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

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Chapter I

General Introduction

Brief Description

The cheetah (*Acinonyx jubatus*) is unique amongst the cats as its taxonomic position lies between the 'big cats' of *Panthera* and the 'small cats' of *Felis* (Hunter & Hamman 2003). Research into felid genetics shows that the cheetah is in fact more closely related to the puma (*Puma concolor*) and the jaguarondi (*Herpailurus yaguarondi*) (Durant *et al.* 2008) than the 'big cats' that it superficially resembles (O'Brien *et al.* 1987). The cheetah stands alone within felid evolution as an extreme specialist and the only remaining sprinting cat. The cheetah displays many differing morphological features, including semi-retracting claws, hyper-extendable spine and unusual skull design, which allows for greater inflow of air. These characteristics enable the cheetah to be the fastest mammal, with explosive bursts of speed, and a specialised hunter. While highly adapted as a hunter, the cheetah has faced many struggles for survival within its history.

Original ancestors of the cheetah are believed to have been as widespread as Europe, Africa, Asia and North America (Hunter 2000). However, environmental pressures and global changes at the end of the Pleistocene Epoch, more than 10,000 years ago, caused a period of mass extinction (Press & Siever 1998). Along with many other species, the cheetah experienced an extreme loss in numbers and its distribution became limited to the African and Asian continents (O'Brien *et al.* 1985). Today, cheetahs are found in the southern regions of Africa, including South Africa, Namibia, Tanzania and Zimbabwe (Marker *et al.* 2007 and Durant *et al.* 2008) as well as a small population in Iran (Charruau *et al.* 2011).

Over the past few centuries, numbers of cheetahs have reduced further due to ever encroaching human civilisation (Marker & Dickman 2003c). Loss of habitat to farming in conjunction with hunting by poachers (for fur and pet trades) has placed the cheetah under further threat (Hunter & Hamman 2003). The cheetah currently faces extinction and has an International Union for Conservation on Nature listing of Vulnerable (Marker *et al.*2007) with an estimated population of 7500 and the Asian subspecies *Acinonyx jubatus venaticus* believed to be as few as 70-110 and being listed as critically endangered (Durant *et al.* 2008) .

Biology

The cheetah is a diurnal animal that occurs in savannah grasslands. It is a medium-sized cat, as males weigh between 29-65 kg and females weigh between 21-63 kg (Hunter &

Hamman 2003). Their nose to tail length ranges from 172-224 cm for the male and 170-236 cm for the female (Caro 1994). Males stand 74-94cm high at the shoulder and females stand 67-84 cm high (Hunter 2000). Only a small degree of sexual dimorphism is seen between the sexes and this monomorphism is unique to the cheetah, with a high degree of sexual dimorphism observed amongst the other large felids (Hunter & Hamman 2003). The cheetah is a slim animal, with a large rib cage and extensive lungs to facilitate increased airflow and a hyper-extendable spine to increase stride length. They have evolved to be capable of intense bursts of speed with reduced stamina as a trade-off. Cheetahs are unable to maintain high speed sprints over long distances and only pursue prey at top speed for 300-500 metres on average (Hunter & Hamman 2003).

The gestational period of cheetahs is 90-98 days and the average litter size is 3-5 cubs, with a maximum of 9 (Laurenson *et al.* 1992). Cubs are reared by the mother for approximately 18 months (Caro 1994). At this point mixed-sex groups of siblings move away from the mother but remain together for a further 4-5 months (Laurenson *et al.* 1992). Females then move away from their brothers which typically remain together, forming coalitions (Caro & Collins 1987a and Caro 1994). Cheetahs can live up to 21 years in captivity (Marker 2000) but this is considerably reduced in the wild, to approximately 12 years (maximum) (Hunter & Hamman 2003). Females are able to conceive at approximately 2 years of age and males mature after 1 year, but they do not usually breed until they are 3 years old (Wildt *et al.* 1993).

Associations Between Cheetahs and Humans

The cheetah was one of the first exotic animals to be kept in captivity (Rawlins 1972) and they have been associated with human civilisation for over seven thousand years (Hunter & Hamman 2003). The earliest records depict their use for hunting and sport by the Sumerians and Egyptians in about 3000 BC (Marker-Kraus 1997a and Saleh *et al.* 2001). In Ancient Egypt, the cheetah was also worshipped as the goddess ‘Mafdet’ or ‘Runner’ (Jequier 1913, Osborn & Osbornová 1998 and Malek 1992), with frequent symbols and hieroglyphs of cheetahs noted within tombs (Bonnet 1952). Cheetahs have been kept as pets and game hunters for centuries. From the 10th Century, hunting with cheetahs was popular for European nobility and the sport flourished until the 16th Century. However, the most detailed records of this activity come from India where maharajahs would use the cheetah for coursing. Coursing involved taking hooded cheetahs into the fields to hunt, removing the hood when a suitable prey had been

chosen (Divyabhanusinh 2002) and allowing cheetahs to pursue the prey. Once the prey was captured, the Maharaja rewarded the cheetah if it had killed a male gazelle or deer but would punish it for killing a female (Divyabhanusinh 2002).

During the reign of Akbar the Great (1556–1605) it was reported that 1000 cheetahs were stabled at once and that over 9000 cheetahs were kept throughout his 50 year reign (Hunter & Hamman 2003). Unfortunately, little focus was placed on the cheetah's reproductive biology (Hunter & Hamman 2003). In fact, it was noted that within the stable of over 1000 cheetahs there was only one record of cheetahs breeding. There was no apparent benefit in breeding cheetahs, as they had observed that captured cubs generally made poor hunters. They preferred to continually replenish their numbers with adult cheetahs from the wild (Divyabhanusinh 2002) as they recognised the need for cubs to learn hunting skills from their mother (Divyabhanusinh 2002 and Hunter & Hamman 2003). Hence, while the cheetah has been kept in captivity and associated with civilisation for thousands of years, little focus had been placed on captive breeding.

Cheetahs in Zoological Parks

The cheetah has been officially kept in zoological collections since 1829 (O'Brien *et al*. 1985). There has been less research undertaken on the biology and behaviour of captive cheetahs than other cat species, such as lions (*Pantera leo*) and leopards (*Pantera pardus*) (Rawlins 1972), despite a similar length of captivity in modern facilities. Many of the enclosures and husbandry practices developed for the cheetah were based on information from other felids (McKeown 1991)

During their early captive history, the cheetah had an exceptionally poor breeding success rate (Marker-Kraus 1997a). The first scientifically recorded birth of a cheetah in captivity was in 1956 (Florio & Spinelli 1967). However, it was not until 1970 that a zoo was able to successfully rear a litter of cubs to adulthood (Rawlins 1972 and Marker 2000). Since then success has been sporadic. Substantial breeding success has only been achieved during the last decade (Marker & Echement 2010). Very few zoos publish information on breeding attempts and data on unsuccessful breeding trials rarely reach the literature. Many reports of successful breeding were published throughout the 1970s, but these reports were of single litters and events in isolation. No facility reported a protocol for breeding cheetahs that had been empirically tested. Substantial research has been performed on the benefits and limitations of captive breeding programs (Allendorf 1993, Conway 1986 and Snyder *et al.* 1996), but there

has been minimal focus on the requirements of cheetahs specifically (Caro 1993, Grisham 1993, Marker & Grisham 1993 and Wildt *et al.* 1993).

Research on Wild Cheetahs

Research on wild cheetahs progressed at a faster rate than captive programs for cheetahs. This work began in 1969 (Bertram 1978) and has generally been based throughout the Serengeti Plains in Tanzania and in South Africa and Namibia (O'Brien *et al.* 1986, Kelly *et al*. 1998, Kelly & Durant 2000, Marker 2000, Durant *et al.* 2007 and Gottelli *et al.* 2007). Research has included distribution and demographic studies (Kelly & Durant 2000, Durant 2000b and Purchase *et al.* 2007); physiological studies focused on genetics and morphological abnormalities (O'Brien *et al.* 1983, 1985, 1986, Wildt *et al.* 1986, 1993 and Crosier *et al*. 2007 and 2009); male fertility (O'Brien *et al.* 1986, Howard *et al.* 1993, Lindberg *et al.* 1993 and Crosier *et al.* 2007) as well as behavioural studies, including male social structure (Frame & Frame 1980; Caro & Collins 1986, 1987a&b, Caro *et al*. 1989 and Caro 1994); female behaviour (Laurenson *et al.* 1992 and Gottelli 2007); mother–cub relationships and cub mortality (Laurenson *et al.* 1992, Kelly *et al*.1998 and Durant 2000a). Many of these studies have been driven by the need to understand the cheetah's poor reproductive rate. While there have been behavioural studies focusing on female cheetahs with young, reproduction has not been extensively examined. This is primarily due to the secretive behaviour of cheetahs, as very few examples of mating have been witnessed in the wild (Caro 1994 and Hunter, T. pers. comm 2002). The lack of observed courtship and mating places constraints on research possibilities in this area.

More recently, extensive research has been performed on cheetahs within Namibian farmlands (Marker-Kraus 1997a&b, Marker *et al.* 2003c, Marker & Dickman 2003a&c, Marker 2008, Munson *et al.* 2004 and Terio *et al.* 2003). Considerable census information is kept on the Namibian population of approximately 3000 animals (Marker 2008) and research is being performed in order to save the estimated 7500 animals that remain (Durant *et al.* 2008). This research has included work in conjunction with local farmers to more accurately investigate the population. The focus initially was to obtain as much information on current demographics as possible and determine the morphological and physical condition of cheetahs within this population (Marker *et al.* 2003a&b and Marker & Dickman 2003a). This research enabled better conservation practices through the Cheetah Conservation Fund (CCF) and provided local farmers

with alternatives to eradicating cheetahs from their farmlands (Marker-Kraus & Kraus 1994, Marker & Dickman 2003c, 2004 and Marker *et al.* 2003b&c). Through education and the promotion of ecotourism, this work has supported new conservation efforts for the cheetah (Marker *et al.* 2003b).

Recognising the Need for Help

Due to their vulnerable status and poor breeding success, it was recognised that a sustainable captive breeding program for cheetahs was needed to maintain a minimum viable population (MVP) in the wild (Soulé 1987). This captive-bred stock would reduce exploitation of the dwindling wild population and provide a reservoir that could be used to replenish suitable wild populations (Soulé 1986, Caro 1993 and Wielebnowski 1998). Hence, this population of captive cheetahs "could act as a final buffer against extinction and as a source of future introductions" (Caro 1993). The goal of this breeding program was to achieve a self-sustaining captive population, without the need to supplement numbers from the wild.

Consequently, in 1971 the National Zoological Gardens of South Africa developed an extensive plan for the breeding of cheetahs in captivity (Brand 1980 and O'Brien *et al*. 1985). This plan included setting up the Cheetah Breeding and Research Centre at De Wildt, South Africa. Initially, the centre only had minor successes, with low birth rates and high juvenile mortality. However, the plan was instrumental in progressing two fields of research; the genetics of cheetahs and the behaviour of cheetahs. Yet, while the research flourished, the Centre continued to only have limited breeding success and consequently the development of a species survival plan (SSP) for the cheetah was approved in 1983 (Wildt & Grisham 1993).

The aim of the SSP was to integrate reproductive, genetic and behavioural research (Wildt & Grisham 1993 and Wildt *et al.* 1993). The development of the SSP led to the entire North American population of captive cheetahs (128 animals in 18 facilities) being declared a research population. The physiology of this population was studied intensively to determine if there were any unique or unusual characteristics about cheetahs and to define any major reproductive problems (Wildt & Grisham 1993 and Grisham 1997). In conjunction with this work on captive animals, extensive behavioural work on wild cheetahs was also underway in the hope that a complete 'picture' of the cheetah would be achieved (Caro 1993, Frame & Frame 1980 and Laurenson 1993).

Research performed within the SSP covered many different areas and specialists from all fields took part. Scientists focused on the reproductive biology of captive cheetahs (Lindburg *et al*. 1993 and Wildt *et al*. 1993) as well as the behaviour of wild cheetahs (Caro 1993 and Laurenson 1993). The biological research included analysis of seminal, vaginal and rectal samples (Howard *et al*. 1993), assessment of reproductive status and fertility (Wildt *et al.* 1993) and evaluation of the diseases of captive cheetahs (Munson 1993, Evermann *et al.* 1993 and Terio *et al.* 2004). Studies focusing on reproductive fitness found that, while captive cheetahs had a number of physiological and behavioural abnormalities including malformed sperm, par-ovarian cysts and congenital defects (Wildt *et al*. 1983, 1986 and 1993), the cheetah was still capable of breeding. These results were not significantly different from those of wild cheetahs, with studies showing similar abnormalities (O'Brien *et al.* 1985 and 1987). However, SSP research studies did show that the cheetah displayed a lack of genetic variability and hence were more susceptible to disease (Howard *et al.* 1992 and Munson 1993).

Following this extensive study, two arguments were put forward to explain the cheetah's poor breeding success. Firstly, that the cheetah had suffered a substantial loss of genetic variability after moving through one or more bottlenecks in its recent past. It was proposed that this loss of genetic diversity was putatively responsible for defects and abnormalities that both prevented conception and also created a variety of birth defects due to inbreeding. The second argument proposed that husbandry and captive management were to blame for poor breeding success rates and high juvenile mortality in captivity. The researchers believed that behavioural problems, particularly those of females which led to neglect and maternal cannibalism, were the major contributors to low birth and survival rates. These two arguments will be discussed further.

Research on Genetics and Physiology

Bottlenecks, Inbreeding and Genetic Monomorphism

Captive environments are notorious for creating genetic problems. Inbreeding occurs due to reduced possibilities for suitable mate selection and can cause many genetic problems, such as reduced genetic variability or homozygosity and inbreeding depression when deleterious recessive alleles appear in the phenotype (Hedrick 1987). O'Brien *et al.* (1983, 1985 and 1986) attribute the cheetah's poor breeding success to its loss of genetic variability and suggested that the cheetah had passed through one or more bottlenecks, where numbers had dropped dramatically and inbreeding occurred.

These bottlenecks may have been caused by contraction of the geographical range of cheetahs due to human encroachment and poaching, and also by the period of mass extinction at the end of the Pleistocene (O'Brien *et al*. 1983 and Press & Siever 1998). These bottlenecks resulted in a dramatic loss of genetic information, severe reduction in numbers (reported by O'Brien *et al.* (1985) to possibly be as low as 10-12 individuals) and possible inbreeding in the remaining population.

O'Brien *et al*. (1985) strongly supported the theory that cheetahs were suffering from inbreeding depression, citing evidence of their extreme level of homozygosity. They examined 55 South African cheetahs and found that they were genetically monomorphic at each of the 47 allozyme loci examined, showing that the cheetah had significantly less genetic variation than was seen in other cats. This lack of genetic variation led O'Brien and his colleagues to report that all cheetahs were as genetically similar as siblings.

Due to the loss of genetic information, O'Brien *et al*. (1985, 1986) argued that the cheetah has been evolutionarily weakened. During the early to mid-1980s there was an increase in the reporting of low genetic variability (O'Brien *et al*. 1983, 1985, 1986 and Wildt *et al*. 1983, 1986). This body of research showed that the cheetah had a loss of vigour caused by inbreeding depression, and that this was the cause of many of their reproductive problems.

Wildt and colleagues (1983 and 1986) also supported the theory that loss of genetic diversity was directly affecting the cheetah's ability to breed. Their studies in 1983 examined the morphological structure and motility of spermatozoa of cheetahs and found that it was highly irregular. They reported that over 75% of the sperm of cheetahs was malformed or irregular in some way. This can be compared to 29% spermatozoal malformation in domestic cats (Wildt *et al*. 1993). In another study, Wildt *et al*. (1986) compared sperm morphology, quantity and various hormone productions in a selection of North American captive cheetahs to the sperm and hormones of free-ranging Tanzanian cheetahs. They found no significant differences between the two groups, and suggested that this helped to explain the low birth and survival rates found in captive cheetahs. They further surmised that this finding was also true for wild cheetahs, due to their equally low survival rates.

Females were also considered to have a high number of physiological problems caused by genetic homozygosity (Wildt *et al*. 1993). Captive female cheetahs can have a high rate of aborted foetuses, still births and cubs with congenital defects (O'Brien 1986 and Wielebnowski 1996). These defects were attributed to severe inbreeding. It

was concluded that many cubs that are born in captivity are either abandoned or eaten, with cheetahs displaying a high level of maternal cannibalism (Laurenson 1993). As very few cubs emerge from lairs in the wild (Laurenson *et al.* 1992), it was proposed that this further supported the theory of maternal cannibalism (Wildt *et al.* 1993).

Research on Behaviour

Behavioural Research in Zoos

Unfortunately due to many constraints such as time and the number of animals needed on exhibit, behavioural research is difficult to undertake at zoological parks and breeding facilities. Hence there are very few comprehensive or longitudinal studies that can be compared to longitudinal data recorded from the wild (Augustus *et al. 2*006 and Bertschinger *et al* .2008). Sexual interactions between male and female cheetahs are difficult to observe in captivity (Beekman *et al.* 1997, Bertschinger *et al.*1998 and 2008) as in the wild. Initially, reports from captivity were often anecdotal and not usually part of a controlled experiment (Florio & Spinelli 1967, 1968, Vallat 1971, Benzon & Smith 1975 and Brand 1980).

Considerable debate occurred on the elements needed for successful captive breeding and ranged from the social environment cheetahs need to stimulate interest in mating (Florio & Spinelli 1967, Vallat 1971 and McKeown 1991) to levels of aggression between male cheetahs to stimulate interest from females (Benzon & Smith 1975).

Breeding Cheetahs in Captivity: Comparison to the Wild

The captive environment is usually very unnatural for many species and can cause many behavioural problems, such as stereotypical behaviour patterns (e.g. pacing) or destructive behaviours (e.g. self-mutilation) (McKeown 1991). Caro (1993 and 1994), Laurenson (1993 and *et al.* 1992) and Wielebnowski (1998 and 1999) predicted that poor breeding success can be attributed to the behavioural problems of cheetahs. It is thought that poor breeding can be related to maternal neglect in the wild, with factors such as environmental conditions in conjunction with predator responses influencing cub survival. Laurenson *et al.* (1992) noted that low cub survival rates in the wild are due to predation from lions and spotted hyena (*Crocuta crocuta*). In comparison, the reasons proposed for poor breeding in captivity are stress and high juvenile mortality

from congenital defects, cannibalism and maternal neglect that may be due to husbandry and management techniques (Wielebnowski 1996). Unsuitable management practices of captive cheetahs can lead to females being stressed, and hence stillbirths, abandonment or cannibalism of young (McDougall *et al.* 2006).

In captivity, cheetahs are usually unable to display a natural repertoire of behaviours as they are forced into unnatural social situations. Historically, males have often been kept in isolation in order to reduce aggression, but males in the wild are usually found in sibling groups (Caro 1994). Conversely, females have been kept in pairs or trios whereas they live in isolation in the wild. These unnatural holding situations, disrupting male and female sociality, may cause undue stress (Caro 1993, 1994 and Augustus *et al.* 2006). Brown and Wielebnowski (1998) also reported stress-related factors when studying captive female cheetahs and found evidence of reproductive suppression in females forced to share enclosures. They found that females living together ceased coming into oestrus and that this suppression could last for one or two months to over a year in a small number of females. While only a small amount of research has been done in this area (Brown & Wielebnowski 1998, Wielebnowski 1999 and Wielebnowski *et al.* 2002) these findings could have vast implications for captive breeding.

Effects of Captivity

There are also a large number of logistical problems that could contribute to poor breeding in captive cheetahs. Housing and enclosure design may cause lower breeding success in cheetahs, as the enclosure environments are unnatural (Grisham 1997). Usually these enclosures do not provide long views or climbing areas, elements that seem vital for cheetahs to maintain natural behaviour patterns (Caro 1994). The proximity to other carnivores/predators is also considered problematic. Cheetahs moved away from enclosures of other large felids show a marked increase in breeding success (Grisham 1997). Hence, housing conditions appear just as significant as behaviour when trying to determine the reasons for a lack of breeding in captive cheetahs.

Captive lifestyles are notorious for reducing both an animal's behavioural repertoire and activity budget. The lack of stimuli and exercise in enclosures is a concern for managers of captive cheetahs. In captivity, cheetahs tend to become severely sedentary, resulting in weight gains that may also reduce breeding success. Weight gain is also compounded by unnatural feeding regimes. Caro *et al*. (1987) found that captive cheetahs were fed 25% more food than wild cheetahs eat, yet they exercised

considerably less. Rawlins (1972) has also reported problems with the captive environment of cheetahs. He reports that a lack of privacy is a concern for cheetahs, as they are shy animals and must be given the opportunity for seclusion in the captive environment to reproduce. The captive environment seems to be a likely contributor to the myriad of problems faced by the cheetah.

Discussion

While initially a loss of genetic diversity, inbreeding depression and monomorphism appear to be valid reasons for low breeding rates in captive cheetahs, current evidence supports the argument that inappropriate husbandry plays a considerable role. The theory of genetic-based reproductive problems has been negated by captive cheetahs that have bred quickly on release into the wild (Caro 1994). This discrepancy can only be attributed to husbandry techniques and the effect they have on reproduction in cheetahs. In captivity, it has often been found that mother cheetahs will abandon or eat their young, particularly if the mothers have been hand-reared (Wielebnowski 1996). However, these behaviours were not observed in extensive field studies of wild females (Laurenson *et al.* 1992).

Wielebnowski (1996) also refutes the arguments of O'Brien *et al* (1985 and 1987) that the homozygosity of cheetahs results in many birth defects and still births. Wielebnowski found a marked increase in congenital defects when parents were related, in her research on the relationship between juvenile mortality and genetic monomorphism. This suggests that in spite of the homozygosity of cheetahs there could still be significant effects of inbreeding depression. This study demonstrates that there is still enough genetic diversity in the cheetah to support further study into their genetic heritage, and hence there is a strong need for studbooks and genetic bloodline management.

Findings from Marker-Kraus (1997a), Grisham (1997) and Wielebnowski (1996) also suggest that there has been an increase in the number of litters being born in captivity over the last two decades. Work by O'Brien and his colleagues on genetic monomorphism cannot account for this increase, as little to no genetic variability would result in minimal breeding success and not the varied results that have been seen over time. Nor can they explain the varying degrees of success achieved by different institutions as seen in studbooks (Marker 2000 and Marker *et al.* 2007).

Current Research: A Trend for Behavioural Solutions

Caro (1993, 1994) believes that while there have been many studies on wild cheetahs, the level of study on captive cheetahs has been a disappointing. Areas that need to be examined include male coalition formation and social hierarchy as well as female behaviour and reproduction. Caro states that while some information can be inferred from wild populations, captive populations need to be thoroughly analysed for husbandry benefits and captive breeding programs. It is only when extensive captive population studies are undertaken that institutions such as zoos will have the knowledge to breed cheetahs on a regular and reliable basis.

In the mid 1990s, reports suggested that there were various behaviours that were displayed by female cheetahs leading into oestrus (Caro 1994, Beekman *et al.* 1997 and Wielebnowski & Brown 1998). These behaviours, which may be indicative of oestrus, included rubbing, rolling, sniffing, scent marking, grooming and vocalising. These behavioural indicators have not been studied extensively and no agreement has been reached on the specific behavioural or indicator types. No research has been conducted on any male behavioural changes when females leading into oestrus are present.

While a considerable amount of research has been performed on wild cheetahs, there are still many research gaps, particularly in the areas of captive behaviour and management. Specifically, very little focus has been given to the importance of male behaviour in the reproductive field. To date, efforts have focussed on female behaviour within the areas of oestrus and fertility as well as maternal behaviour and cub survival.

In this study, I aim to examine the behavioural repertoire of the captive cheetah to provide an extensive description of their behavioural suite. Once the numerous captive behaviours have been explored, I aim to look at the behaviours of male and female cheetahs in the context of varying degrees of sociality and differing captive management processes. Finally, I aim to look at male responses to female behaviour to determine if there are any behavioural changes that could indicate female receptivity.

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