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

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Chapter VII

General Discussion

The cheetah (*Acinonyx jubatus*) has lived in association with humans for thousands of years (Hunter & Hamman 2003). The earliest records depict their use as companion animals and game hunters by the Sumerians and Egyptians around 3000 BC (Marker-Kraus 1997). However, while cheetahs have had a long association with humankind, relatively little study has been performed on their needs in captivity (Wildt *et al.* 1993). The cheetah has been officially kept in zoological collections since 1829 (O'Brien *et al.* 1985). Since this time, only a small proportion of research has been performed on the cheetah compared to many other captive species. The primary focus of this research has been the physiology and genetics of the cheetah (O'Brien *et al.* 1985 and Wildt e*t al.* 1993). Limited work has been undertaken on captive behaviour of cheetahs (Caro 1993, Wielebnowski & Brown 1998, Wielebnowski 1999 and McKay 2003), as extensive behavioural studies on cheetahs in the wild are used to understand their needs in captivity (Eaton 1972, Frame & Frame 1980, Caro & Collins 1986, 1987a&b, Laurenson *et al.* 1992, Caro 1994, Kelly *et al.* 1998, Durant 2000, Durant *et al.* 2007 and Gottelli *et al.* 2007). There are considerable differences between wild and captive populations in terms of breeding success and there are still vast gaps in the knowledge of captive behaviour of cheetahs. These are particularly evident in the behaviour of male cheetahs (Caro 1993 and Wildt *et al.* 1993) and reproductive behaviour (Wielebnowski & Brown 1998).

The History of Breeding Cheetahs in Captivity

Throughout the early ages of interactions between humans and cheetahs, little focus was placed on the requirements of captive cheetahs or their reproductive biology (Divyabhanusinh, 2002 and Hunter & Hamman 2003). Births in captivity were rare, with the first reported birth in 1956 (Florio & Spinelli 1967). Varying husbandry practices were used to attempt to breed cheetahs (Vallat 1970, Rawlins 1972 and Benzon & Smith 1975), but relatively few organisations have had any real success until the last decade.

Detailed studbooks have been kept to manage the captive populations of cheetahs (Marker 2000). In the 1999 Studbook, Marker (2000) reports that only 48 animals (22:26, male:female) had successfully bred of the 1296 (668:620:8, male:female:unknown) cheetahs held in 272 captive facilities, even though most facilities had intended to breed cheetahs during the year. These statistics continue through the 2000s, where approximately 4% of captive cheetahs successfully bred each year, with only 3.4% in 2000 (Marker 2002), 5% in 2001 (Marker 2002) and 4.6% in

2005 (Marker *et al.* 2007). The 2005 studbook reports that 6.4% of the captive female cheetahs worldwide have produced at least one litter of cubs. These reports contrast to the data from the wild, where it is reported that 95% of females produce at least one litter in their lifetime (Laurenson *et al.* 1992 and Caro 1994).

Research from Wild Populations

Research on wild cheetahs had been extensive and, over the past 40 years, considerable effort and resources have been placed into the study of reproductive biology and behaviour of wild cheetahs on the Serengeti Plains, Tanzania (Frame & Frame 1980, O'Brien *et al.* 1985, 1986, Laurenson *et al.* 1992, Caro 1994, Kelly *et al.* 1998, Kelly & Durant 2000, Durant *et al.* 2007 and Gottelli *et al.* 2007). This research has included physiological tests, including seminal quality and genetics (O'Brien *et al.* 1985, 1986) and various longitudinal behavioural studies (Caro 1994 and Durant *et al.* 2007). These behavioural studies have focused on male territoriality (Caro & Collins 1986, 1987a&b), sociality (Caro 1994) as well as mother–cub relationships and cub mortality (Laurenson *et al.* 1992, Laurenson 1993 and Caro 1994). Many of these studies focus on females with young or male social behaviour. However, male/female interactions have been limited because they are very difficult to observe in the wild (Gottelli *et al.* 2007). Indeed Caro (1994) and Hunter (pers. comm. 26 July 2002) report never seeing a natural mating even though both have spent more than a decade researching wild cheetahs.

The information that has been obtained from these longitudinal studies is vital to aid in the understanding of a species' population dynamics and the factors that influence survival (Soulé 1986). However, not all information can be extrapolated from the wild to captive populations. Further research is needed to understand not only the differences in these environments, but to examine behaviours that cannot be observed in wild populations.

The Current Study

A major goal of the current study was to analyse the behaviour of captive cheetahs. Long term studies on animals are rare (Durant *et al.* 2007). Analysis and records from captive facilities are rarely compiled over time (Augustus *et al.* 2006 and Bertschinger *et al.* 2008), except in studbooks (Marker 2000, Marker *et al.* 2007 and Marker & Echement 2010). This longitudinal study was required to examine a wide range of behaviours and develop an extensive analysis of the cheetah's behavioural repertoire in

captivity. Cheetahs at MZP were studied for approximately four years and four main areas of inquiry were selected as described below.

Ethogram

I developed the ethogram (Chapter 3) to provide a description of behaviours that could be used in subsequent analyses within this study and then easily related to past or future studies. A total of 70 behaviours and 19 behavioural states were recorded. The initial statistical analysis illustrated that the behaviour of cheetahs was complex. Behaviour accumulation curves (BAC) were used to estimate what proportion of the total repertoire was recorded. The initial analysis was not adequate to reveal the entire behavioural repertoire, but the scores were close to the asymptotes as was predicted.

In the initial study, I found large differences between male and female behaviour, with males displaying 48 behaviours compared to 38 for females. While males generally had a larger behavioural repertoire over the study, there was one male which had a substantially lower score, with only 33 behaviours observed. This repertoire was equal to that seen by the lowest scoring female and suggests there is considerable difference between animals over observations.

The descriptive ethogram was continually updated during my data collection to improve its quality and comprehensiveness. Behaviours such as courtship and mating were not observed in the initial analysis, but were added later to the descriptive ethogram.

Behavioural Cues to Oestrus in Captive Female Cheetahs

I studied the behaviour of female cheetahs in Chapter 4. PCA was used to analyse the extensive information recorded for females. This analysis highlighted some very interesting behavioural patterns, particularly within PC1. Here I observed that the principal behaviours loading on to this component were the same for the females and these were Tail Rolling and Tail Swishing. These behaviours were highly correlated and accounted for over 20% of the total behavioural variability observed in female cheetahs. The remaining PC's showed high levels of variability between individuals.

In further examination of female behaviour I found that Tail Rolling and Tail Swishing showed strongly cyclic patterns of expression. For Pinda in particular, this cyclicity occurred for more than a year of intense observation. Lula showed variation in her patterns of expression. Bouts of Tail Rolling occurred at different times within the study and were linked to key husbandry events within the facility. Increases in Tail

Rolling were observed when two females were given hormone therapy for an artificial insemination attempt. Changes were also noted when other females were moved in and out of the facility. Lula was successfully mated when at a peak in Tail Rolling and it was concluded that this behaviour is a possible cue to receptivity in female cheetahs.

As cyclical expression of Tail Rolling was approximately half a lunar month in length, I examined the data to see whether the lunar cycle may have provided cues for the oestral cycle. I compared Tail Rolling with the luminescence of the moon to rule out any possible effect on behaviour. This analysis suggested that the lunar cycle was not a driver for Tail Rolling cyclicity and that this behaviour was not temporally synchronous between the females.

I observed, in particular with Lula and to an extent with Pinda, that social housing had an impact on Tail Rolling. When housed either with males or females, the cyclicity of Tail Rolling behaviour declined or disappeared and the frequency of Tail Rolling observations was considerably reduced. This reduction in Tail Rolling was seen when Lula was housed either with males or other females. Even when Lula was held in an adjoining enclosure to Bopha or Zilkaat, without a visual barrier, her Tail Rolling behaviour appeared to be suppressed.

This suppression of behaviour was also seen to a lesser degree with Pinda. For this animal it appeared that Tail Rolling was suppressed while she was housed with male and female cheetahs. However, the same level of suppression was not observed when she was being housed in adjoining yards with some visual access to other females. This housing situation appeared to have little or no impact on her behaviour.

This study provides evidence for a hierarchical basis for oestrus suppression. Previous research (Wielebnowski & Brown, 1998) initially hypothesised that oestrus suppression was equal for all females in a facility. Wielebnowski *et al.* (2002) extended this examination, finding that some females appear to be totally suppressed while others showed minimal effect from being housed together or in close proximity. The results of this study support the latter finding. The hierarchical suppression of oestrus has further implications for captive management, supporting the idea that cheetahs should be housed with their natural social requirements in mind, which does not involve adult female cohabitation.

Behaviour of Male Cheetahs and the Impacts of Captive Husbandry

A similar analysis for the behaviour of male cheetahs was outlined in Chapter 5. I used PCA to determine any key behaviours in the repertoire of five males. Male behaviour

was shown to be highly complex, with considerably more variation among individuals than was seen in the females. However, as I found for females, PC1 showed some similarity among the males, though to a lesser degree. While the other behaviours loading on to this component varied for the males, four of the five males displayed high positive scores for Fighting within this component. However, unlike females, male cyclicity was not observed throughout this study, with the exception of behaviours that appeared to be responses to female oestrus (see below).

I examined male behaviour for relationships within pairs and trios. There were large changes over the study, with patterns of both long steady trends (increases or decreases) in behaviour or short spikes in behaviours relating to husbandry events. These patterns of behavioural change occurred at times of key events within the facility, such as the removal of animals, mating and births. Males appeared to accept levels of sociality within the group and changes in the behaviour of male pairs were noted over the study.

My analysis showed distinct changes in the behaviour of two males over the study, Izipho and Nyomfoza. These two males were brothers and their behavioural patterns were very similar at the beginning of the study when housed with a third brother Umballa. The three males were observed to spend considerable time together Lying and Grooming. However, as the study progressed Umballa was removed from the facility. From this time, Izipho showed a preference to socialise with the remaining males, Induna and Ndonda rather than Nyomfoza. It was also noted that Fighting and Spraying behaviours increased for Izipho over the study and that towards the end of 2004, rates of these behaviours equalled the dominant male, Induna.

It is possible that male/male aggression is needed to develop dominance relationships for the male group and that these relationships may have an effect on courtship behaviours. Initially, Induna displayed the highest level of aggression and territoriality and he was also the only male to mate. As the study progressed and Fighting increased between Induna and Izipho, it was eventually Izipho that mated.

The aggression observed within the study is concordant with the idea that aggression occurs when coalitions are formed. Changes in sociality were noted and, after Umballa was removed from the facility at the end of 2001, a new coalition was developed involving Induna, Ndonda and Izipho. This coalition appeared to be quite stable by 2004. All males excluded Nyomfoza by the end of the data collection period and I noted that he chose to sit away from the male group.

Responses of Males to Female Cues in the Cheetah

Finally, I examined male responses to females in Chapter 6. Again, behaviour was studied over time and long term analysis was performed. Males were given 30 minute periods to investigate female yards for olfactory and visual cues. Key male behaviours were selected for analysis which included Sniffing, Chassé, Stutter Call, Lying, Calling and Pacing. Interestingly, the behaviours linked to aggression and territoriality were rarely observed while males were investigating females.

Behaviour patterns varied both between males and within individual males over the course of the study. The behaviours of Sniffing, Chasse and Stutter Call displayed cyclicity that had not been previously observed in male cheetahs. These behaviours were examined and compared to female Tail Rolling, as this too had shown cyclicity. These behaviours were shown to be highly correlated between Induna, Ndonda and Izipho, whereas no correlation was evident for Nyomfoza. Nyomfoza displayed a completely different set of behavioural patterns to the other males.

I noted considerable changes during the study for Izipho. While his behavioural patterns were similar to Nyomfoza at the beginning of 2002, I observed that by mid 2002 these patterns appeared to be changing. By the end of the study, Izipho's behaviour had aligned with Induna's behaviour. While his correlations to Tail Rolling were not as strong as Induna/Ndonda, his patterns of behaviour were becoming more and more like a dominant male.

Again, as was seen from the previous study, Nyomfoza became excluded from the group of males. While initially showing behavioural patterns like his brother Izipho, Nyomfoza never displayed interest in investigating female signals. His behavioural expression was entirely different to the remaining males, and this is a possible reason for his exclusion from the coalition.

Conclusions

A number of key findings have come from this study. The cheetah's behavioural repertoire varies widely, both between the sexes and within the sexes. Males displayed a higher rate of variability in their repertoire than females, exhibiting 10 more behaviours during the study period. One male was found to display considerably lower rates of behaviour, matching those of females. Later analysis of the males determined that this male's behavioural suite was different to the others and he was excluded from multi-male interactions over the study period.

Analysis of female behaviour found oestrus to be a major driver of behavioural variation. Tail Rolling and Tail Swishing appear to be good behavioural indicators of oestrus. The ability to determine oestrus behaviourally is important as it means that zoo staff could use focussed behavioural observations to identify receptive periods of females, without the costs and time constraints of undertaking hormonal assays. This may be particularly important for smaller zoos where costs may prohibit regular hormonal monitoring.

Further analysis of female reproductive cues found that housing females in social situations, with either females or males, may inhibit oestrus and therefore decrease the likelihood of successful breeding. Oestrus suppression was observed to varying degrees among the females, from complete suppression as seen in Lula, caused by sociality or close proximity of either sex, through to suppression only while housed with males as seen in Pinda. Oestrus suppression due to social housing is an important factor for captive management.

Analysis of male behaviour determined that captive males formed coalitions similar to their wild counterparts. Introductions of unrelated males could occur past the previous age considered limiting to their acceptance of each other without considerable negative responses. Further analysis of the male behavioural repertoire found that males exhibit a high level of inter- and intra-individual variation and a major part of this appears to be linked to aggression within coalitions. Key behaviours appeared to determine coalition membership, with increased aggression equating to dominance. This may represent a natural aspect of coalition formation in the wild and may be important for successful breeding in captivity.

Male dominance within a coalition may be a predictor of which males are likely to be successful breeders. This success may be due to the dominant male having greater access to females or they may be more attractive to females. The driver behind the preference for dominant males is still unclear, but it may be important when designing introductions in captivity.

Finally, variations in key male behaviours were shown to occur in response to female olfactory signals. These variations in behaviour were highly correlated to the female behaviour of Tail Rolling and also appeared dependant on coalition membership. This finding further supports the benefits of holding captive males in groups.

Final Comments

Frequent breeding in the wild occurs despite low genetic variability and high degrees of physiological defects in both male and female cheetahs, so these factors cannot be regarded as the major impediment to breeding in captivity. As both male and female cheetahs appear capable of reproduction, it is still concerning that there are consistently low reproduction rates reported from captivity.

The facilities that do report breeding success are typically large, hold numerous animals and are not open for public viewing. They have multiple large enclosures allowing for separation between the sexes and provide conditions similar to what cheetahs would experience in the wild. However, as seen from studbook data, the majority of cheetahs held in captivity can be found in small zoos and not large open range facilities. Further knowledge of the problems with breeding cheetahs in smaller zoos and facilities is needed, as many facilities do not have the luxury of large open spaces, multiple options for pairings and exclusion from other species and visitors. Research on captive management and housing conditions is needed to maximise the breeding potential of cheetahs as well as improve the well-being of animals in smaller zoos.

The current study has shown that there are many parallels between what is observed for captive and wild cheetahs, particularly the responses of forced female social environments and the development and maintenance of coalitions. These findings mean that examining captive populations may be more useful for looking at natural social behaviour than has been previously recognised.

Further research needs to be conducted in a number of areas relating to the effect of captivity on cheetahs. Firstly, for females, the possibilities of oestrus suppression need to be examined and the levels of sensitivity that females have for one another need to be determined. This sensitivity needs to be examined in order to develop minimum requirements for spacing when housing female cheetahs and prevent the periods of anoestrus caused by suppression. Secondly, the behavioural cues to oestrus need to be thoroughly analysed in conjunction with hormonal assays. While the current results show a strong trend for Tail Rolling as a behavioural cue to oestrus, hormone analysis is needed to confirm these results.

Thirdly, further research needs to be performed to understand how male coalitions develop and subsequently explore ways to prevent males being excluded from multi-male groups. This study indicated that there are benefits of group living in captivity. Coalition formation needs to be examined further with respect to the impact

of group living on reproductive success. By understanding the drivers of social and reproductive behaviours in captivity, captive managers will improve their understanding of the needs of cheetahs in the captive environment and be able to provide them with suitable enclosures.

With the use of studbooks, captive managers aim to manage populations and genetics in order to maintain a minimum viable population throughout all regions. The prosperity of cheetahs is highly reliant on good management techniques. Zoos are needed to provide a backup to management and reintroduction programs in the wild. Ultimately the goal is to ensure that zoological parks, big and small, are able to provide suitable enclosure to prevent boredom and dysfunctional behaviours, while maximising the animals' breeding potential. These achievements will enable zoos to not only replenish their own stocks without being a drain on wild populations, but to act as a reservoir for future re-introduction programs and conservation projects.

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