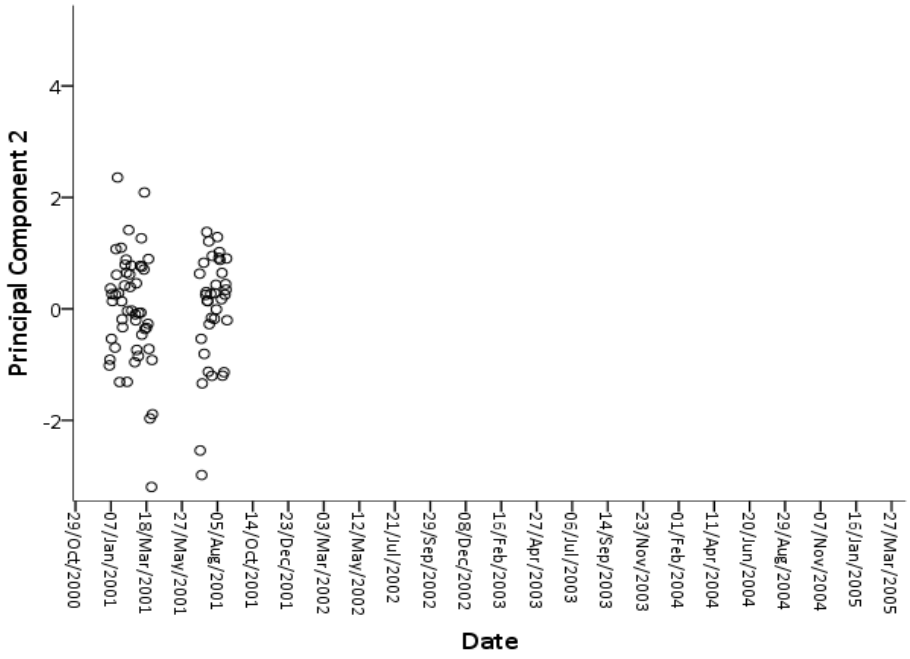


Figure 18. *Principal Component 2 scores for Umballa, plotted against days. Days are for 2001 dates only, as Umballa was sent to Orana Park, New Zealand, on breeding loan.*

The relationship between behaviours for PC2 is depicted in Figure 18. Again, the trend for these behaviours remains relatively stable over the observation periods, but a high level of variation was noted with these behaviours.

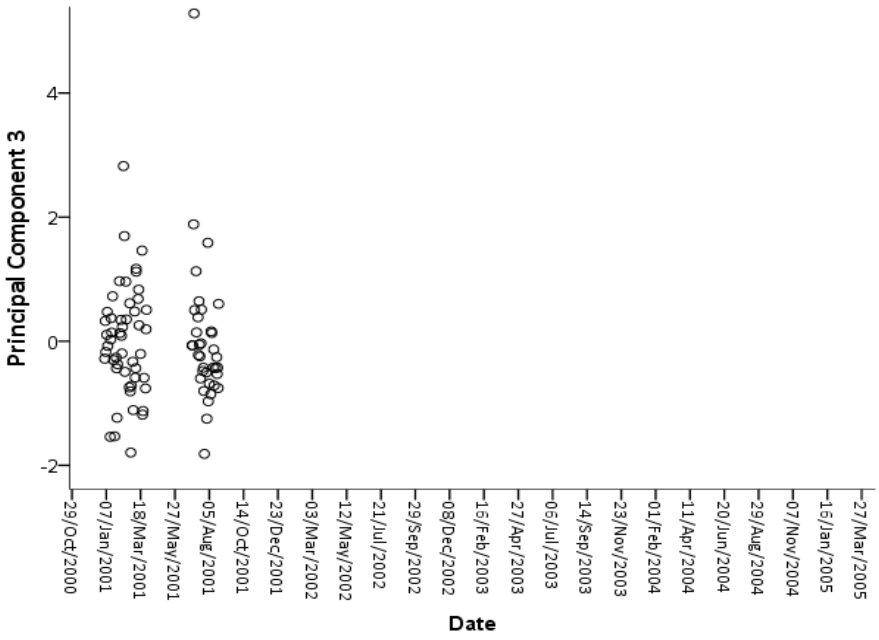


Figure 19. *Principal Component 3 scores for Umballa, plotted against days. Days are for 2001 dates only, as Umballa was sent to Orana Park, New Zealand, on breeding loan.*

Figure 19 illustrates PC 3 for Umballa. There is a considerable increase in the trend here from the January-March observations to the July-September observations.

Lastly, Figure 20 shows that the behaviours loading onto PC4 are very different to what was observed for the other males.

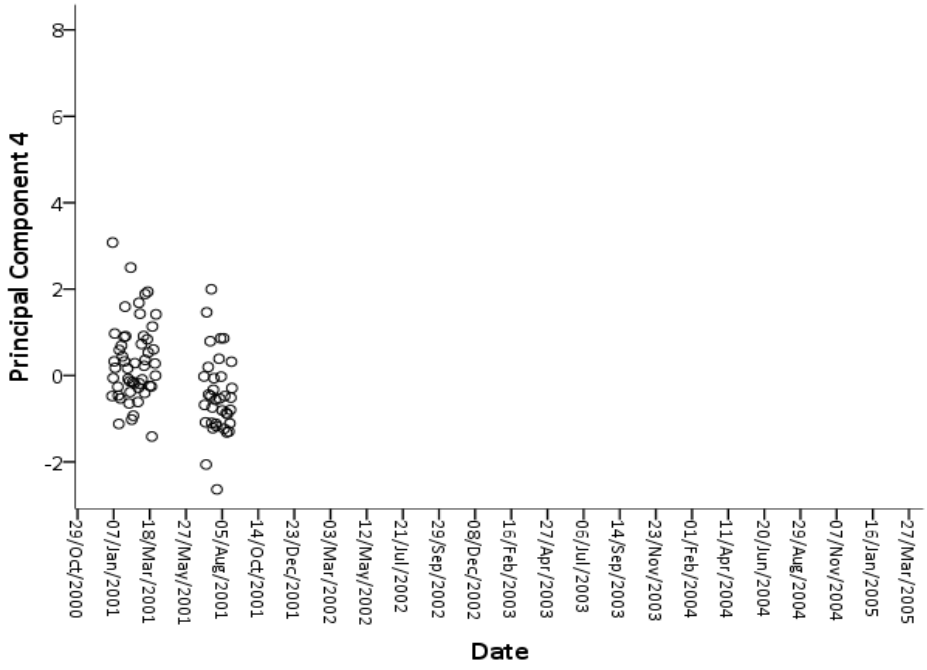


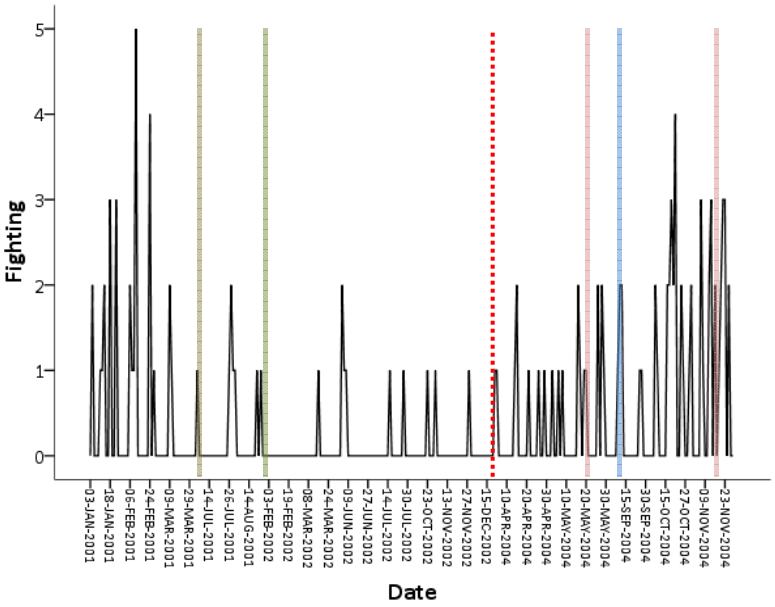
Figure 20. *Principal Component 4 scores for Umballa, plotted against days. Days are for 2001 dates only, as Umballa was sent to Orana Park, New Zealand, on breeding loan.*

Key Male Behaviours

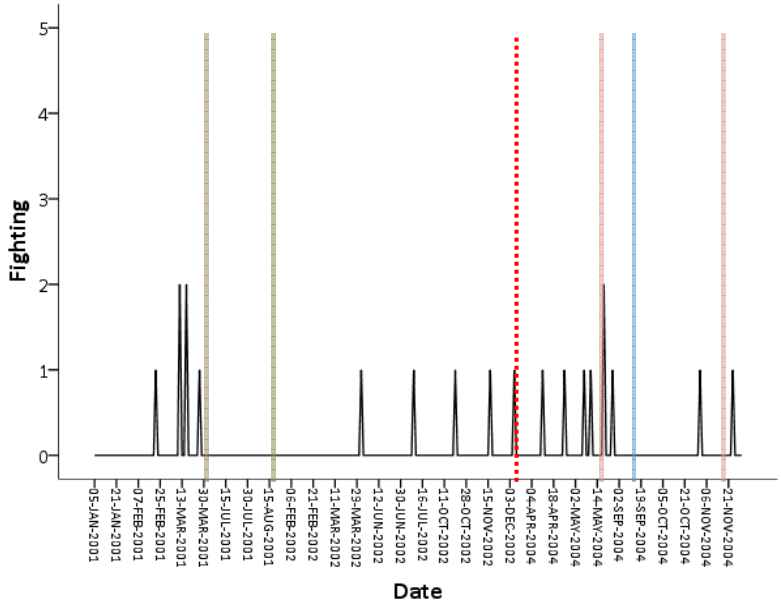
Due to the variation in key behaviours and in the principal components over the study period, as well as the high level of variation between individuals, the behaviours of Fighting, Spraying, Tail Twitches and Grooming were examined further for each male. Data for these variables were obtained between the 3rd of January 2001 and the 29th of November 2004 (excluding 2003).

In the following sections I examine whether behavioural changes in males were linked to several key events in the facility, particularly relating to the female cheetahs. These events were the separation of males and females and housing in separate yards, an assisted reproduction attempt (during December 2001), mating (occurred during work on mate choice and the receptivity of males to female signals- see Chapter 6), and subsequent births in the facility. Relevant events will be indicated in each analysis.

In Figures 21, a-d, the male behaviours are represented by line graphs, where each observation day is represented contiguously, rather than spaced by the absolute amount of time between observations. This is done to make any relationships between events and the male behaviours more apparent than in the scattergrams shown previously, where many data are densely clustered. Each male is represented in a separate graph, allowing comparison between males and to examine how changes in husbandry and housing may have impacted differently on individual males. Initially, Fighting for Induna, Ndonda, Izipho and Umballa was examined. Nyomfoza was only observed Fighting once in the study and was therefore omitted from this analysis.



a) Induna



b) Ndonda

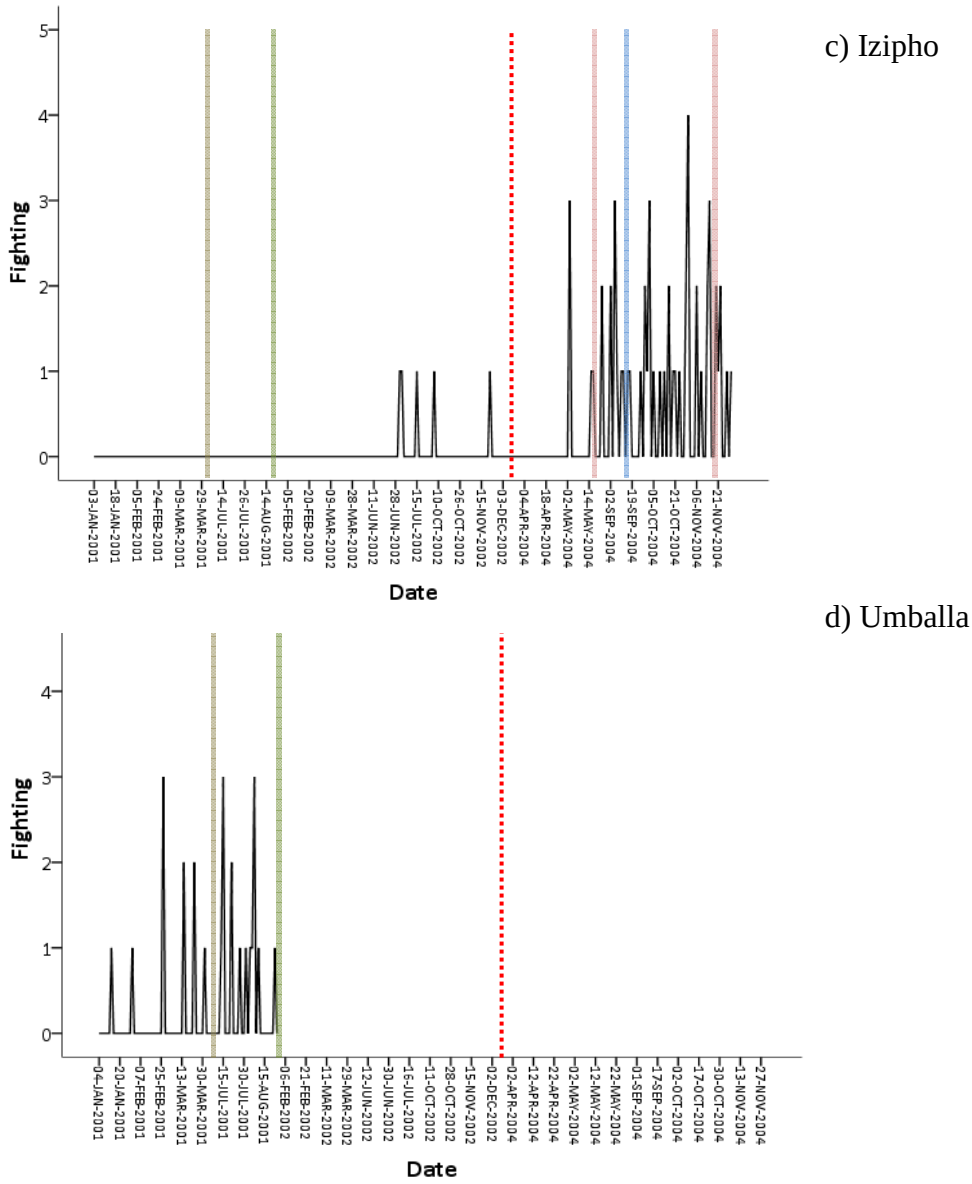
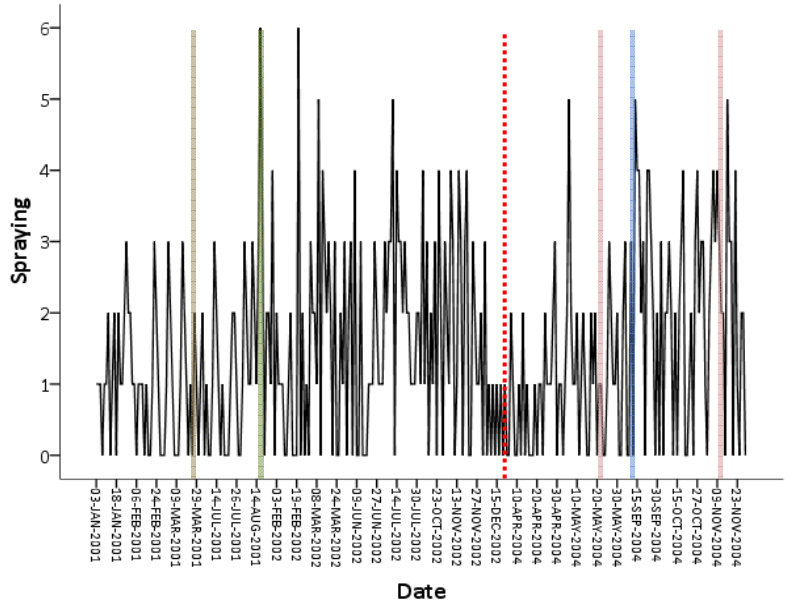


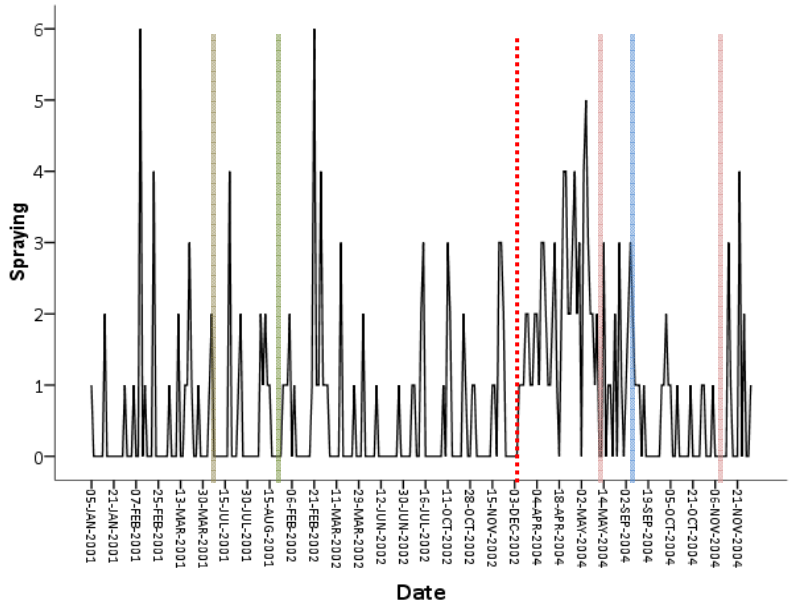
Figure 21. *Scores for individual males for Fighting during the study, showing: a) Induna, b) Ndonda, c) Izipho and d) Umballa. Colour-coded vertical lines indicate key husbandry events within Monarto Zoological Park. Tan represents the point when males and females were moved to be housed separately; green represents the Artificial Insemination procedure; pink represents mating within the facility and blue represents births within the facility. The dotted red line indicates the end of 2002 and the beginning of 2004 with the intervening period not represented. Umballa was only observed during 2001, therefore his graph only depicts that year.*

Figure 21 shows the considerable variation between individuals in Fighting. Each graph represents Fighting that was instigated by the particular male. Nyomfoza was excluded from this set of graphs as he was only seen to instigate one fight with another male during the study period. Induna showed increased Fighting at the

beginning of the study through to July 2001, and then Fighting increased again at the end of observations in 2004. Izipho displayed very little aggression and was not seen to instigate Fighting until July 2002. These fights were very uncommon until 2004, when Izipho was regularly seen to fight with Induna and occasionally Ndonda. Ndonda did very little Fighting throughout the study period.



a) Induna



b) Ndonda

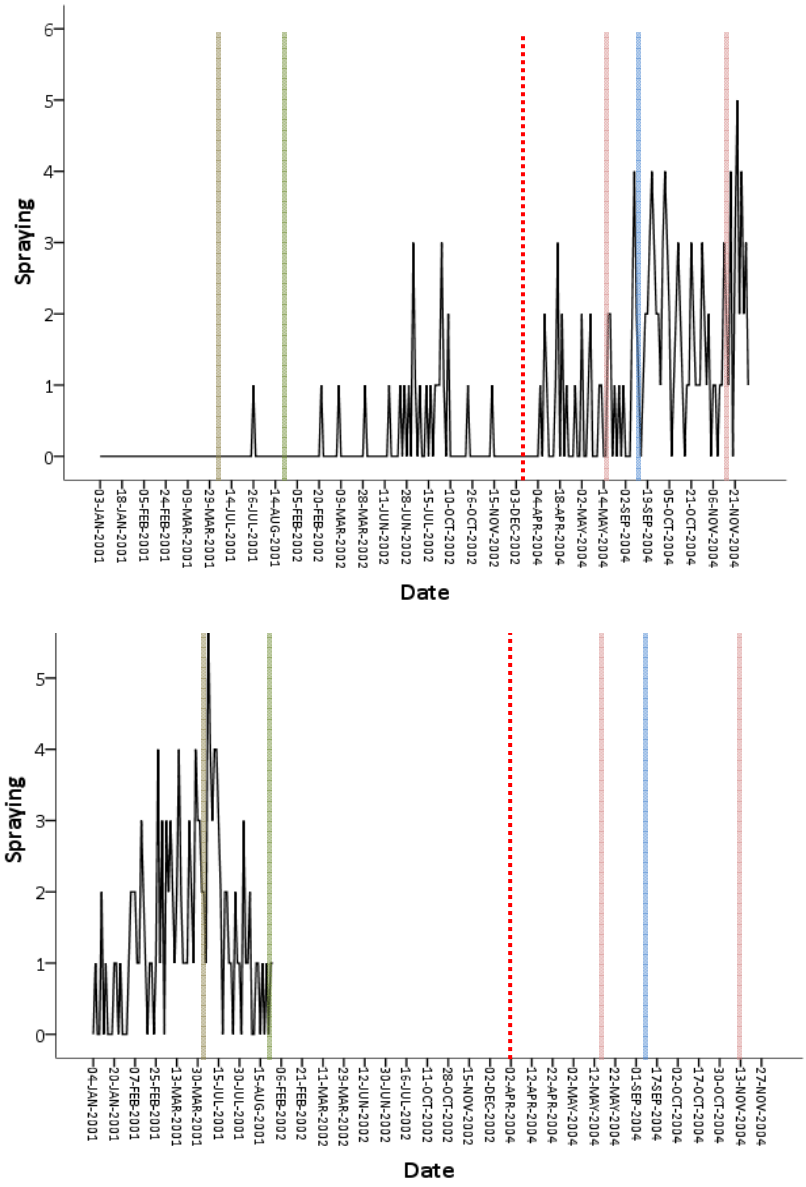
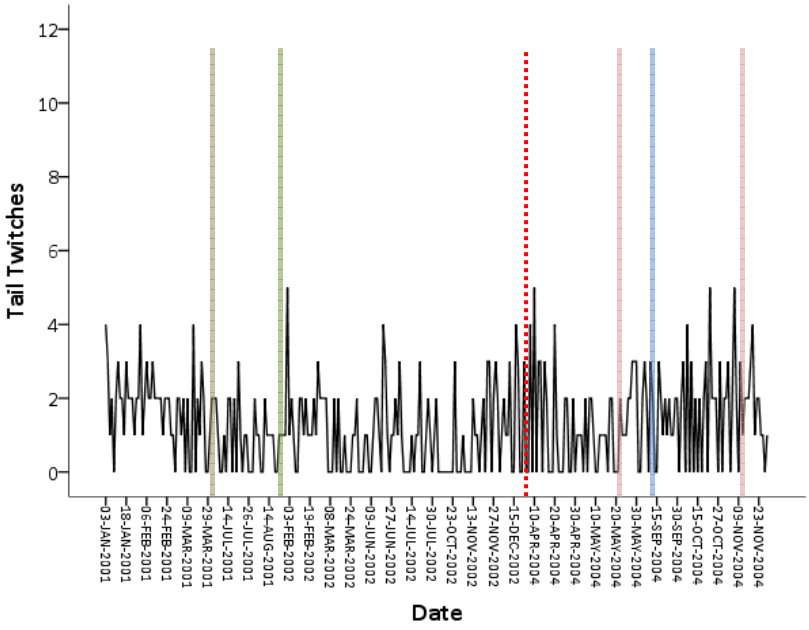


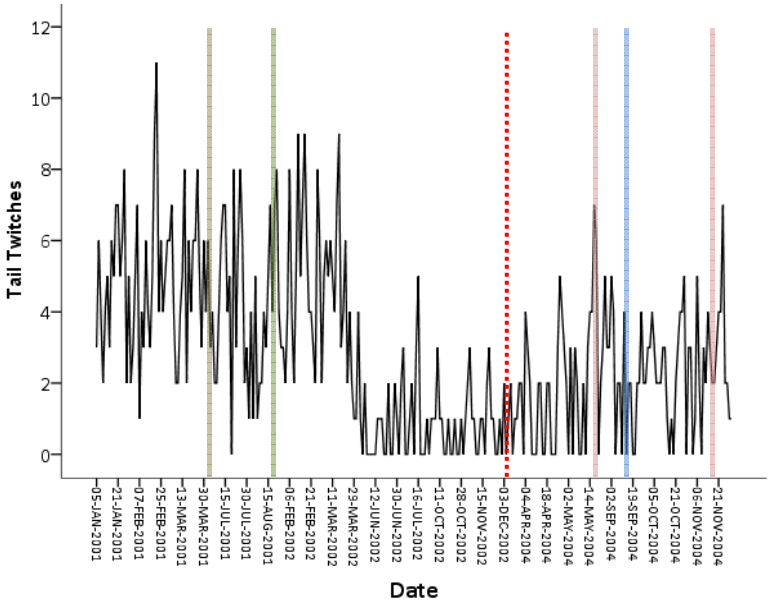
Figure 22. *Scores for individual males for Spraying during the study, showing: a) Induna, b) Ndonda, c) Izipho and d) Umballa. Colour-coded vertical lines indicate key husbandry events within Monarto Zoological Park. Tan represents the point when males and females were moved to be housed separately; green represents the Artificial Insemination procedure; pink represents mating within the facility and blue represents births within the facility. The dotted red line indicates the end of 2002 and the beginning of 2004 with the intervening period not represented. Umballa was only observed during 2001, therefore his graph only depicts that year.*

Figure 22 illustrates the frequency of Spraying for individual males over the study. Individuals sprayed at different rates, with high levels of Spraying from Induna, Ndonda and Umballa. Spraying increased in the latter half of the study for Izipho, with

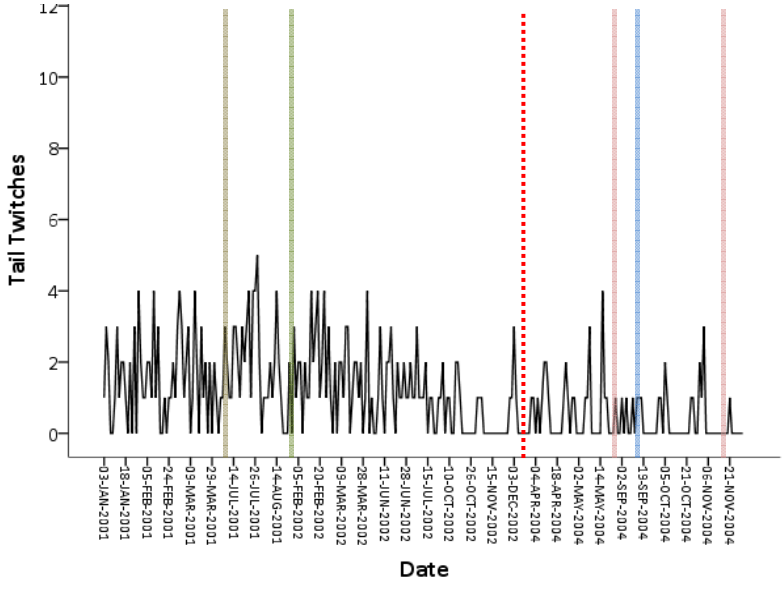
quite a distinct increase during 2004. No Spraying was observed from Nyomfoza and he was omitted from the analysis.



a) Induna



b) Ndonda



c) Izipho

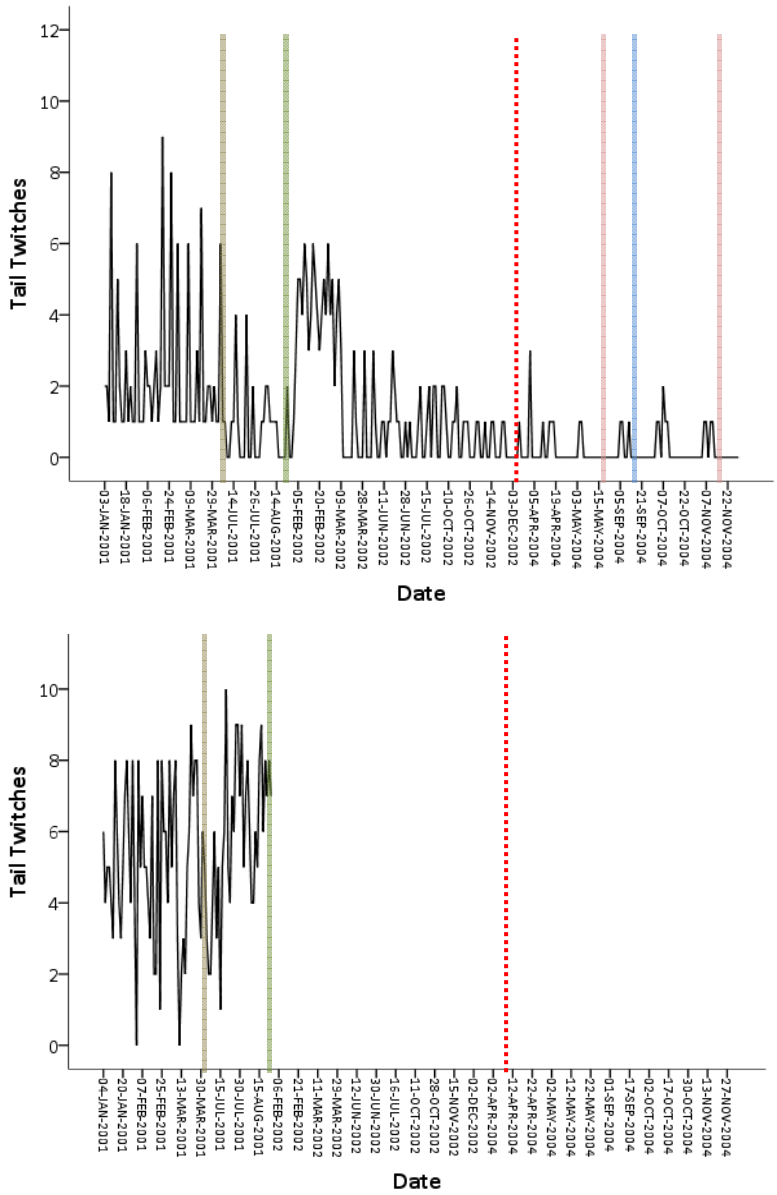
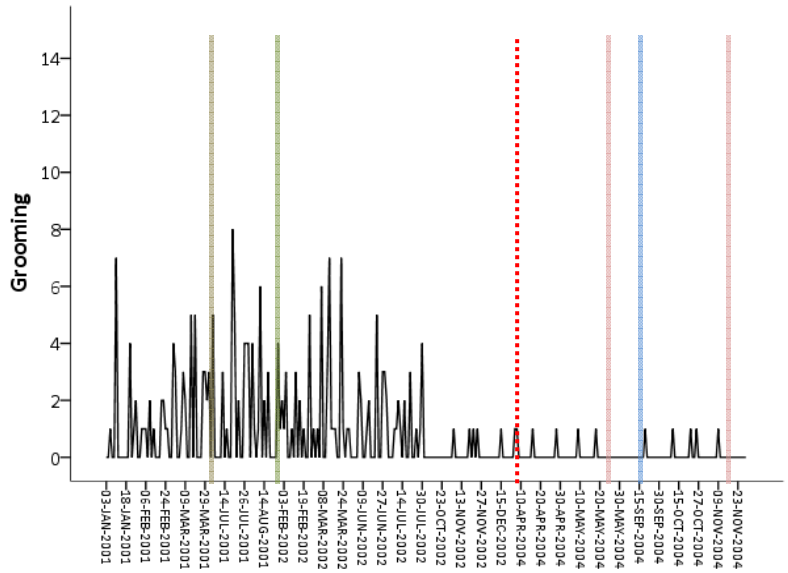


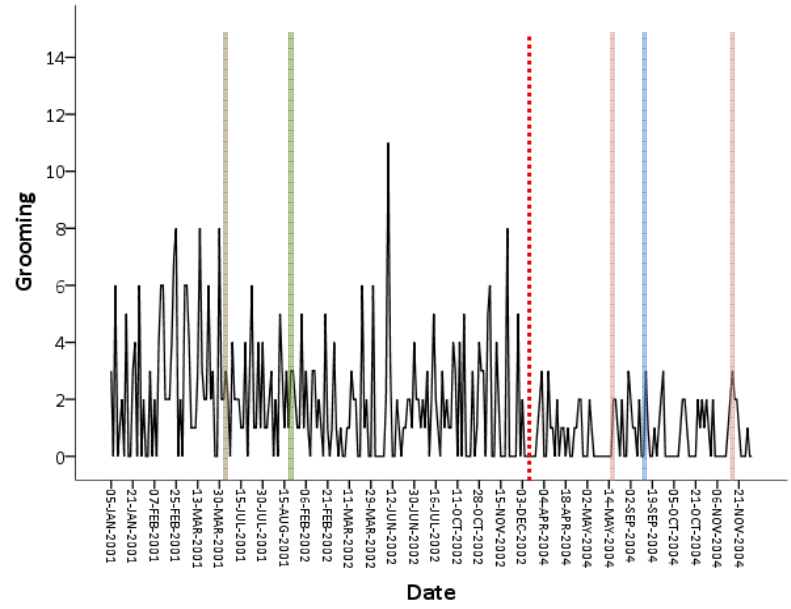
Figure 23. *Scores for individual males for Tail Twitches during the study, showing: a) Induna, b) Ndonda, c) Izipho, d) Nyomfoza and e) Umballa. Colour-coded vertical lines indicate key husbandry events within Monarto Zoological Park. Tan represents the point when males and females were moved to be housed separately; green represents the Artificial Insemination procedure; pink represents mating within the facility and blue represents births within the facility. The dotted red line indicates the end of 2002 and the beginning of 2004 with the intervening period not represented. Umballa was only observed during 2001, therefore his graph only depicts that year.*

It is evident from Figure 23 that there is a considerable amount of variation in the expression of Tail Twitches between individuals over the observation period. Tail Twitching was observed throughout the study for Induna and Izipho, but with generally

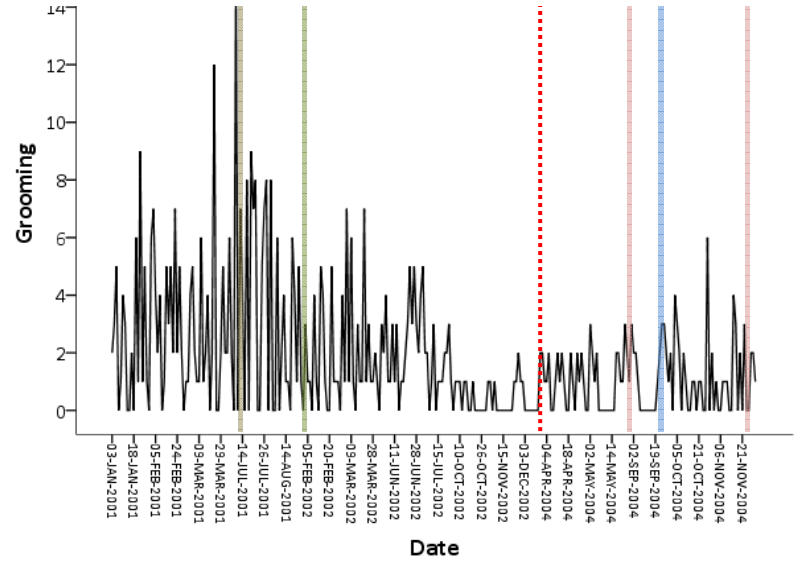
higher levels of expression in the first part of the study. Ndonda and Nyomfoza initially had a high rate of Tail Twitches but expression of this behaviour lessened in the second half of the study. Umballa also had a high level of Tail Twitches, increasing towards the end of 2001.



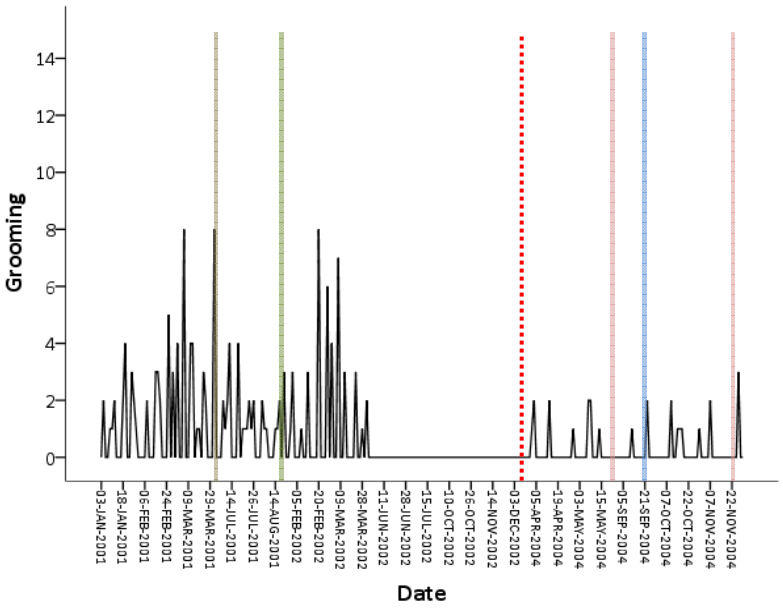
a) Induna



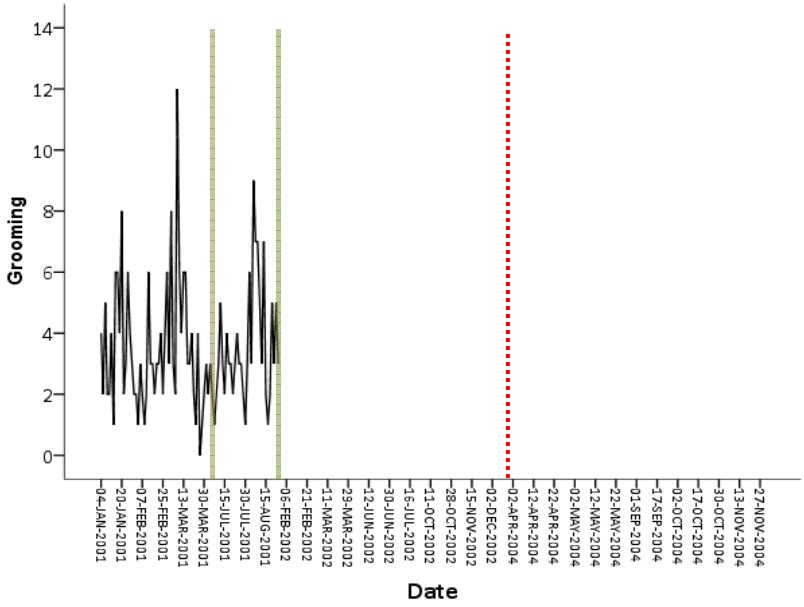
b) Ndonda



c) Izipho



d) Nyomfoza



e) Umballa

Figure 24. *Scores for individual males for Grooming during the study, showing: a) Induna, b) Ndonda, c) Izipho, d) Nyomfoza and e) Umballa. Colour-coded vertical lines indicate key husbandry events within Monarto Zoological Park. Tan represents the point when males and females were moved to be housed separately; green represents the Artificial Insemination procedure; pink represents mating within the facility and blue represents births within the facility. The dotted red line indicates the end of 2002 and the beginning of 2004 with the intervening period not represented. Umballa was only observed during 2001, therefore his graph only depicts that year.*

Finally, Figure 24 illustrates differences observed in the rates of Grooming between males. Higher levels of Grooming were observed for Induna and Izipho in the first part of the study than in the latter part. A quite different pattern was observed for

Nyomfoza, as no Grooming occurred at all during a considerable part of 2002. Grooming was very low and episodic in the second part of the study. Ndonda had relatively consistent Grooming which reduced in 2004, and Umballa displayed a moderate amount of Grooming during 2001.

It can be seen from all four graphs that a number of behavioural changes coincided with husbandry events. Initially it was evident that there was an increase in Fighting during 2004. This increase in Fighting coincided with increased introductions to the females and frequent reproductive activity within the facility.

Similar changes were observed for Spraying for Izipho during 2004. Where he had previously shown minimal Spraying behaviour, by April 2004 this behaviour had increased considerably. Then with a birth in the facility, his Spraying increased further. This change contrasts to Induna's Spraying behaviour. While Induna was seen to spray frequently throughout the study, his behaviour changed at the time of the artificial insemination/Umballa's removal. At this point in the study, the frequency of his Spraying doubled and remained high throughout 2002. Increased Spraying was also recorded for Umballa at the time the sexes were separated.

Tail Twitches patterns varied amongst the males. While this behaviour remained stable for Induna over the study, there was a pronounced fluctuation at the beginning of 2002 for Ndonda and Nyomfoza, with both males showing an increase in this behaviour. This increase in Tail Twitches was followed by a steady reduction that was observed for Ndonda, Izipho and Nyomfoza during mid-2002.

There were changes in Grooming for all males, with a pronounced reduction in Grooming for all males over the study. Interestingly, this behaviour also changed when the sexes were separated. Izipho displayed an increase in Grooming, whereas Ndonda and Umballa showed a reduction in Grooming. By 2004, when there was frequent reproductive activity in the facility, Grooming was considerably reduced.

Relationships Between Male Cheetahs

Relationships between pairs of males were investigated by analysing Fighting and Grooming. Pairs were observed to determine the levels of acceptance between males, by examining if there were higher levels of Grooming or Fighting between related versus unrelated pairs.

Table 11 shows consistently high correlations for both Fighting and Grooming for the majority of male pairs. This suggests that patterns of both Fighting and

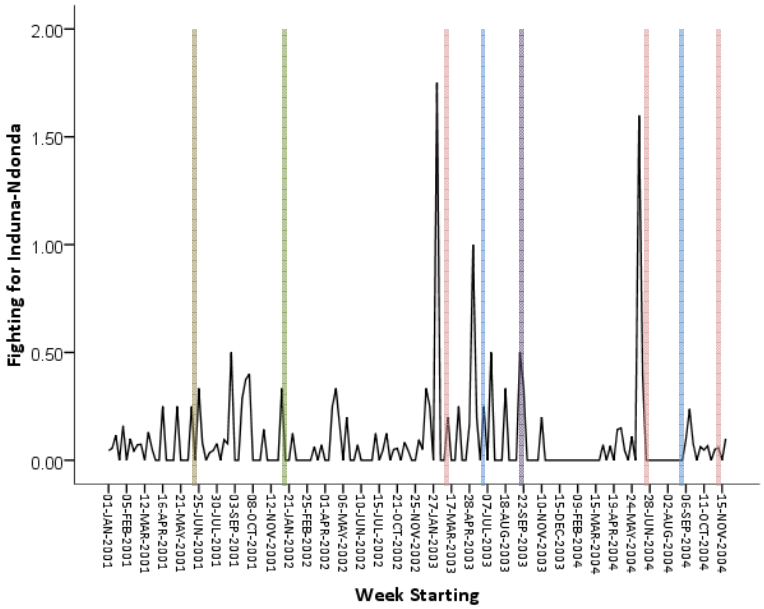
Grooming are not constrained to just individual pairs, but have implications throughout the males as a group. The only exceptions to this were the pairing of Induna/Nyomfoza and Ndonda/Nyomfoza for Fighting and Ndonda/Izipho for Grooming.

Table 11. *Correlations between pairs of males for Fighting and Grooming (values above the diagonal give correlations between pairs for Fighting, and values below the diagonal give correlations between pairs for Grooming)*

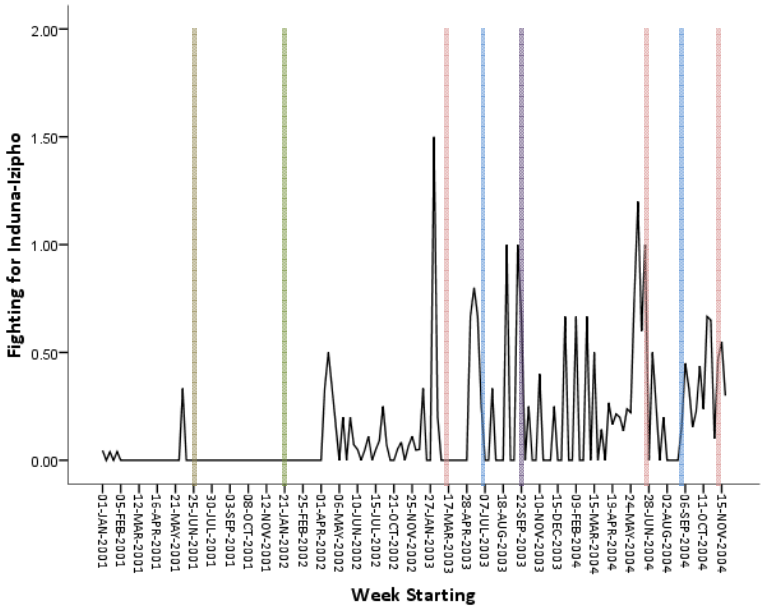
	Induna/ Ndonda	*Induna/ Izipho*	*Induna/ Nyomfoza*	*Ndonda/ Izipho*	*Ndonda/ Nyomfoza*	*Izipho/ Nyomfoza*
Induna/ Ndonda	--	r = 0.514 p < 0.001	r = 0.143 p = 0.062	r = 0.705 p < 0.001	r = 0.530 p < 0.001	r = 0.415 p < 0.001
Induna/ Izipho	r = 0.606 p < 0.001	--	r = 0.242 p = .001	r = 0.583 p < 0.001	r = 0.308 p < 0.001	r = 0.368 p < 0.001
Induna/ Nyomfoza	r = 0.412 p < 0.001	r = 0.531 p < 0.001	--	r = 0.228 p = 0.003	r = -0.007 p = 0.931	r = 0.650 p < 0.001
Ndonda/ Izipho	r = 0.364 p < 0.001	r = 0.426 p < 0.001	r = 0.114 p = 0.136	--	r = 0.494 p < 0.001	r = 0.425 p < 0.001
Ndonda/ Nyomfoza	r = 0.406 p < 0.001	r = 0.316 p < 0.001	r = 0.238 p = 0.002	r = 0.207 p = 0.007	--	r = 0.255 p < 0.001
Izipho/ Nyomfoza	r = 0.323 p < 0.001	r = 0.307 p < 0.001	r = 0.271 p < 0.001	r = 0.301 p < 0.001	r = 0.495 p < 0.001	--

Fighting

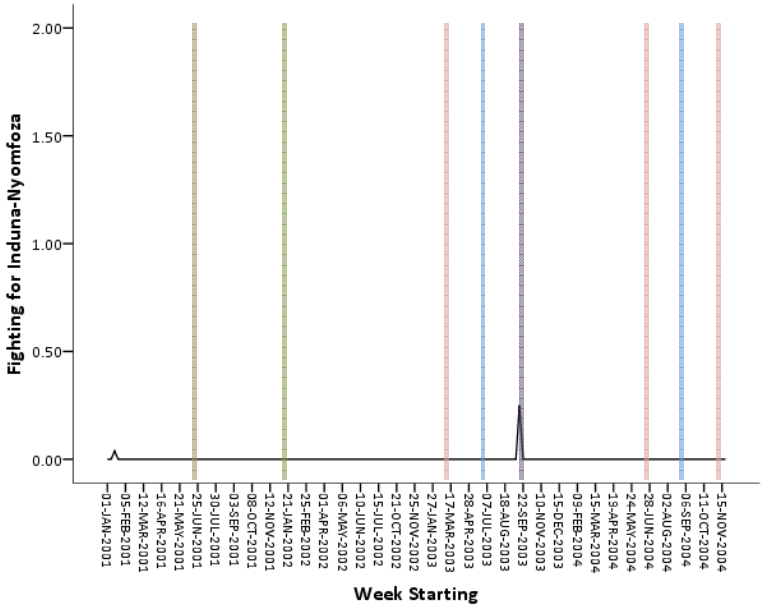
Fighting between pairs of males was examined to determine if there were particular pairs of cheetahs that showed higher levels of aggression towards one another. Analysis of pairs was performed to determine if there was a greater tolerance between related or unrelated males. Again, a key to the behavioural events within the facility was developed. As there are data included from 2003, additional bars have been added for events within this year. Continuous investigation was used, observing the cheetah for 2-8 hours per week during the breaks from the intensive data collection occurring in 2-3 month blocks. In order for the data to be comparable, behaviours have been converted to scores based on a percentage of hours that cheetahs were observed.



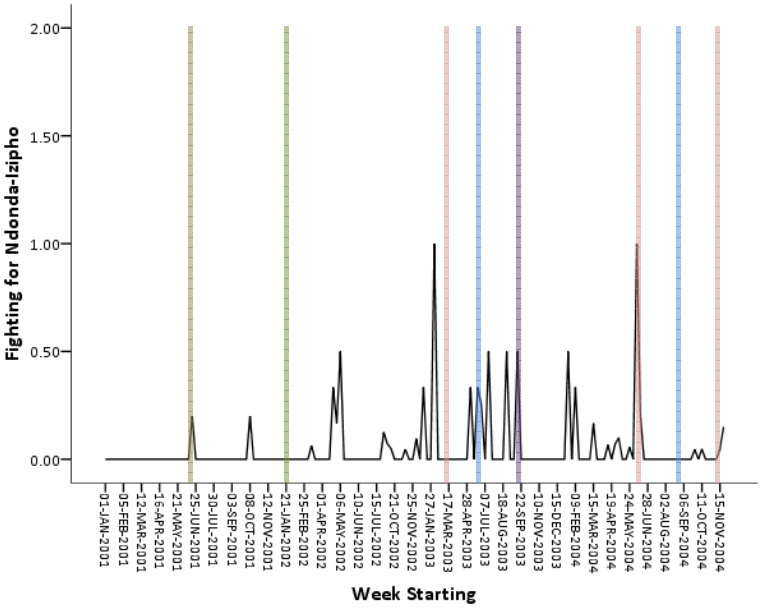
a) Induna/Ndonda



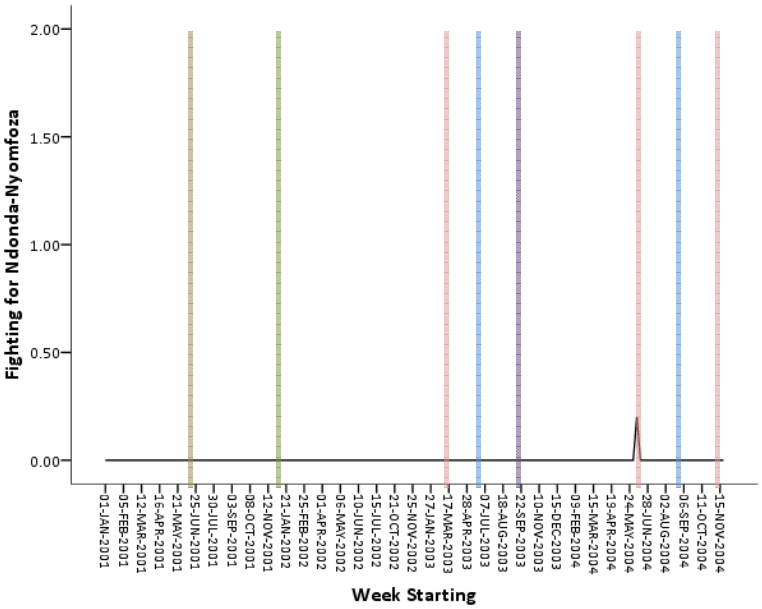
b) Induna/Izipho



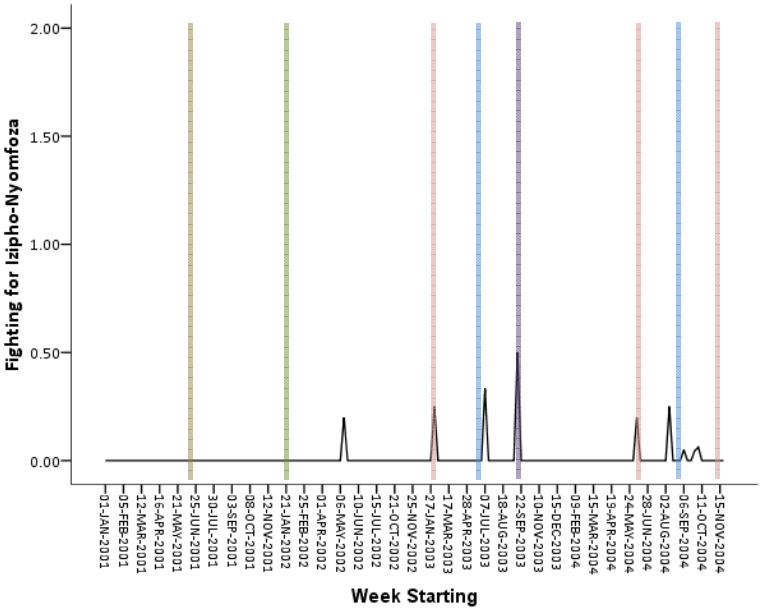
c) Induna/Nyomfoza



d) Ndonda/Izipho



e)Ndonda/Nyomfoza



f)Izipho/Nyomfoza

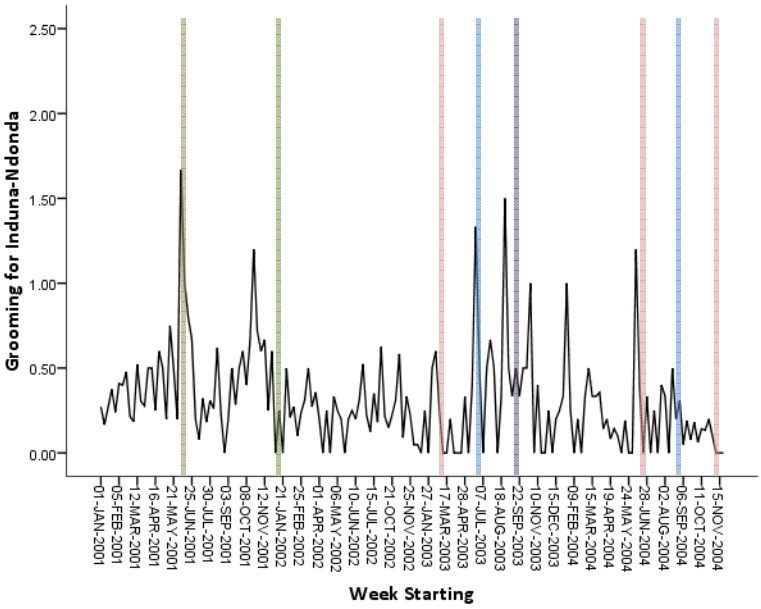
Figure 25. *Adjusted scores for Fighting observed for pairs of males over the study. Colour-coded vertical lines indicate key husbandry events within Monarto Zoological Park. Tan represents the point when males and females were moved to be housed separately; green represents the Artificial Insemination procedure; pink represents mating within the facility; blue represents births within the facility and purple represents when cubs were released into an adjoining yard to the males.*

Figure 25 illustrates Fighting for all of the pairs of male cheetah observed over the study period, with Fighting scores adjusted for amount of observation time. It can be seen that Fighting varies considerably between the different pairs, with high levels of Fighting observed between Induna/Ndonda, Induna/Izipho and Ndonda/Izipho. This high level of Fighting is between unrelated males and contrasts with lower levels of Fighting between Izipho, Nyomfoza and Umballa, the trio of brothers housed at Monarto Zoological Park. Interestingly, in the 625 hours of observations of these particular males, Izipho and Nyomfoza were observed Fighting 10 times, Izipho and Umballa were observed Fighting three times and Umballa and Nyomfoza were never seen Fighting. This can be contrasted to the unrelated males, where in over 1794 hours of observation there were 122 fights between Induna and Ndonda, 200 fights between Induna and Izipho and 45 fights between Ndonda and Izipho.

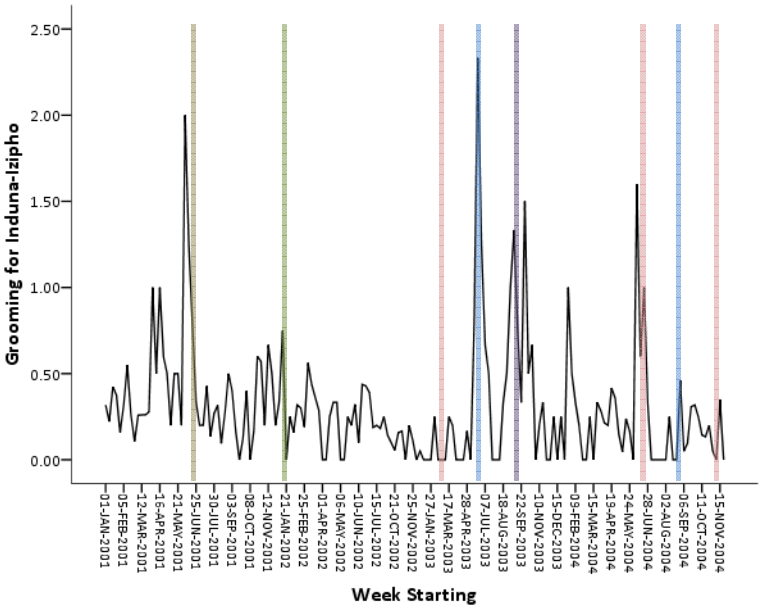
It was apparent that Induna was involved in the majority of Fighting observed within this group of cheetahs. Figure 25 a-c presents Fighting scores, adjusted for amount of observation time, for Induna with the other males. There are frequent spikes in this Fighting behaviour that appeared to correspond with husbandry and breeding events within the facility. There was a distinct increase in Fighting evident at the time of matings, firstly on the 7th of February 2003 and then again on the 11th of June 2004. Smaller peaks in Fighting were observed when cubs were born and when the cubs were released into the adjoining exhibit. These increases are evident for both the pairs of Induna/Ndonda and Induna/Izipho. At the beginning of the study, the majority of Induna's Fighting was with Ndonda. However this changed from mid-2002, when he began Fighting with Izipho. While initially only few fights were observed between this pair, (Figure 25b) there was a considerable increase in Fighting from mid-2002. Further increases in Fighting were observed in mid-2003, at approximately the time of the first birth within the facility, and continued to increase throughout 2004. In November 2004, Izipho mated for the first time.

Grooming

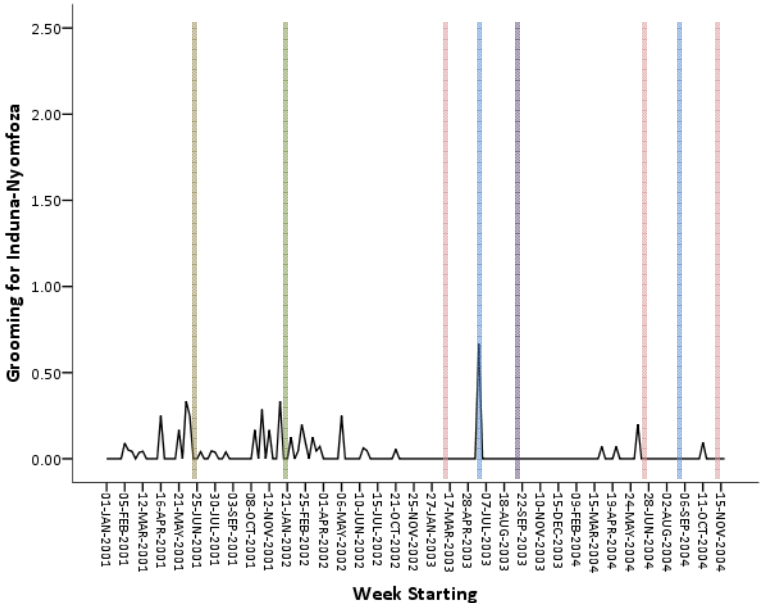
Grooming can be a key indicator of acceptance between males as seen in studies of wild cheetahs (Caro 1994). Grooming between pairs of males was also analysed to determine which cheetahs were the most tolerant of others and to identify any differences between related and unrelated males in Grooming.



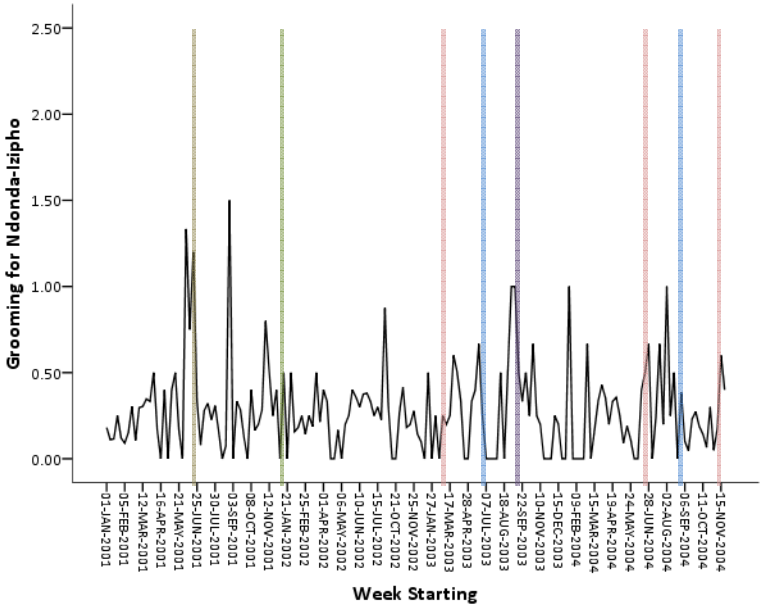
a) Induna/Ndonda



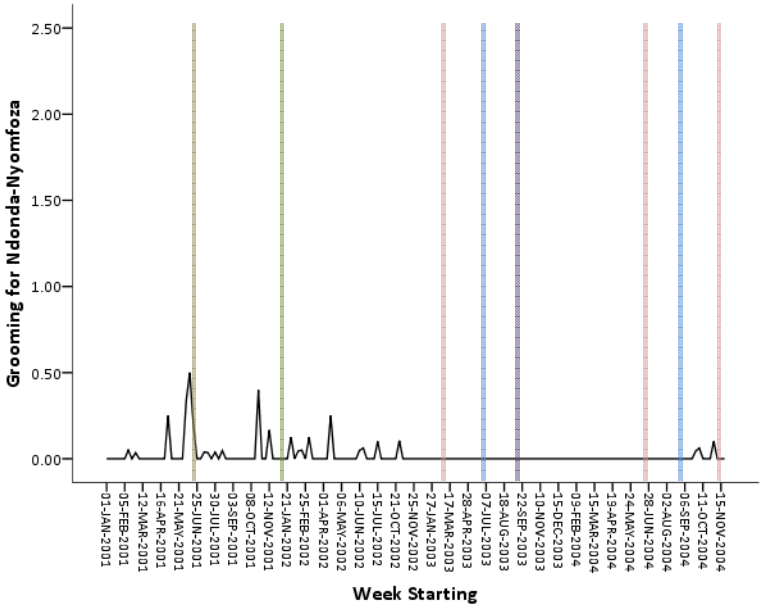
b) Induna/Izipho



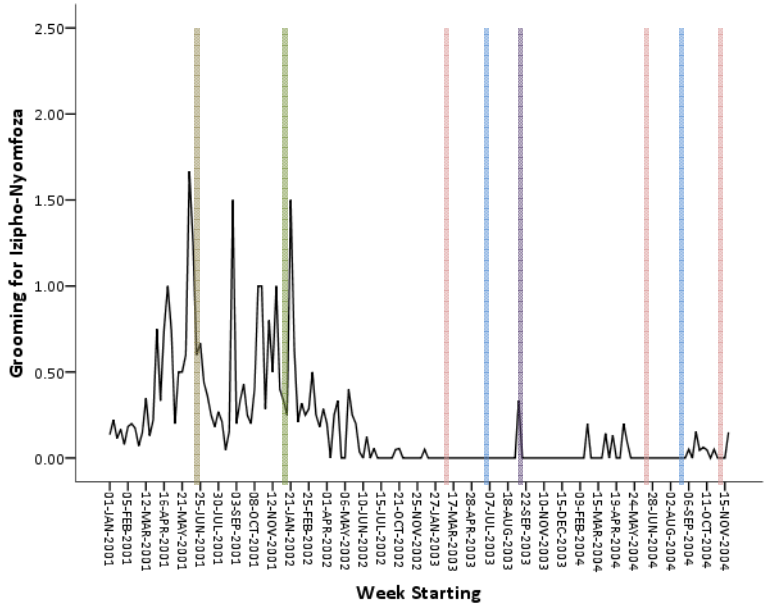
c) Induna/Nyomfoza



d) Induna/Izipho



e) Ndonda/Nyomfoza



f) Izipho/Nyomfoza

Figure 26. *Adjusted scores for Grooming observed for pairs of males over the study. Colour-coded vertical lines indicate key husbandry events within Monarto Zoological Park. Tan represents the point when males and females were moved to be housed separately; green represents the Artificial Insemination procedure; pink represents mating within the facility; blue represents births within the facility and purple represents when cubs were released into an adjoining yard to the males.*

High levels of Grooming were observed for many pairs of male cheetahs. Figure 26 illustrates the complex relationships that were observed within cheetahs in this behaviour. All pairs of males displayed some involvement in mutual Grooming, but the rates in which males were groomed varied widely. Differences occurred between different pairs of males and the rate of Grooming also changed over time. Scores for Grooming were adjusted for the amount of observation time.

Again, as was seen for Fighting, significant increases in Grooming coincided with a number of husbandry events within the facility. It should be noted that there was an increase in Grooming for pairs at the time the sexes were separated, with a spike for all pairs. Further spikes in behaviour appeared to coincide with the birth and matings within the facility.

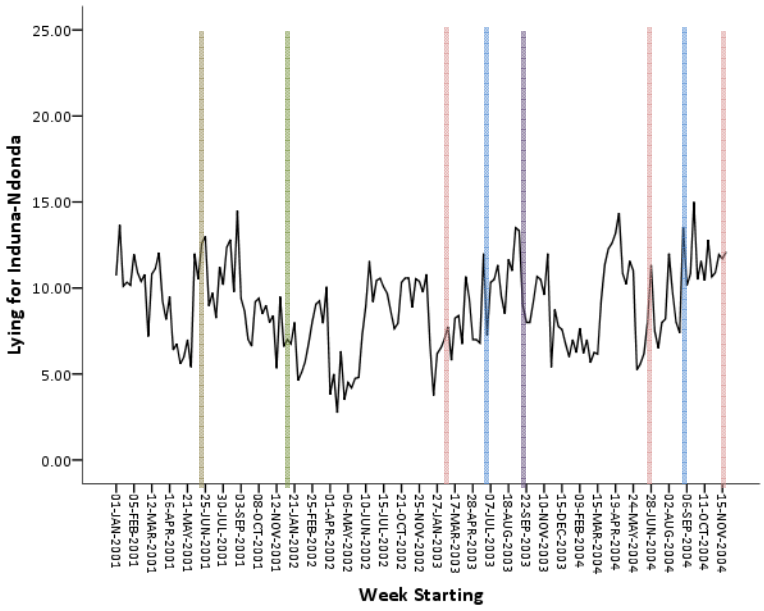
There were considerable differences in the Grooming relationships depending on individuals. Figure 26 a-c displays the Grooming involving Induna. Grooming remains relatively steady over the study period, and Induna is in relatively equal Grooming bouts with Ndonda and Izipho.

Induna's consistency is in stark contrast to the Grooming relationships involving Nyomfoza where there was a considerable decline in Grooming behaviour over the study (Figure 26 c, e and f). By 2004 Nyomfoza was virtually excluded from all mutual Grooming sessions. It can be seen that even his brother Izipho was excluding him from Grooming in the latter part of the study (Figure 26 f). Where Grooming was seen at a relatively high rate in 2001, by the end of 2004 Nyomfoza had been excluded from Grooming altogether. While for many of the unrelated pairs, Grooming remained consistent, there was a marked reduction in the rate of Grooming between the brothers over the study.

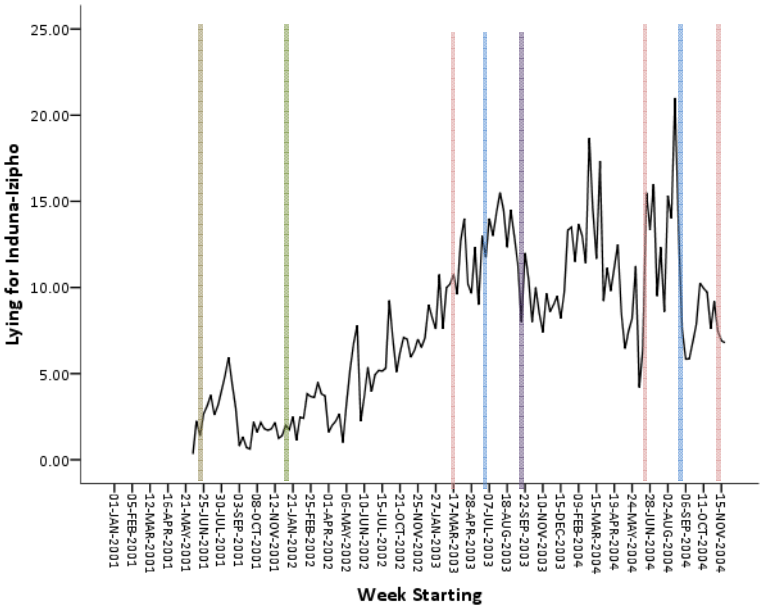
Lying Together

Relationships between pairs and trios of males for Lying together were then analysed. Combinations were examined to establish the levels of acceptance between males and to determine any differences between related and unrelated males. Not all pairs or trios were analysed as some combinations were either not observed or only observed very infrequently.

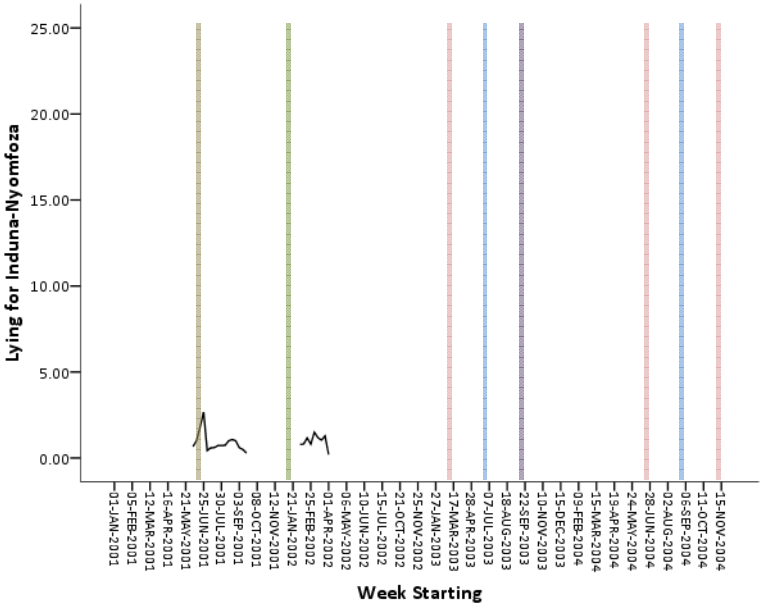
Again, as with Grooming, the relationships between pairs of males Lying together was highly complex. However, there were some very distinct trends within the data. Figure 27 depicts the relationships between males for Lying over the study.



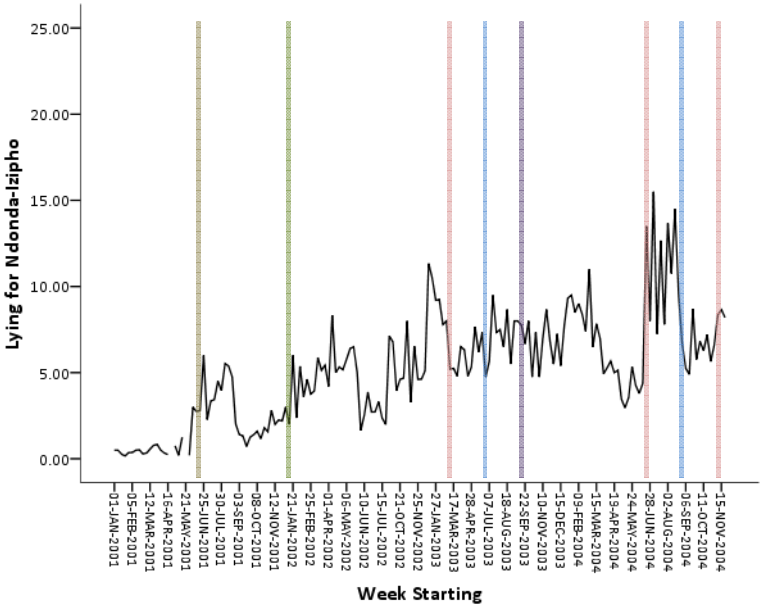
a) Induna/Ndonda



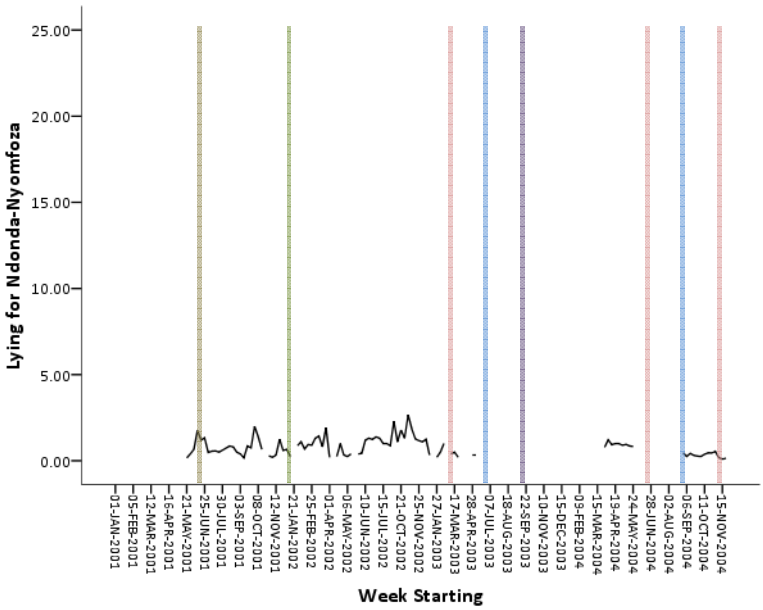
b) Induna/Izipho



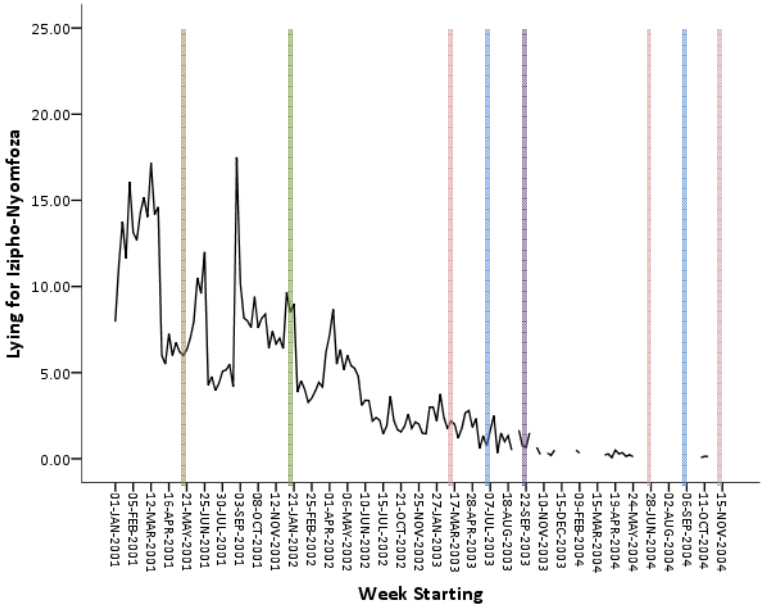
c) Induna/Nyomfoza



d) Ndonda/Izipho



e) Ndonda/Nyomfoza



f) Izipho/Nyomfoza

Figure 27. *Adjusted scores for Lying observed for pairs of males over the study. Colour-coded vertical lines indicate key husbandry events within Monarto Zoological Park. Tan represents the point when males and females were moved to be housed separately; green represents the Artificial Insemination procedure; pink represents mating within the facility; blue represents births within the facility and purple represents when cubs were released into an adjoining yard to the males.*

Lying together illustrates the complexity of the relationships within the group of male cheetahs. There were strong increases and decreases in Lying over the study for the different pairs of cheetahs. This was quite different from the other behaviours with Lying displaying long term gradual trends rather than spiked variation (Figure 27).

There are also considerable differences between scores for different pairs of cheetahs, with some pairs displaying high scores for Lying and other pairs rarely observed together. The relationships were explored further, examining individual pairs and trios.

Figure 27a depicts the relationship between Induna and Ndonda on the behaviour of Lying. The frequency of this behaviour is relatively high over the study with occasional dips, particularly at the beginning of 2002 and again towards the end of 2003 start of 2004. These results contrast with the data for Lying between Induna and Izipho. Figure 27b shows the change in this behaviour for the pair of males over the study with no instances of Lying until July 2001. From early 2002 there is a steady increase in Induna and Izipho Lying together, with a peak in August 2004.

Again Figure 27d indicates a steady rise in Lying for Ndonda and Izipho. While this increase is not as pronounced as that seen for Induna and Izipho, they appeared to spend more time Lying from mid-2002 through to the end of 2004.This relationship was explored further by examining these males as a trio. Figure 28 illustrates the scores for the males Induna, Ndonda and Izipho when Lying as a trio. The same trend is evident as in the pairs. The occurrence of Lying behaviour was minimal until July 2001, when there was a sudden increase. The behaviour then steadily increased from mid-2002 until a peak during late July/August 2004.

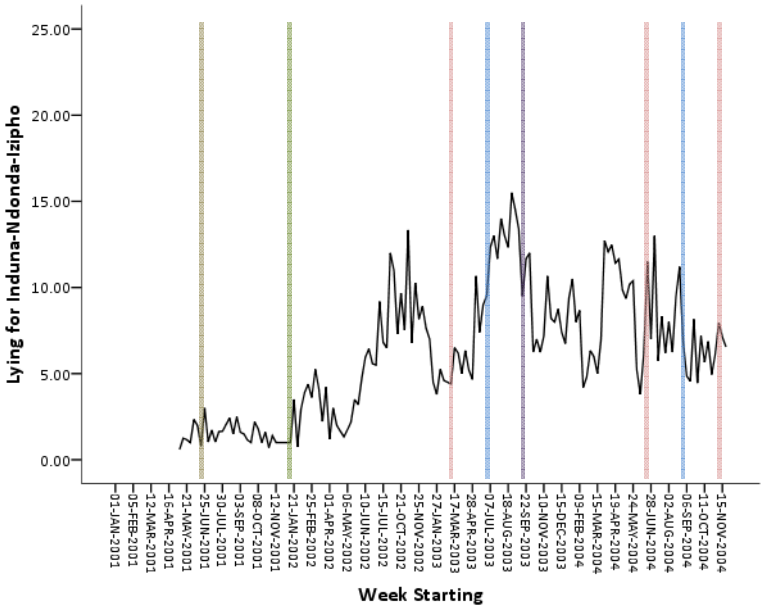


Figure 28. *Adjusted scores for Lying observed for between Induna, Ndonda and Izipho over the study. Colour-coded vertical lines indicate key husbandry events within Monarto Zoological Park. Tan represents the point when males and females were*

moved to be housed separately; green represents the Artificial Insemination procedure; pink represents mating within the facility; blue represents births within the facility and purple represents when cubs were released into an adjoining yard to the males.

Finally, Figure 27f illustrates the relationship for Lying between Izipho and Nyomfoza. It can be seen to show a very different trend than what was seen for the other pairs of males. Initially, the behaviour was observed frequently, but the instances of Lying reduced dramatically over the study. By the beginning of 2002 the scores were halved, and continued to decrease until the first observation day on the 1st of September 2003 where Izipho and Nyomfoza were not recorded to lay together.

Discussion

While male cheetahs have been studied extensively in the wild (Caro 1989, 1994, Caro & Collins 1987a&b, Durant 2000 and Durant *et al.* 2007) there has been little research on their behaviour in captivity (Caro 1993 and Ruiz *et al.* 1998). Studies on the behaviour of captive cheetahs have focussed on the female, examining receptivity and reproductive behaviours (Wielebnowski 1996, 1999) as well as hormonal assays and reproductive biology (Asa *et al.* 1992, Wildt *et al.* 1993 and Brown & Wielebnowski 1998). Research on male cheetahs in the wild suggests varying levels of sociality, with a high proportion of males living together in coalitions (Caro & Collins 1986, Caro 1994 and Gottelli *et al.* 2007). This sociality appears to play an important role in their welfare and survival, with group living males being rated as healthier and having much greater chance of holding territories and gaining access to females than single living males or 'floaters' (Caro & Collins 1987a). The factors behind group living in male cheetahs are still not fully understood, with multiple reasons for sociality being proposed (Caro 1994). Even less is known about how these factors operate in captive environments. The current study aimed to identify and record the behaviour of captive male cheetahs and determine if they formed coalitions like their wild counterparts. Observation of the general behaviour of captive males provides information on the dynamics of group living, including the formation of hierarchies and the reasons for the inclusion or exclusion of particular males.

Principal Component Analysis and Correlated Behaviour

In my initial analyses of the male cheetahs' behaviour, I found high levels of variability in the frequencies of behaviours with fluctuations seen over short periods of time, such as weeks, as well as over longer periods of time, spanning years. The frequency and rate of behaviours fluctuated differently for different individuals. I used Principal Component Analysis (PCA) to examine the frequencies and relationships of behaviours and uncovered some interesting patterns.

Firstly, it was observed that principal components compositions were very different between males. There were some similarities in the behavioural composition of PC 1, but the remaining three principal components analyses showed that there were complex differences between the behaviours loading on each separate component. There were also differences between positive and negative relationships within the components.

Fighting was consistently observed positively loading on to PC 1, suggesting that there may be a common driver behind these behaviours associated with aggression. However, all other behaviours in this component vary between the males, suggesting that if there is a common driver, all males have different ways of responding to PC 1. Principal component 1 explained varying levels of male behaviour, with 10% of variation explained for Induna through to 17.9% of variation explained for Izipho. Behaviours loading on to this component varied among males, as did the trend of behaviour. Induna and Izipho showed increases in behaviour over the sampling periods in 2004, Ndonda's results were stable over the years, where as Nyomfoza's results show greater variation within the individual behaviours loaded on to PC1.

I observed considerable variation within the remaining principal components. The results from PC 2, 3 and 4 for males indicated marked differences between all individuals, with variables failing to correlate. There was a considerably higher level of structuring to the three brothers' behaviours, with significant loadings on a number of variables and positive and negative relationships observed within each principal component.

Each male displayed a considerable difference in their behavioural loadings for components two to four. Those differences are also reflected in the cumulative percentages of variation explained by the principal components, ranging from 34% for Induna to 45.4% for Nyomfoza. The principal components analysis defined Nyomfoza as a somewhat unique male among the group, showing very different behaviours

loading on to all of his components and very different patterns in the dispersal of scores in those components.

Relationships Between Male Cheetahs: Coalition Formation

I observed many relationships within the group of five male cheetahs housed at Monarto Zoological Park. Initially, due to zoo practices, the unrelated males Induna and Ndonda were paired together and the three brothers were housed together. The relationship between these two males was relatively stable – while they are not related, they had been housed together for the longest period, being together since their arrival at Monarto Zoological Park in 1999. At the beginning of July 2001, all five males were housed together and all females were removed. There was a considerable rise in the majority of behaviours at this time. After an initial period of settling, behaviours returned to levels previously observed.

The males developed into a loose form of coalition. All five males were observed frequently Lying together, but there appeared to be some division in the group with Induna and Ndonda often forming a pair without the three brothers. As a pair and as a trio, members of these two groups were observed to groom other members within the group frequently. Yet there were only infrequent observations of Grooming seen between individuals between these two groups.

Each male displayed varying levels of territory marking. As Induna displayed the most Spraying and territorial behaviour, and was the predominant individual involved in fights among males, he was considered the dominant male within this newly formed coalition. Ndonda and Umballa also displayed elevated levels of these behaviours, while Izipho and Nyomfoza failed to show territory marking or aggressive behaviour. Increased Grooming was observed between brothers compared to the unrelated males.

At the end of 2001, this coalition of males was fractured when Umballa was sent to New Zealand. This action appeared to cause a number of behavioural changes within all of the males in the group. Induna showed changes in his Spraying behaviour, and increased levels of Spraying and Grooming were observed in Ndonda. By mid-way through 2002 changes were also evident with Izipho's behaviour. While previously he was not noted to spray or fight, these behaviours steadily increased over the study. Increased Grooming and Lying together was also noted for Izipho. Concurrent to these changes, variations were also noted for Nyomfoza. He gradually became excluded from

the remaining males, with instances of Lying and Grooming ceasing altogether. The behaviours of Fighting, Grooming and Lying are discussed further.

I also examined key events within the facility as possible drivers of male behaviour There were a number of changes with female cheetahs held at Monarto Zoological Park that appeared to correspond to changes in male behaviour. Male behavioural changes were particularly related to mating and births within the facility, but there were also changes that corresponded with other husbandry events.

Fluctuations in male behaviour were observed when males and females were initially separated. This was expected, as males had their first opportunity to establish in an all-male group with associated changes in behaviours. Males displayed considerably more Spraying and Grooming behaviour at this time. Spikes in the overall behavioural patterns were observed, with males appearing to take time to adjust to living in an all-male group. These fluctuations in behaviour settled approximately 2-3 months after the initial peak in activity.

Male behaviour also changed substantially when the artificial insemination procedure was performed. This procedure also coincided with the removal of Umballa from the facility. Changes in behaviour were obvious during early 2002. As seen by Earley and Dugatkin (2006) with their work on swordfish, dominance orders can emerge after long static periods. The males had appeared to be settled in their behaviour. However, by sending Umballa out of the facility, the social order seemingly became unstable and was followed by a period of readjustment. At this time there was increased Spraying and Tail Twitches and the patterns of male behaviour appeared to change considerably.

Further changes were observed when females were moved in and out of the facility including when Bopha was sent to Victoria, and when Zilkaat was introduced for two month periods at the end of 2001 and 2002. Fluctuations in behaviour were also observed when the females were isolated from each other during the male receptivity experiments (see Chapter 6). Through a number of male-female introductions, mating and births occurred with indications of impacts on male behaviours. These were further emphasised by a change in behaviour that was linked to the release of a litter of cubs into the yard adjoining the main enclosure.

Key Behaviours

Males were assessed based on the relationships they held within pairs and trios within the facility. Relationships between Induna and Ndonda remained relatively stable over the study. However, there was a distinct change in Izipho's behaviour during mid-2002 when he was observed Fighting for the first time. Fighting increased through to 2004. The sudden onset of Fighting for Izipho may have been caused by an interest in courtship and mating. Through the male receptivity experiments run concurrently to this study, (see Chapter 6), Izipho was given access to receptive female cheetahs. It is particularly noteworthy that peaks in Fighting with Izipho coincided with key husbandry events, including both mating and births.

Peaks of behaviour at these times also occurred for Induna and Ndonda. The trend of this behaviour appears to fluctuate frequently, with changes happening rapidly. Spikes in Fighting behaviour coincided with events relating to the females, with increases seen particularly at times of mating, birth and also when cubs were released into their exhibit.

Grooming was relatively common among males until mid to late 2002. By 2004 the behaviour had almost ceased. Grooming had been relatively high between Izipho and Nyomfoza during 2001. However, from mid-2002 rates of Grooming between these two males dropped considerably. By 2004 Nyomfoza was excluded from almost all Grooming activities.

As seen for Fighting, Grooming behaviour appears in spikes with the frequency of behaviour fluctuating very quickly at times during the study. Peaks occurred when males were separated from females, when Umballa was removed from the group and at times of mating and birth. There were variations between pairs, with different pairs seeming to respond to different events.

The behaviour Lying was the most distinct and was unlike any of the other behaviour patterns. Observations for this behaviour changed slowly over the study, and did not spike like the other behaviours. There was an overall reduction of Lying behaviour at the beginning of 2002. While high frequencies were initially recorded between Izipho and Nyomfoza, this changed over the study. The change in trend can possibly be attributed to the breaking up of the male coalition when Umballa was sent out of the facility. Changes to a hierarchy after a long static period can cause a number of behavioural fluctuations (Ensminger & Crowley 2007). This change could possibly be the contributing factor for the substantial change observed in the males' behaviour.

Nyomfoza: Declining Health and Change of Status

While many similar patterns of behaviour were observed for the males, Nyomfoza's behaviour was the most distinct. Nyomfoza had repeated fur ball problems, causing gastric distress prior to the study and early during 2001. These problems would result in him being kept in the night-yard on occasion for veterinary treatment. He was also injured during early 2002. This injury kept him in the night-yard for a week. Due to Nyomfoza showing signs of severe distress on being left alone, he was not isolated from all the males. His brother Izipho was removed from the other males and was kept with him for company.

During late 2002 it was apparent that Nyomfoza was being excluded from the coalition to effectively become a 'floater' as described by Caro and Collins (1987a) and Caro (1994). Unlike Caro, who could not be sure whether ill health or 'floating' came first, for Nyomfoza the sequence of events was clearer. He was initially a member of the coalition, albeit a subordinate one, but as his health declined over the study he was slowly excluded from the group. By 2003 he was excluded from most social activity, including behaviours such as Lying and Grooming. By 2004 Nyomfoza chose to remove himself from the other males, electing to sit away from them when in the main enclosure.

Trio of Males

While Induna, Ndonda and Izipho were all unrelated, they formed a close bond. By 2004 this coalition had fully developed and they spent a considerable amount of time Lying and Grooming. This relationship was very different to the relationship observed between the brothers Izipho and Nyomfoza. Initially, while the third brother Umballa was at MZP, they spent a substantial amount of time together. However, after Umballa was sent to New Zealand, the relationship between Izipho and Nyomfoza began to deteriorate. Further illness in Nyomfoza appeared to break the bonds between the two completely. Izipho moved away from Nyomfoza, choosing to spend his time with Induna and Ndonda. While Induna, Ndonda and Izipho were past the age Caro (1994) believed is suitable for coalition formation, they appeared to bond with each other. By 2004, Grooming between the males was observed, a behaviour Caro (1994) reported as an indicator of acceptance of a new member.

There are a number of possible reasons why Izipho chose to bond with Induna and Ndonda rather than his brother. Firstly, with changes to the group (when Umballa

was removed) there was a period of re-adjustment and re-ordering of the males. Secondly, Induna and Ndonda were a stronger choice of allies than his sickly brother Nyomfoza, hence he may have chosen to align himself with the stronger males. Thirdly it is possible that Nyomfoza was electing to remove himself due to his declining health, leaving Izipho the choice of remaining solitary or choosing to spend time with the remaining males. One further possible explanation for the changes in Izipho's behaviour throughout 2002 concerns the male receptivity trials (see Chapter 6). Izipho began to display an interest in females throughout the receptivity trials. At this time the levels of Fighting and Lying with males also increased. Izipho changed his social bonds to Induna and Ndonda instead of his brother Nyomfoza, which resulted in Nyomfoza being ostracised from the coalition. The change in Izipho's behaviour and his social groupings may have all been triggered by movement of Umballa out of the facility. Umballa's removal changed the group dynamics.

Overall, there was a considerable change in the behaviour of this group of cheetahs from mid-2002. As will be explored further in Chapter 6, this also coincided with Izipho's increased interest in females.

Conclusions

Over the study period males showed a higher and more complex patterning in their behaviour compared to females. All males displayed varying behavioural trends, suggesting that if there was a similar driver to behaviours, males responded differently to that driver. Some similarities were noted for the brothers, but Nyomfoza was unique among the males and displayed a very different behavioural pattern. Males appeared to form coalitions which changed during the study period. Induna and Ndonda spent the longest time together without interruption and initially formed a pair. The increased levels of spraying and aggression displayed by Induna suggested he was the dominant male in the pair. This dominance was later reflected in his breeding status. Izipho then formed a group with Induna and Ndonda and this is seen in a steady increase in Lying behaviour for this trio.

The dynamics of the male group changed over the study. Izipho in particular changed his alliance during the study, which appeared to coincide with the removal of Umballa. Izipho could either remain with his brother Nyomfoza or bond with the dominant male Induna, already paired with Ndonda. Izipho's alliance shifted to Induna and Ndonda and hence Nyomfoza became a 'floater'. Nyomfoza's multiple health issues may have played a significant role in this change.

Many patterns of male behaviour appeared to be related to key events in the facility such as husbandry changes and mating. Behavioural trends showed great variability over the study. Behaviours either occurred as sharp spikes, with behaviour frequencies changing rapidly, or as long, slow trends, with frequencies of observations changing over months or years.

Behaviours such as Fighting and Grooming occurred as spikes. Frequencies of these behaviours changed rapidly, and peaks in these behaviours corresponded to mating and births in the facility. The behaviour of Lying was very different to other behaviours with increasing/decreasing trends slowly changing over time. Lying is very different as it becomes stable over time, while Fighting and Grooming were highly variable. Overall, it was apparent that males would be seen Lying with each other much sooner than they would groom each other. The same result was reported by Caro (1994) in his wild studies. Fighting occurred regularly and it was apparent that the males were still sorting out the hierarchy. Fighting and Grooming increased for the trio towards the end of the study, suggesting that the males were reorganising their group. Fighting between Induna and Izipho began in mid-2002 and increased through 2003-2004. Interestingly this increase in Fighting led up to Izipho mating in November 2004. Aggression-related behavioural variation in males, but not females, is not surprising given that males live in coalitions where we would expect to see dominance relationships that may influence mating.

Until the current study, we had little understanding of how male cheetahs socialise in captivity, extrapolating information from various wild studies (Caro & Collins 1986, 1987a and Caro 1989, 1994). This study on captive male cheetahs shows that not only do coalitions of males form in captivity, but that the relationships within these coalitions vary. Mature unrelated males, past the age of 20 months, were seen to not only to accept the presence of each other, but were seen Lying and Grooming one another. The ages of these males were considerably older than those previously reported from studies on wild males (Caro 1994), suggesting that older males can be safely introduced to form coalitions in captivity. Males were also seen to vary in their social status in captivity, with the majority of males forming a coalition yet one male becoming a ‘floater’. Considerably different behavioural patterns were observed for this male, who over the study chose areas of seclusion to remove himself from other males. While initially a member of the coalition, repeated illnesses and injury resulted in his exclusion from grooming activities and therefore isolation resulted.

Management and husbandry practices can have a major impact on the behaviour of captive cheetahs. Housing decisions can dramatically affect the social dynamics and behaviour of male cheetahs. The current study shows that while aggression-related behaviour was common and coalitions were dynamic, this kind of behaviour is natural, given the existence of coalitions in the wild. Husbandry practices may need to allow aggressive behaviour and the formation of coalitions as these seem to be elements that are observed in wild cheetahs. Allowing captive cheetahs to act upon the same social instincts as wild cheetahs appears to be beneficial and may even play a role in enhancing breeding in captivity.

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