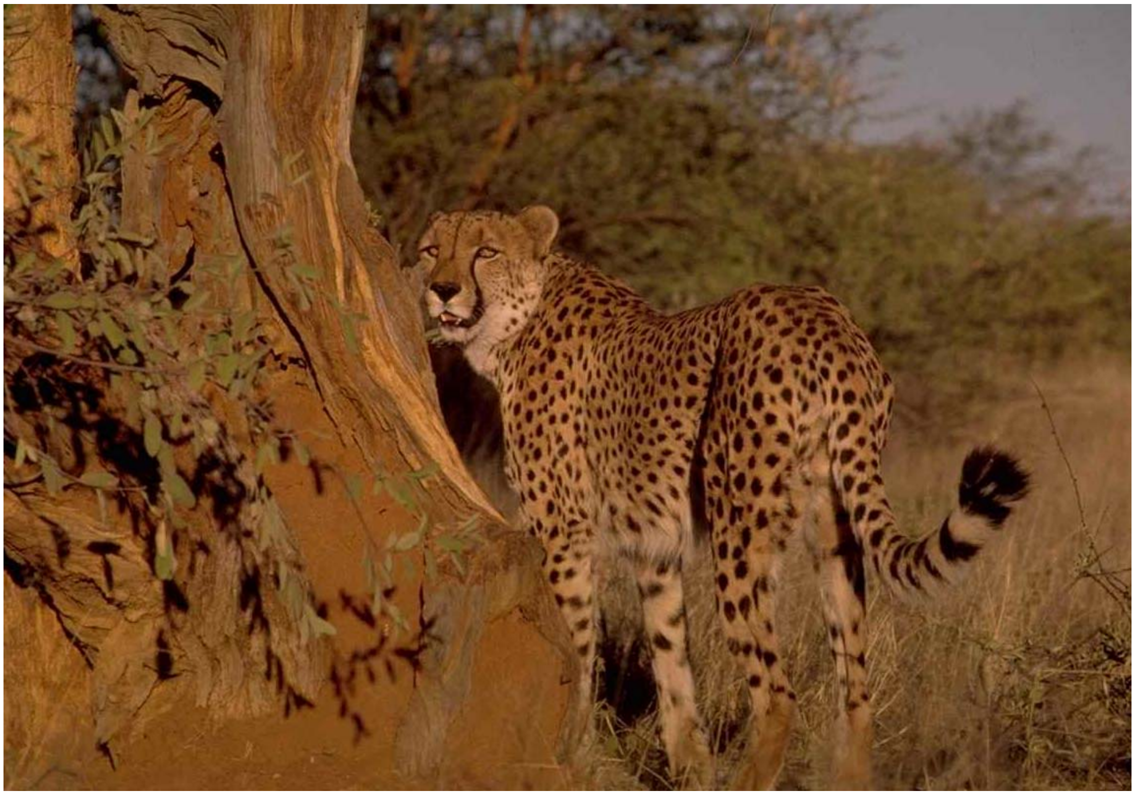
Aspects of Cheetah (*Acinonyx jubatus)* Biology, Ecology and Conservation Strategies on Namibian Farmlands



by
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ASPECTS OF CHEETAH (*ACINONYX JUBATUS*) BIOLOGY, ECOLOGY AND CONSERVATION STRATEGIES ON NAMIBIAN FARMLANDS

Summary

In an increasingly human-dominated environment, the task of successfully conserving large carnivores, such as cheetahs, is difficult due to real or perceived threats resulting in conflict and often their local extirpation. This research describes the causes and potential solutions to this conflict in Namibia. Cheetah biology and ecology were studied through physical examination, laboratory analysis, radio-tracking and human perceptions using survey techniques.

Between 1991 and 2000 data collected on over 400 live-captured and dead cheetahs showed that a perceived threat to livestock or game was the reason for 91.2% (n = 343) of cheetahs captured and 47.6% (n = 30) of wild cheetah deaths. Both were biased towards males, with 2.9 males being captured for every female, despite an apparent equality of sex ratio. Human-mediated mortality accounted for 79.4% (n = 50) of wild deaths reported, of which the majority involved prime adult animals, with a peak at around 5-6 years of age.

Polymorphic microsatellite loci were used to assess 313 Namibian cheetahs' variation, gene flow, paternity and behavioural ecology. Genetic analysis showed limited regional differentiation supporting a panmictic population and that persistence in Namibia depends on dispersal from regions throughout the country; therefore efforts of connectivity throughout the country should continue. Relatedness values confirmed family groups, and 45 new potential sire/dam offspring and 7 sibling groups were identified, providing information on dispersal and the success of translocation. Sera from wild cheetah were assessed for exposure to feline and canine virus antibodies to CDV, FCoV/FIP, FHV1, FPV, and FCV; antibodies were detected in 24%, 29%, 12%, 48%, and 65%, respectively, showing infection occurs in wild cheetahs; although there was no evidence of disease at time of capture, these diseases are known to cause serious clinical disease in captive cheetahs. Neither FIV antibodies nor FeLV antigens were present in any wild cheetahs tested, however, the first case of FeLV in a non-domestic felid is described in a captive Namibian cheetah. Concern for contact with domestic animals is discussed. Focal Palatine Erosion (FPE), a dental abnormality found in captive cheetahs, was discovered in over 70% of the wild cheetahs and was correlated with dental malocclusions, and is of concern to the long-term health of wild cheetahs.

Namibian cheetahs have a mean 95% kernel home range of 1642.3 km^2 ($\pm$ 1565.1 km^2), the largest home ranges yet defined. Habitat type significantly affected the cheetah's spatial distribution and prey density. Radio-collared female cheetahs were more closely related to other cheetahs in the study area than males, indicating male dispersal. Continual cheetah perturbation may partially explain the unusually low density of cheetahs in this area (estimated at only 2.5 cheetahs per $1000km^2$) despite the apparent abundance of prey.

Namibian farmers originally surveyed revealed a mean removal of 19 cheetahs per year/farm, even when not considered a problem, and higher removals occurred on game farms. Evidence for actual livestock depredation was negligible, only 3% of reported captures. Scat analysis revealed cheetahs' selection for indigenous game, however 5% of scats contained evidence of livestock. Research conducted on methods of conflict resolution showed that placing Anatolian Shepherd livestock guarding dogs proved to be effective, with 76% of farmers reporting a large decline in livestock losses since acquiring an Anatolian. Such solutions appear effective in increasing farmer's tolerance for cheetahs, and by the end of the study period cheetah removals dropped to a mean of 2.1 cheetahs/farm/year. Implementing strategies such as these could be significant for reducing human-carnivore conflict in the many other places in which it occurs.

To Khayam,

who showed me the path and provided the vision

Here with Loaf of Bread
beneath the Bough,
A Flask of Wine, a Book
of
Verse - and Thou
Beside me singing in the
Wilderness –
And Wilderness is
Paradise enow.
In: Rubaiyuat of Omar Khayyam

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Although only one name appears on the cover, this thesis would not exist without all those who have given so generously of their time and energy over the last several years.

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This research was conducted with the generous support of the Namibian farmers who provided access to cheetahs and allowed their release back into the wild, and who spent hours answering questions about the Namibian farmlands. In particular, Dr. Arthur Bagot- Smith for first showing me the problems facing the Namibian cheetah, the Kruger's for making me apart of their family, and the Waterberg Conservancy farm families for being great neighbours with a great conservation vision for the future. I am thankful to the Namibian Government, particularly the Ministry of Environment and Tourism, which supported this research. And, to His Excellency, Dr. Sam Nujoma, the President of Namibia and the International Patron for the Cheetah Conservation Fund, for his interest learning about the Namibian cheetah

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On a more personal note, I would like to thank my parents Marline and Ralph Bushey for teaching me that the world is an open door and one is only constrained to venture into the world by one's own fears. They told me I could do anything I put my mind to.

L.M. - Sept 2002

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FOREWORD

In support of my research, I co-founded the Cheetah Conservation Fund (CCF) in 1990, as the first international organisation to focus on the cheetah's survival in the wild. CCF's mission is 'to secure habitats for the long-term survival of cheetah and their ecosystems through multi-disciplined and integrated programs of conservation, research and education.' In 1991, CCF became a Namibian Trust with a Namibian Board of Directors. Additionally, CCF has an International Scientific Advisory Board that is actively involved in CCF's collaborative research.

Although prior research had identified the need for conservation action, particularly with respect to the ability of the cheetah to survive in the changing habitats of the agricultural and livestock lands (Myers 1975, 1986, Wrogemann 1975, Joubert 1984, Hamilton 1986, Stuart & Wilson 1988, Wilson 1987, Laurenson 1991, Caro 1994), minimal conservation action took place prior to my development of the Cheetah Conservation Fund (CCF) in 1990. Working in cooperation with the Namibian Ministry of Environment and Tourism, my field research in Namibia began in 1991. I set up a permanent base on a farm in north central Namibia, the centre of Namibian cheetah habitat, to better understand the issues facing the cheetah and to develop conservation based research and education programmes to assist with the species' survival throughout its range.

CHAPTER 1

GENERAL INTRODUCTION

Chapter 1: Table of Contents

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1.1 The importance of carnivores

Carnivores are important indicators of functioning ecosystems and, through predation, impact on all aspects of the system, by diverting what they do not need for their own energetic requirements to scavengers, detritivores, and microorganisms (Ricklefs 1990). However, large carnivore populations are declining globally, with 22 of 30 large carnivore species considered endangered (Fuller 1995), and all are subject to a multitude of pressures, including habitat degradation, conflict with agriculture, hunting, disease and commercial trade (Sillero-Zubiri and Laurenson 2001). Of the carnivores, all the 36 species of Felidae are either classified as threatened or endangered, except for the domestic cat (*Felis catus*) (Nowell and Jackson 1996).

Through their evolutionary history, carnivores have helped shape the evolution of their prey by hunting selection, which has provoked the development of fitness-enhancing anti-predator strategies (Logan and Sweanor 2001). In addition, carnivores have influenced human evolution by enhancing our senses against predation, and we may in part owe the evolution of our large brain and reasoning abilities to carnivores (Wilson 1980). Through scavenging predator kills for themselves, early hominids were provided a high-quality food source that may have enabled them to emerge from Africa and inhabit the globe (Blumenschine 1991, Logan and Sweanor 2001).

Carnivores are still influencing human lifestyles through predation on livestock, pets and people. However, their beauty, intelligence and cryptic behaviour has garnered our human curiosity to investigate carnivore species' evolution, biology and ecology and the consequences for them of living in today's human dominated landscape. Felids, in particular, are intriguing, and not only provide us with sources of companionship but have provided us with knowledge on genetic links to hereditary defects and diseases that affect both humans and cats through the collaboration between the felid genome organisation and the Human Genome Project (Nash and O'Brien 1982, Rettenberger et al. 1995, Wienberg et al. 1997).

Through the study of cheetahs in the early 1980s, today we possibly know more about this species than most other cat species (Caro 1994, Nowell and Jackson 1996, O'Brien et al. 1985, O'Brien et al. 1983), and yet its survival is still in question. In this introduction I summarise information on the cheetah and review its current status, including reasons for its decline. I introduce the background and aims of the research conducted for this thesis, and summarise the contents of each chapter.

1.2 Cheetah evolution

An evolutionary history of the cheetah has been constructed by paleontologists from fossils and, more recently, by geneticists using DNA (Adams 1979, Driscoll et al. 2002, Johnson and O'Brien 1997, Menotti-Raymond and O'Brien 1993, van Valkenburgh et al. 1990). Present records date carnivores to the Eocene epoch (Vaughan 1997), about fifty million years ago, with the specialised family Felidae evolving in the Miocene about twenty million years ago. In the middle Miocene, early felids began their radiation into other cats with conical canines including the early cheetahs, *Miracinonyx* and *Acinonyx,* during the Pliocene and Pleistocene epochs, about eight million to twelve thousand years ago (Hunt 1996).

The cheetah is considered one of the earliest divergences in felid evolution, about 8.5 million years ago, compared to the large cats of the *Panthera* group, which still shared a common ancestor about 6 million years ago (Adams 1979, Hemmer 1978, Johnson and O'Brien 1997, Neff 1983, Pecon-Slattery and O'Brien 1998, van Valkenburgh et al. 1990). The species known as *Acinonyx pardinensis* (Adams 1979), which is larger than the modern species, migrated from North America to Asia, India, Europe, and Africa. The modern cheetah evolved into its present form about 200,000 years ago. Genetic research has shown that today’s cheetah populations are descendants of but a few animals that remained after the Pleistocene era about 10,000 years ago, at which point the population experienced a founder event generally referred to as a population bottleneck (Menotti-Raymond and O'Brien 1993, O'Brien et al. 1985, O'Brien et al. 1983). The cheetah somehow survived this time of mass extinction and the population gradually increased.

The cheetah was first classified as *Felis jubatus* (Schreber 1776), but early taxonomists soon realised that the cheetah was unique from all the other cats and placed it into the monospecific genus *Acinonyx* Brooks (1828), of which there is only the one species *jubatus*. The translation of the cheetah’s scientific name *Acinonyx jubatus* is a reference to the species’ semi-retractile pointed claws. In Greek, *a* means not, *kaina*, means a thorn, and *onus*, means a claw (Gotch 1979). A more direct translation may be non-moving claws, and *jubatus,* in Latin means maned, as young cheetahs have a crest or mane on the shoulders and back.

Although seven subspecies have been identified, five subspecies are considered valid by most taxonomists (Smithers 1975). These are *Acinonyx jubatus venaticus* (Griffith 1821), *Acinonyx jubatus hecki* (Hilzheimer 1913), *Acinonyx jubatus soemmeringii* (Fitzinger 1855), *Acinonyx jubatus raineyii* (Heller 1913), (Schreber,

1776) and *Acinonyx jubatus raddei* (Hilzheimer 1913) and details of their distribution are given in Appendix 1. This thesis concerns *Acinonyx jubatus jubatus,* which is found in Southern Africa.

1.3 Cheetah anatomy and behaviour

The cheetah is markedly different in both anatomy and behaviour than the other 35 species of Felidae (Ewer 1973, O'Brien et al. 1983). It is the fastest land mammal over short distances (300-400m) (Gray 1968), and has the optimum body size and stride length to reach these high speeds. Nearing full speed, the cheetah is running at about one stride per 0.28 seconds or 3.5 strides per second (Hildebrand 1959, Hildebrand 1961).

Due to the cheetah's specialisation for speed, it has developed many morphological and physiological adaptations. For aerodynamics, it has a small head, lightweight and thinly-boned skull, flat face, and a reduced length of muzzle that allows the large eyes to be positioned for maximum binocular vision, enlarged nostrils, and extensive air-filled sinuses (Ewer 1973). Its body is narrow and lightweight with long, slender feet and legs and specialised muscles, which act, simultaneously, for high acceleration and allow for greater swing to the limbs (Hildebrand 1959, Hildebrand 1961, Neff 1983). The cheetah is the only cat with short, blunt claws, which lack skin sheaths, making the claws semi-retractable, thus providing added traction like a sprinter's cleats (Ewer 1973).

To facilitate the explosion of energy necessary to reach such high speeds, cheetahs are endowed with a powerful enlarged heart, oversized liver, adrenals, bronchi, lungs and large, strong arteries (Eaton 1974, O'Brien et al. 1983). During its high-speed chase in pursuit of prey, the cheetah's respiratory rate climbs from 60 to 150 breaths per minute, and its body temperature has been measured at 40^0 C (105^0 F; 4^0 F higher than normal) during a 375-metre sprint (Chinery 1979). For increased intake of air, the nasal passages have become enlarged, crowding the roots of the cheetah's canine teeth, thus the reason for their smaller size relative to other felids (Ewer 1973).

The distinguishing marks of a cheetah are the long tear-drop shaped lines on each side of the nose from the corner of its eyes to its mouth. The cheetah's coat is tan to a yellow-buff colour, with smaller, less distinct spots between larger spots, and a white belly. Near the end of the tail, the spots merge to form several dark rings. The tail often ends in a bushy white tuft. Although male cheetah are often slightly bigger than females (Caro 1994, Eaton 1974, Wrogemann 1975) and have slightly larger heads, males and females are difficult to tell apart by appearance alone. Cubs are born fully furred and with black spots on a greyish coat. Within two weeks the cubs eyes are open and the fur on the cub's back begins to grow; by six weeks old the cubs have a long mantle of tan and black fur.

Until recently, the cheetah has generally been considered to be an animal of open country and grasslands. This impression is probably due to the ease of sighting cheetahs in the shorter grass, and the long-term studies conducted on cheetahs in East Africa (Caro 1994, Caro and Laurenson 1994, Schaller 1968). However, cheetahs use a wider variety of habitats and are often found in dense vegetation, e.g. the Kora Reserve in Kenya, Botswana's Okavango Delta, and Namibian farmlands (Broomhall 2001, Marker-Kraus et al. 1996).

Even though it is customised for speed, the cheetah can run only 300 to 400 metres before it is exhausted; at this time the animal is extremely vulnerable to other predators, which may not only steal its prey but attack it as well (Caro 1994). Cheetahs are primarily diurnal, possibly due to the nocturnal behaviour of competing predators (Nowell and Jackson 1996). It has been suggested that the cheetah has larger litter sizes as a strategy to offset high juvenile mortality caused by lions and hyaenas (Burney 1980, Caro 1994, Hamilton 1986, Laurenson et al. 1995). Cheetahs have been observed scavenging and returning to a kill, but this is not common behaviour (Burney 1980, Caro 1982, Graham 1966, Pienaar 1969, Stander 1990). Cheetahs also are known to remain on kills in areas where lions and hyaenas are not present (Nowell and Jackson 1996).

Cheetahs are considered more social than most other felids, with the exception of the lion (Caro 1994). Large groups of cheetahs (up to 19 individuals of different age groups) have been observed and reported in Namibia and east Africa (Graham 1966, Marker-Kraus et al. 1996, McVittie 1979). Male and female siblings tend to stay together for several months after independence from their dam (Caro 1994), and male littermates remain together in coalitions (Caro 1994). Males in coalitions have been reported to better hold and defend territories (Caro 1994), were found to be in better physical condition and had better access to females for breeding than solitary males (Caro 1994, Caro and Collins 1987).

There is considerable variation in cheetah prey, ranging from Thomson's gazelle (*Gazella thomsoni*) on the Serengeti plains (Schaller 1968), impala (*Aepyceros melampus*) in Kruger National Park (Broomhall 2001, Mills and Biggs 1993, Pienaar 1969) to kudu (*Tragelaphus strepsiceros*), gerenuk (*Litocranius walleri*) and dik-dik (*Madoqua kirkii*) in the arid areas of northern Kenya (Hamilton 1986). Other species reported as prey include puku (*Kobus vardoni*), kob (*Adenota kob*) and oribi (*Ourebia *ourebi*) (Nowell and Jackson 1996), springbok (*Antidorcas marsupialis*) (Mills 1990, Nowell and Jackson 1996, Smithers 1975), wildebeest (*Connochaetes taurinus*) (Eaton 1974, Skinner and Smithers 1990), hare (*Lepus spp.*) (Labuschagne 1979), and seasonally a large proportion of prey consumed consists of immature ungulates (Burney 1980, McLaughlin 1970). Although, in the central livestock farmlands of Namibia, kudu, warthog (*Phacochoerus aethiopicus*), red hartebeest (*Alcelaphus buselaphus*), gemsbok (*Oryz gazella*), steenbok (*Raphicerus campstris*) and duiker (*Sylvicapra grimmia*) have been noted as regular prey species (Marker-Kraus et al. 1996, Morsbach 1987), there has been no quantification of prey consumed in farmland areas.

1.4 The cheetah's early association with humans

The earliest record of the cheetah's long association with humans dates back to the Sumerians, 3,000 BC, where a leashed cheetah, with what appears to be a hood on its head, is depicted on an official seal (Grzimek 1972, Guggisberg 1975). It was believed in Egyptian history that the cheetah would quickly carry away the Pharaoh's spirit to the afterlife (Wrogemann 1975)and symbols of cheetahs have been found on many statues and paintings in royal tombs (Guggisberg 1975).

Cheetahs were used for hunting in Libya during the reign of the pharaohs (Harper 1945). Cheetahs were not hunted to obtain food, but for the challenge of sport, known as coursing (Guggisberg 1975, Kingdon 1977). In Italy, cheetahs were coursed during the fifth century (Guggisberg 1975, Harper 1945). Russian princes hunted with cheetahs in the 11th and 12th centuries, and, at the same time, crusaders saw cheetahs being used to hunt gazelles in Syria and Palestine (Grzimek 1972). The best records of cheetahs having been kept by royalty, from Europe to China, are from the 14th, 15th and 16th centuries

(Guggisberg 1975). Cheetahs also were used for hunting in Russia (Novikov 1956). Eighteenth and 19th century paintings indicate that the cheetah rivalled dogs in popularity as hunting companions (Wrogemann 1975).

During his 49-year reign as an Indian Mogul in the 16th century, Akbar the Great had more than 39,000 cheetahs in total, which were called Khasa or the Imperial Cheetahs, and he kept detailed records of them (Caro 1994, Guggisberg 1975). However, all the cheetahs kept for hunting and coursing purposes were taken out of the wild from free-ranging populations. Because of this continuous drain on the wild populations, the numbers of cheetahs declined throughout Asia. In the early 1900s, India and Iran began to import cheetahs from Africa for hunting purposes (Pocock 1939).

In Africa, the cheetah was important to many local ethnic groups: the San hunting communities of southern Africa ate cheetah meat for speed; traditional healers used cheetah foot bones for fleet-footedness; and kings wore cheetah skins for dignity (Nowell and Jackson 1996, Wrogemann 1975). These practices, combined with exportation to other countries, contributed to the beginning of the cheetah's decline in Africa.

1.5 Current status of the cheetah and population threats

The cheetah was once one of the most widely distributed of all land animals (Wrogemann 1975). Through the course of time, the cheetah migrated over land bridges from North America into China, through Asia, India, Europe, and finally to Africa (Adams 1979, Kurten 1968, Kurten and Anderson 1980, Martin et al. 1977, Martin and Bateson 1986, van Valkenburgh et al. 1990), settling in its worldwide range as recently as 20,000 years ago (Adams 1979, Wrogemann 1975).

In 1900, approximately 100,000 cheetahs were found in at least 44 countries throughout Africa and Asia (Myers 1975, Figure 1.1). The current free-ranging African populations of cheetahs are found in small, fragmented areas spread in 29 African countries of North Africa, the Sahel, East and southern Africa, and it is estimated that around 15,000 animals remain (Marker 1998, Nowell and Jackson 1996, see Figure 1.1), representing a decline of nearly 90% over the century (Marker 1998, see Appendix 1).

However, current information about the status of the cheetah in many countries, especially countries that have been engaged in long civil wars, is lacking (Breitenmoser 1998, Breitenmoser and Breitenmoser 2001, Nowell and Jackson 1996). The information from North and West Africa is particularly limited, and the cheetah's future in these areas is questionable (Marker 1998, O'Mopsan 1998). The remaining strongholds are Kenya and Tanzania in East Africa, and Namibia, Botswana and Zimbabwe in southern Africa (Marker 1998).

Cheetah numbers throughout their ranges are declining due to loss and fragmentation of habitat, and a declining prey base (Nowell and Jackson 1996). Intra-guild competition from more aggressive predators decrease cheetah survivability in protected game reserves, causing larger numbers of cheetahs to live outside protected areas and therefore coming into conflict with humans (Caro 1994, Marker 1998, Nowell and Jackson 1996).

As human populations change the landscape of Africa by increasing the numbers of livestock and fenced game farms throughout the cheetah's range, addressing this conflict may become the most important factor in their conservation.

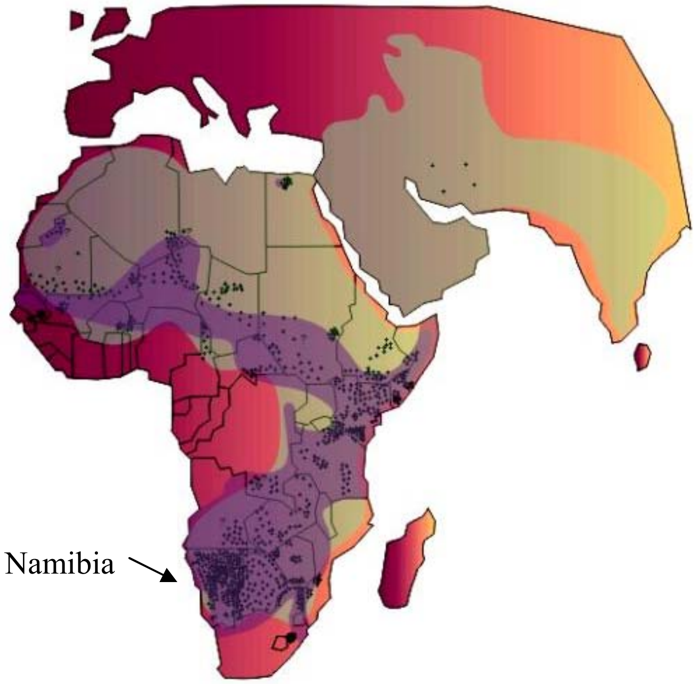


Figure 1.1 Distribution of cheetahs throughout Africa and Asia (in Iran) in 1900 (grey), showing 1975 range (purple) and current range (dots) (Marker 1998).

A further concern is that cheetahs breed poorly in captivity (Marker 2002) and wild populations have continued to sustain captive ones (Marker 2002, Appendix II). Until the 1960s, most cheetahs were imported from East Africa (Marker-Kraus 1997) but, as the numbers of cheetahs decreased in this region, Namibia became the major exporter of cheetahs (Marker-Kraus 1997). Today more than 90% of all cheetahs in captivity are descendants of Namibian cheetahs (Marker 2000, Marker-Kraus 1997). This additional pressure, together with ineffective captive breeding programmes, further endanger cheetah populations.

A potentially critical factor for the long-term persistence of the cheetah is its lack of genetic variation relative to other felids. The genetic structure of the cheetah has received considerable attention over the past several years (Driscoll et al. 2002, May

1995, Menotti-Raymond and O'Brien 1993, Merola 1996, O'Brien et al. 1985, O'Brien et al. 1987, O'Brien et al. 1983). It has been suggested that the genetic homogeneity could make the species more susceptible to ecological and environmental changes (Menotti-Raymond and O'Brien 1993, O'Brien et al. 1985, O'Brien et al. 1987, O'Brien et al. 1983). This has been interpreted in the context of two potential risks, including the expression of recessive deleterious alleles, and increased vulnerability to viral and parasitic epizootics that can affect genetically uniform populations (Brown et al. 1993, Evermann et al. 1988, Heeney et al. 1990, Munson et al. 1993, O'Brien et al. 1985). Given the lack of genetic diversity, monitoring the overall health of cheetah populations is an important component of understanding and promoting long-term viability (Munson and Marker-Kraus 1997).

Over the past few years, the impact of infectious diseases on endangered species has become well known (Burrows et al. 1994, Munson et al. 1993, Roelke et al. 1993, Roelke-Parker et al. 1996). Cheetahs are known to be very susceptible to several feline diseases, and are possibly more vulnerable to such diseases due to the lack of heterogeneity in the population (Evermann et al. 1988, Munson 1993, Munson et al. 1993, O'Brien et al. 1985). In addition, captive populations world-wide have been known to have a high prevalence of unusual diseases that are rare in other species, and these diseases impede the goal of maintaining self-sustaining populations (Bartels et al. 2001, Munson 1993). Although the specific causes of these diseases are not known, the character of these diseases implicate stress as an important underlying factor, and genetic predisposition and diet are possible confounding factors. While it is assumed that these diseases did not historically affect wild populations, there is concern that these diseases may arise in wild animals that are trapped, held in captive facilities and translocated.

Additionally, there is concern that cheetahs may transmit or acquire infectious diseases through these actions.

Viable populations may be found in less than half of the countries where cheetahs still exist. All populations are listed on the Convention on International Trade in Endangered Species of Fauna and Flora (CITES) Appendix I and are classified as Vulnerable or Endangered by The World Conservation Union (IUCN) (CITES 1984, CITES 1992). The largest remaining wild population of cheetahs is found in Namibia (Kraus and Marker-Kraus 1991, Marker 1998), and these are the subjects of this thesis.

1.6 The cheetah in Namibia

Ninety-five percent of Namibia's cheetahs live on the commercial livestock farmland, which covers 275,000 km^2 of the country's north central region (see Figure 1.2) (Marker-Kraus and Kraus 1990, Morsbach 1987). The widespread removal of lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) from commercial farming areas early in the 1900s opened a niche for the cheetah to fill. The abundance of water and natural prey animals on these farms allowed the cheetah to successfully inhabit these areas (Marker-Kraus et al. 1996).

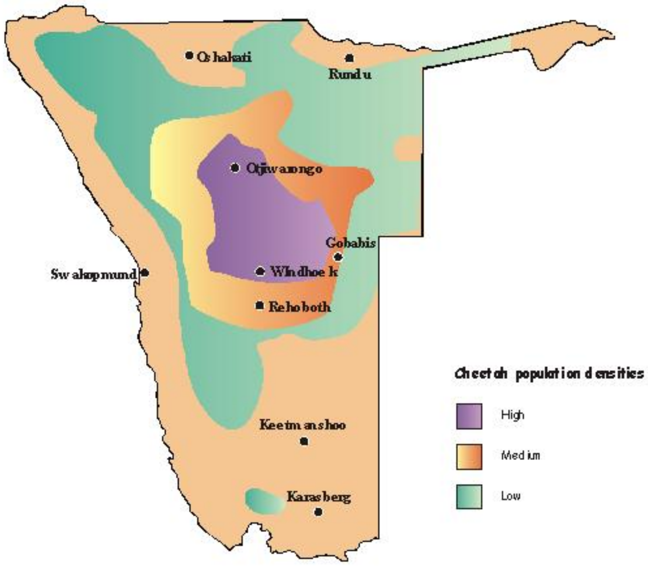


Figure 1.2 Density distribution of Namibian cheetah population.

Although the cheetah has been reported to be declining in numbers throughout its range (Hamilton 1986, Joubert 1984, Kraus and Marker-Kraus 1992, Marker 1998, Marker-Kraus and Kraus 1990, Myers 1986, Stuart and Wilson 1988, Wilson 1987, Wrogemann 1975), little research has been conducted outside fenced game reserves or protected areas, despite the fact these are now the most important habitats for cheetah in Namibia. At the same time, studies on captive cheetah have yielded extensive information about their biology, physiology, and behaviour (Brown et al. 1993, Dierenfeld 1993, Evermann et al. 1988, Howard et al. 1993, Lindburg et al. 1993, Marker-Kraus and Grisham 1993, Munson et al. 1993, Wildt et al. 1993, Wildt and Grisham 1993), but there have been no comparable studies conducted on free-ranging cheetahs.

In southern Africa, cheetahs are killed regularly in farming areas due to their raiding of livestock and the attitudes of the farmers (Marker-Kraus et al. 1996, Marker-

Kraus et al. 1993, Morsbach 1987, Stuart and Wilson 1988, Wilson 1987). Although classified as a protected animal in Namibia, a cheetah can be shot in order to protect one's life or property (Marker-Kraus et al. 1996). Between 1980 and 1991, 6,829 cheetahs were legally removed from the wild Namibian population, mainly through indiscriminate catching in live traps and shooting (CITES 1992). Carnivore-livestock conflict has been exacerbated by a change in husbandry during the past century (Breitenmoser 1998). For instance, in recent decades, domestic livestock is no longer herded or guarded by dogs and as such is more vulnerable to predation. Furthermore, stockmen have lost the tradition of coexistence with large predators and modern protective legislation of carnivores is not matched by positive cooperative attitudes by livestock communities (Breitenmoser 1998). The increasing availability of illegal and legal firearms is also likely to pose a threat so long as the cheetah's skin has any value (Hamilton 1986).

1.7 Livestock management and non-lethal predator control

The key question for management of large carnivores in today's human dominated landscape is what is the impact of predators on livestock? There are a variety of reasons for livestock loss, including disease, poor management, and predation. Because of this, identifying the correct cause of livestock loss is fundamental. Worldwide farmers commonly blame predators for the majority of livestock losses before investigating the cause of loss thoroughly (Marker-Kraus et al. 1996). If predation is discovered as the cause, then identifying the appropriate culprit is necessary for effective management strategies to be undertaken. When the specific predator causing livestock loss has been accurately determined, identifying livestock management strategies to help prevent further losses is then necessary. All information and management practices must be evaluated carefully since every situation is unique, and different methods may be required for reducing predation in each case.

Some farmers, through the world indicate that implementing new livestock protection methods is too much work, as their management was already extensive (Landry 1999). This attitude is unfortunate, as the lack of any predator control or the presence of vulnerable livestock or game may encourage opportunities for predators, and improper methods of farming can create losses to predators. Conversely, proper management can prevent or remedy many problems.

A large variety of management practices have been used successfully in Namibia to reduce livestock loss to cheetahs (Marker-Kraus et al. 1996). Some of these strategies include calving camps, corralling calving herds and utilising guard animals such as donkeys or baboons that can reduce loss to predation. Predation on cattle calves may decline if farms synchronise calving both within their herd and with other farms in the area, as well as with wildlife calving times. High concentrations of cattle calving within a short time period has helped, as there is protection in numbers. This, combined with a fast rotation schedule through smaller camps, has helped several farmers. Farmers that breed more aggressive breeds of cattle have shown to have lower losses to predators, as these breeds are more protective of their calves. Inexperienced heifers calving for the first time should be given additional protection, such as putting them with older cows or in closely observed calving camps. Calving seasons are critical, especially for heifers. It is best for them to calve in mid-summer when there are more wild young, as well as more cows and calves for protection, as the first calves born during the start of a calving season are the most likely to be killed. A cow that fails to reproduce or loses its calf to predation should be culled from the herd.

The use of donkeys to protect livestock from predators has been used in many areas of the world (Landry 1999, Marker-Kraus et al. 1996). Donkeys are generally docile, but are know to have an inherent dislike for intruders such as cheetahs, black-backed jackals, caracals and even domestic dogs. Farmer benefits include low cost, easy management, and a high success rate (Marker-Kraus et al. 1996). Mules also have been used for protection because they are more aggressive than donkeys. Although mules are aggressive guard animals, they have been known to 'steal' calves for themselves, since they cannot reproduce. Zebras, horse stallions and horned oxen have been used successfully to deter predators. The early Namibian settlers commonly kept horned oxen with their calving herds (Marker-Kraus *et al.* 1996). Farmers have also expressed the belief that cattle, especially females, should never be dehorned; and that mature cattle are more successful against predators than heifers (Marker-Kraus *et al.* 1996). A few farmers have used baboons to protect smallstock, however the aggressive behaviour of the baboons eventually prevents even the farmers from getting near the flock (Marker-Kraus et al. 1996).

Other forms of predator control included poison collars on stock to selectively eliminate the specific livestock-killing animal; and both sight and sound repellents, which can be effective temporary aids to protect livestock, but predators soon become accustomed to the repellents (Landry 1999). In addition, taste aversion has been experimented with on canids, causing the predator physical illness after eating treated bait (Gustavson et al. 1976). This method has proved very effective, as it targets the specific problem animal.

Smallstock farmers often use dogs with their herds. The majority of the dogs used in Namibia to protect livestock showed 'herding dog' behaviour instead of the appropriate 'guarding dog' behaviour (Marker-Kraus et al. 1996). Herding dogs use the eye-stalk behaviour to move stock, similar to predators. It is believed that when a predator approaches the herd, the dog instinctively begins to herd the animals, due to the herding instinct. This stimulates the predatory motor pattern of the predator (eye-stalk-chase-trip-bite-consume), causing it to chase and kill the stock.

Conversely, specialised breeds of 'livestock guarding dogs' discourage the predatory behaviour, as guarding dogs act as sentries. When a predator approaches, a guarding dog will bark while moving towards the predator, and then will retreat back into the herd, without causing the herd to run. This pattern is repeated, thus breaking the predatory motor pattern. Predators usually are opportunistic and will seek prey elsewhere once challenged. This may be especially true of the non-aggressive cheetah. Therefore, using a selected breed of livestock guarding dog could be an effective non-lethal predator management strategy for farmers in Namibia.

1.8 Aim of the thesis

The Namibian cheetah population may be the largest and healthiest population of cheetahs left in the world, and understanding their biology and ecology is essential. In the future, as wild cheetah populations become more fragmented, their management will become increasingly necessary in order to maintain genetic diversity, and protect against further population declines due to habitat loss, demographic fluctuations, and conflict with humans. It is hoped that the studies described in this thesis will provide the basis for developing effective conservation strategies for the long-term survival of the wild cheetah.

In this thesis I report on a series of integrated studies on the Namibian cheetah designed to evaluate the: 1) genetic makeup of this population and disease risks; 2) ecology of cheetahs including demography, density, and feeding; 3) home range requirements and spatial utilisation of the cheetah; 4) potential strategies to improve the status of cheetahs through changing farmers' attitudes, resulting in greater tolerance for the cheetah; and 5) specific strategies to reduce conflict with cheetahs through the use of non-lethal predator control methods such as livestock guarding dogs. The summaries below outline the content of each chapter in the thesis.

1.9 Chapter contents

My thesis is arranged in the following way.

Chapters 3 - 13 are papers, all but two (Chapters 5 and 11) of which have been submitted to journals for publication. In some cases, to reduce duplication, the papers have been edited and a complete description of the Study Area, including history of the Namibian farmlands can be found in Chapter 2. Each Chapter presents a detailed methods section for that particular chapter. A full reference list will be presented at the end of the thesis and not at the end of each chapter or section.

Chapter 2. Study Area

I describe the Namibian farmland region where the studies described in the thesis have been conducted.

Chapter 3: Aspects of the Management of Cheetahs Trapped on Namibian Farmlands

In Chapter 3 I investigate the reasons given for the trapping and/or killing of the cheetahs studied. These stated explanations for trapping or killing cheetahs allowed me to determine whether the actual risks for cheetahs on Namibian farmlands matched the data provided by questionnaire surveys in Chapter 12. These data provided insights into how the level of reported removals fluctuated between years, the social structure of the cheetahs removed, and whether or not removals were correlated with actual livestock losses that could be attributed to cheetah predation.

Chapter 4. Morphology, Physical Condition and Growth of the Namibian Cheetah

The Namibian cheetah has never been fully described. This chapter describes the physical condition, morphology, and growth of the Namibian cheetah, and compares these data to those of other subspecies. The data were obtained from biomedical and physical examinations of cheetahs that were opportunistically live-trapped, as described in Chapter 3. A standardised technique was used, which is recommended for comparative studies of cheetahs in other regions.

Chapter 5: Patterns of Molecular Genetic Variation in Namibian Cheetahs

In this chapter I investigate the genetic variation within the Namibian cheetah population, in collaboration with research associates at the National Cancer Institute in the United States. Using microsatellites, I explored if there were any evident barriers to gene flow or recognisable substructure of this cheetah population, whether there were different levels of molecular genetic variation among geographic areas that varied in estimated cheetah densities and demographic patterns, as well as whether relatedness appeared to affect the behavioural ecology of Namibian cheetahs. Data on social and family groups, as well as locations of captures, were used to answer questions regarding population relatedness.

Chapter 6*:* A Serosurvey of Antibodies to Viral Diseases in Wild Namibian Cheetahs

Captive cheetahs are extremely susceptible to several viral diseases, which result in abnormally high morbidity. Since cheetahs are captured on farmland, have very large ranges and travel through many different farms, they often come into contact with domestic felines. Viruses transmitted in this way could be a threat to the wild cheetah population. In collaboration with my colleague from the University of California at Davis, I present the results of my investigations into the prevalence of feline viral diseases, and discuss the disease risks to wild Namibian cheetahs.

Chapter 7: Lymphosarcoma Associated with Feline Leukaemia Virus Infection in a Captive Namibian Cheetah

I present a case report of the occurrence of multicentric lymphosarcoma in a captive cheetah, which had been exposed to another cheetah infected with feline leukaemia virus that had previously been in contact with domestic cats. The cheetah subsequently died and, upon necropsy, Feline Leukaemia Virus was identified from multiple organs. This was the first confirmed case of FeLV-associated lymphosarcoma in a non-domestic felid and illustrated the risks facing the wild cheetahs due to their proximity to domestic animals on Namibian farmlands.

Chapter 8: The Incidence of Dental Abnormalities in Wild-Caught Namibian Cheetahs

A dental abnormality known as Focal Palatine Erosion (FPE) can lead to infection and death in affected animals. I investigate the prevalence of this condition in wild cheetahs, as it had previously only been reported in captive cheetahs. I consider possible genetic causes for this condition and discuss its potential impacts on free-ranging cheetahs.

Chapter 9: Demography of the Namibian Cheetah

Understanding cheetah population dynamics, including reproductive rates, litter sizes, and both juvenile and adult survival, is essential for developing a scientific approach to cheetah management and conservation. In this chapter, I study the life history parameters of the Namibian cheetah population. The results show high human-caused mortality and reveal which age categories were most at risk from human-mediated removals. These results are compared with populations studied elsewhere and their conservation implications discussed.

Chapter 10: Notes on the Diet and Feeding Ecology of the Cheetah on Namibian Farmlands

Gaining an accurate picture of cheetah prey selection and feeding ecology is fundamental to understanding how cheetah predation affects prey populations, and investigating the veracity of farmers' perceptions of cheetah predation. In Chapter 10, I investigate the diet of cheetahs using scat analysis and, through feeding trials, determine a correction factor that enables more accurate interpretation of wild cheetah diet from scat analysis. Through the use of this corrected scat analysis technique, I examine the abundance and types of hair identified in wild cheetah scats, and determine how frequently livestock is found in cheetah diet versus that of wild prey species. The data provided through this scat analysis are compared to data regarding kills observed during the long-term radio-tracking study described in Chapter 11.

Chapter 11: Movements and Spatial Organisation of Cheetahs on North-Central Namibian Farmlands: The Influence of Prey-base, Competition and Perturbation

I used radio-tracking and GIS analysis to examine the spatial distribution of cheetahs on Namibian farmland and investigate the factors that affect home range requirements, spatial utilisation and habitat use.

Chapter 12: Factors Influencing Perceptions and Tolerance towards Cheetahs on Namibian Farmlands

In this chapter I investigate the factors causing cheetahs to be perceived as pests. I explore the factors that mitigated the perception of cheetahs as pests, and whether there is any evidence that attitudes could be changed over time. I used questionnaire surveys to conduct this investigation; one from an initial study in 1991 to 1993 and a follow-up survey conducted in 2000.

Chapter 13: Evaluating the Effectiveness of Using Livestock Guarding Dogs as a Method of Conflict Resolution

In Chapter 13 I evaluate the effectiveness of using of the Anatolian Shepherd Livestock Guarding Dog in Namibia as method of deterring cheetahs from predating upon livestock, thereby reducing losses to farmers, and also the resultant hostility to predators. Using a questionnaire, the owners of dogs that were bred and placed on farms were regularly surveyed, to evaluate the attentiveness, protectiveness and trustworthiness of the guarding dogs, the care given to them by the farmers, and the overall satisfaction of the farmers with their dogs. These results were compared to previous studies on livestock guarding dog behaviour. Behavioural problems, longevity as guardians, and causes of mortality were assessed. Data regarding any changes in the level of livestock loss before and after placement of the dog was used to determine the efficacy of the dogs as a method of reducing livestock depredation.

Chapter 14: General Discussion and Conservation Implications

Finally, I use my results to discuss how conservation and long-term survival strategies necessary for cheetahs could be compatible with the current trends in land use practices and policies in Namibia, and how these management strategies may be used in another countries where cheetah populations are in conflict with people and their livestock or game farming interests.

CHAPTER 2

STUDY AREA

Chapter 2: Table of Contents

CHAPTER 2: STUDY AREA

In this Chapter I briefly describe the land use, climate, and vegetation of Namibia, and give details of the area within Namibia where my studies were conducted. I will go on to outline the social and economic features of Namibia, which are relevant to the Thesis.

2.1 Land use

Called ‘a land between two deserts’ (Schneider 1994), Namibia is an arid country of 82.3 million hectares (2.7% of the African continent) of which 12.65 million hectares are unsuitable for agriculture. Sixteen percent of Namibia’s total area is hyper-arid (defined as true desert: Seely et al. 1994), where agriculture of any kind is excluded; 49% is classified as arid, 32% as semi-arid, and 3% as sub-humid (Marker-Kraus et al. 1996, Seely et al. 1994). Sixty-nine percent of the land is usable for agriculture; this is split between commercial livestock and game farms (approximately 40%) and communal lands (approximately 40%) (Figure 2.1). Details of communal and commercial farms are given in sections 2.5 and 2.6 respectively. Twenty-one percent of the country (112,000km^2) is proclaimed as national parks or protected areas (Figure 2.1).

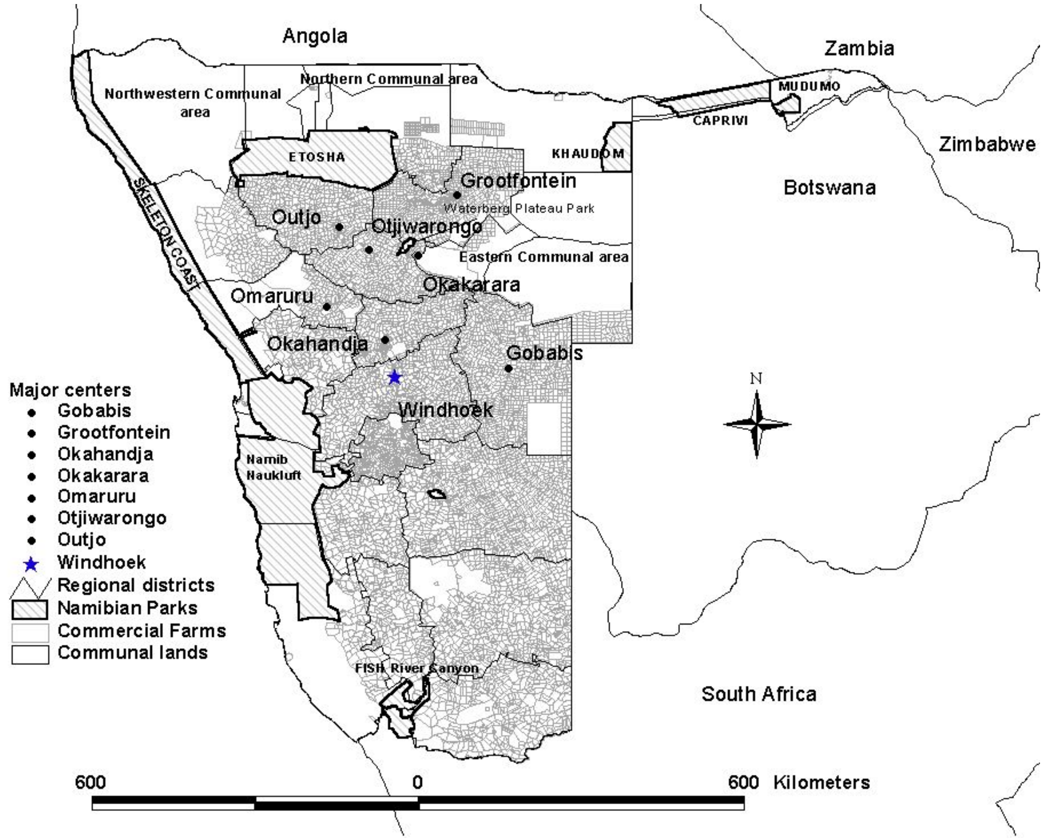


Figure 2.1 Land use map of Namibia, showing National Parks, commercial farms and communal lands.

2.2 Rainfall, climate and vegetation

Land use for agriculture depends on rainfall distribution and water availability. Figure 2.2 shows the country's rainfall distribution. Although rainfall is sporadic and unpredictable, records since the early 1900s show nine to 12-year cycles of wet and dry spells (Berry 1990). Periods of drought have been known to last from four to nine years and are a regular occurrence (Schneider 1994). However, the recent drought phase from 1979 - 1999 lasted nearly 20 years. Most of Namibia's rain falls in summer, from November to April. Temperatures in Namibia can also be varied, with temperatures well over 50^0 and under 0^0 recorded in the same parts of the country.

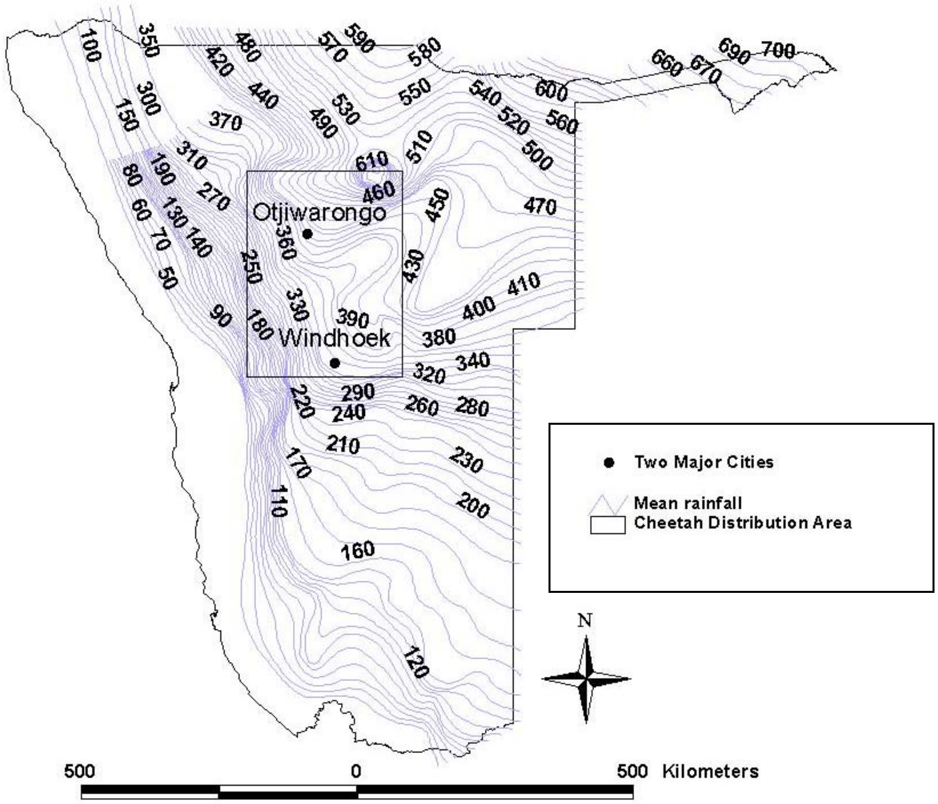


Figure 2.2 Namibia rainfall distribution (source, Ministry of Agriculture, Department of Water and Rural Development, Windhoek, Namibia).

In geological time, the Namib Desert and its adjacent plateaus have been arid or semi-arid for at least 55 million and possibly up to 80 million years (Barnard 1998). The Atlantic Ocean's Benguela upwelling, in addition to the hot interior, has maintained and possibly increased the aridity of the region in recent times (Barnard 1998). Namibia is considered the world's oldest desert, because of both the age of its rocks and sands, and its unique species and biological communities.

Namibia's landscape is dry but varied, includes rocky landscapes, dune coasts, scrublands, thorn savannahs, moist woodlands and tropical floodplains. Namibia's flora and fauna are always affected in various ways by the drought phases.

There are four biomes in Namibia, each with distinct plant and animal communities. The biomes are described as the Namib Desert Biome (along the west coast), the Winter Rainfall Area (in the southwest corner of the country), the Woodland Savannah (in the north east corner of the country) and the Grassland Savannah (through the central part of the country from south to north) (Barnard 1998). It is very difficult to draw a line between two adjacent biomes as flora and fauna change gradually across them, although the climate separates the individual biomes. Additionally, unique species are found in specific biomes. For example, the aridity of Namibia, which has occurred for millions of years, has fostered a variety of arid-tolerant species, some which have unique growth forms and strategies, such as Namibia's famous desert plant the *Welwitschia mirabilis* (Barnard 1998).

The seasonal rains and temperature fluctuations, in addition to the topography and soil, determine the 14 major subdivisions of the vegetation zones (Figure 2.3). Most of Namibia is covered by savannah, in particular thorny shrub and tree savannah of which, Thornbush, Highland and Kamel Thorn Savannahs dominate the central highlands (Barnard 1998). This is the main distribution area where cheetahs occur in the country. The study area for the work described in this thesis is also located within these vegetation zones.

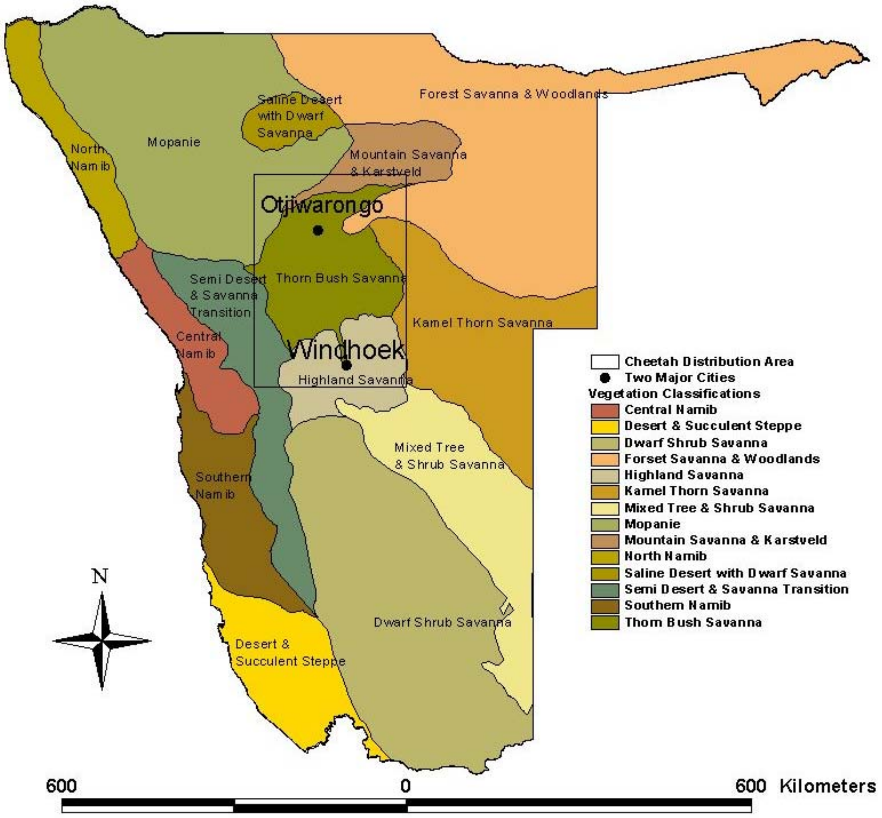


Figure 2.3 Vegetation types of Namibia (Geiss 1971). The main occurrence of cheetahs in Namibia is the North Central Farmlands and is shown within the boxed area, to show vegetation for that area.

2.3 North-central farmlands study area

Within Namibia, the studies presented in this thesis were conducted in the North-central farmlands. These commercial cattle farmlands are where cheetahs historically are known to be problematic and considered vermin. The area covers over 3 million hectares of land and nearly 20% of the commercial cattle farmland (Figure 2.4). The study area spans several districts, including Gobabis, Windhoek, Okahandja, Otjiwarongo, Omaruru, Outjo and parts of the Grootfontein district, in the regions of Omaheke, Khomas, Otjozondjupa, respectively, and lies between 19°30'S to 23°30'S and 16°E to 19°E. The area is predominately thornbush savanna, consisting of grassland with trees and shrubs in dense or open clumps (Joubert and Mostert 1975) (Figure 2.3).

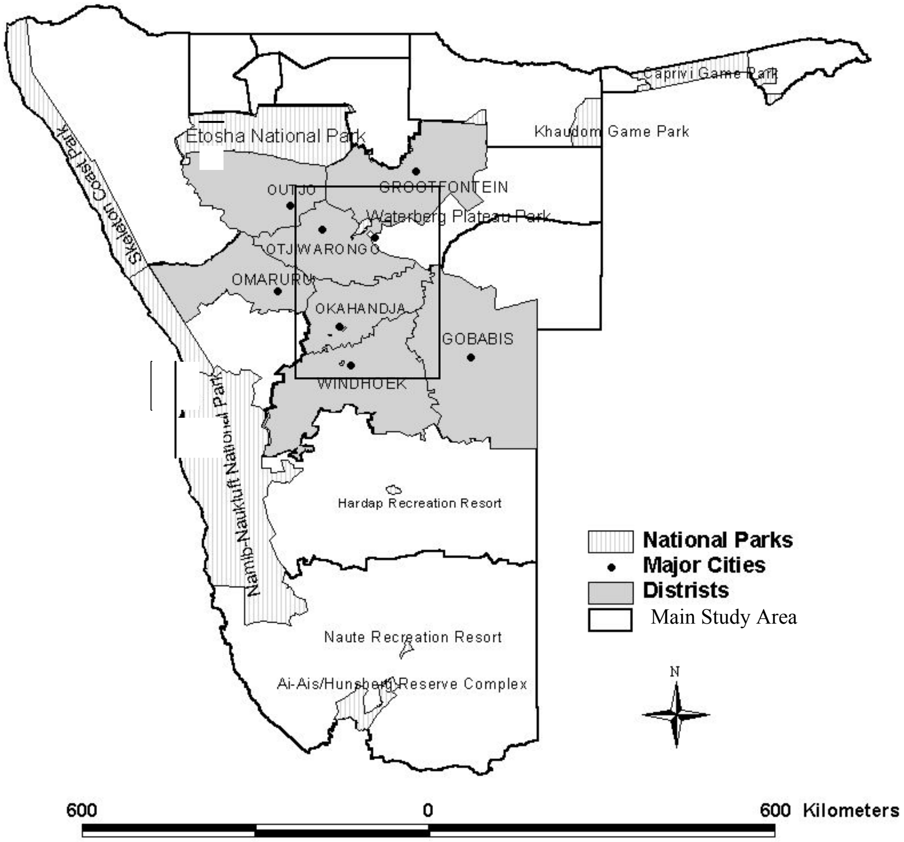


Figure 2.4 Map of Namibia, with districts in the North Central Farmlands highlighted where studies for this thesis were conducted.

From data collected during the survey with farmers (Chapter 12), important information about the farmland was obtained and is summarised in this section. Farmers in the study area were categorised as owning small, medium, or large farms (Table 2.1). Most farms were criss-crossed with 4-wire fences, which allowed rotation of stock through the farm and free movement of game.

Table 2.1 Farm sizes in the study area[a]

Total Farm Size (ha)[b]	No. Farmers	% Farmers	% Land
Small (<7 000)	91	39	20
Medium (7-15 000)	114	48	49
Large (>15 000)	30	13	31

[a] n = 235 (Marker-Kraus et al. 1996)

[b] Total land holding in hectares by individual farmers. A 'Total Farm' may be comprised of several small farms.

2.3.1 The number and ratios of livestock and countable game in the farmland study area

The livestock and countable wild game reported in the study area as reported during the survey presented in Chapter 12, numbered 376,506 head (Tables 2.2 and 2.3). Sixty-six percent of the animals in the area were livestock (cattle, goats, sheep) and the remaining 34% were game. These ratios were considered representative of the entire north-central farmlands. The livestock numbers listed in Table 2.2 were derived from survey questionnaires covering over 14% of the commercial cattle farmland (Marker-Kraus et al. 1996) and represent 10% of the cattle and 1% of the smallstock recorded by Ministry of Agriculture, Department of Veterinary Services Animal Health Inspectors for 1993 (Schneider 1994).

Table 2.2 Livestock numbers reported in the study area

Livestock	No. Reported	No. Farms Reporting
Cattle	165 443	233
Cattle Calves	33 086	157
Goats	16 527	117
Sheep	28 562	96
Unk. Smallstock[a]	354	4
Smallstock uncounted	---	6
TOTAL LIVESTOCK	243 972	233

[a] unknown if goats or sheep

Table 2.3 Numbers of wildlife reported in the survey area

	Free-ranging	On Game Farms[a]	TOTAL
Kudu	31 664	1 764	33 428
Oryx	29 617	3 046	32 663
Springbok	13 423	1 243	14 666
Hartebeest	17 943	2 157	20 100
Eland (*Taurotragus oryx*)	1 291	1 107	2 398
Blesbok[b] (*Damaliscus damaliscus*)	383	809	1 192
Impala[b]	---	500	500
Plains Zebra (*Equus burchelli*)	---	461	461
Mountain Zebra (*Equus zebra hartmannae*)	1 699	226	1 925
Blue Wildebeest	---	1 151	1 151
Black Wildebeest[b] (*Connochates gnou*)	---	645	645
Waterbuck[b] (*Kobus ellipsiprymnus*)	---	320	320
Giraffe (*Giraffa camelopardalis*)	---	340	340
Sable (*Hippotragus niger*)	---	52	52
Roan (*Hippotragus equines*)	---	63	63
Warthog	19 737	1 768	21 505
Ostrich (*Struthio camelis*)	912	156	1 068
Tsessebe[b] (*Damaliscus lunatus*)	--	13	13
Nyala[b] (*Tragelaphus angasii*)	--	14	14
Water Buffalo[b] (*Bubalus bubalis*)	---	16	16
White Rhino (*Ceratotherium simum*)	---	4	4
Lechwe (*Kobus leche*)	---	10	10
TOTAL	116 669	15 865	132 534

[a] 55 Game Farms surveyed, encompassing 246 761 ha
[b] Exotic Species

As presented in Table 2.3, the majority of the reported game (88%) was free-ranging rather than in game-fenced areas. Fifteen percent of the reported species on game-fenced farms was exotic. In the study area, the ratio of game to cattle varied greatly, from a low of 1:19 to a high of 99:1. The average ratio of game to livestock in the study area was 1:2.

2.4 The Waterberg Conservancy

The Waterberg Conservancy, which lies within the larger study area of the North Central Farmlands was the centre of my radio-tracking study area (Chapter 11) and consisted of 200,000 ha of farmlands owned by 11 neighbouring farmers (Figure 2.5). The Conservancy is situated around the southwestern point of the Waterberg Plateau Mountain, which is a national park.

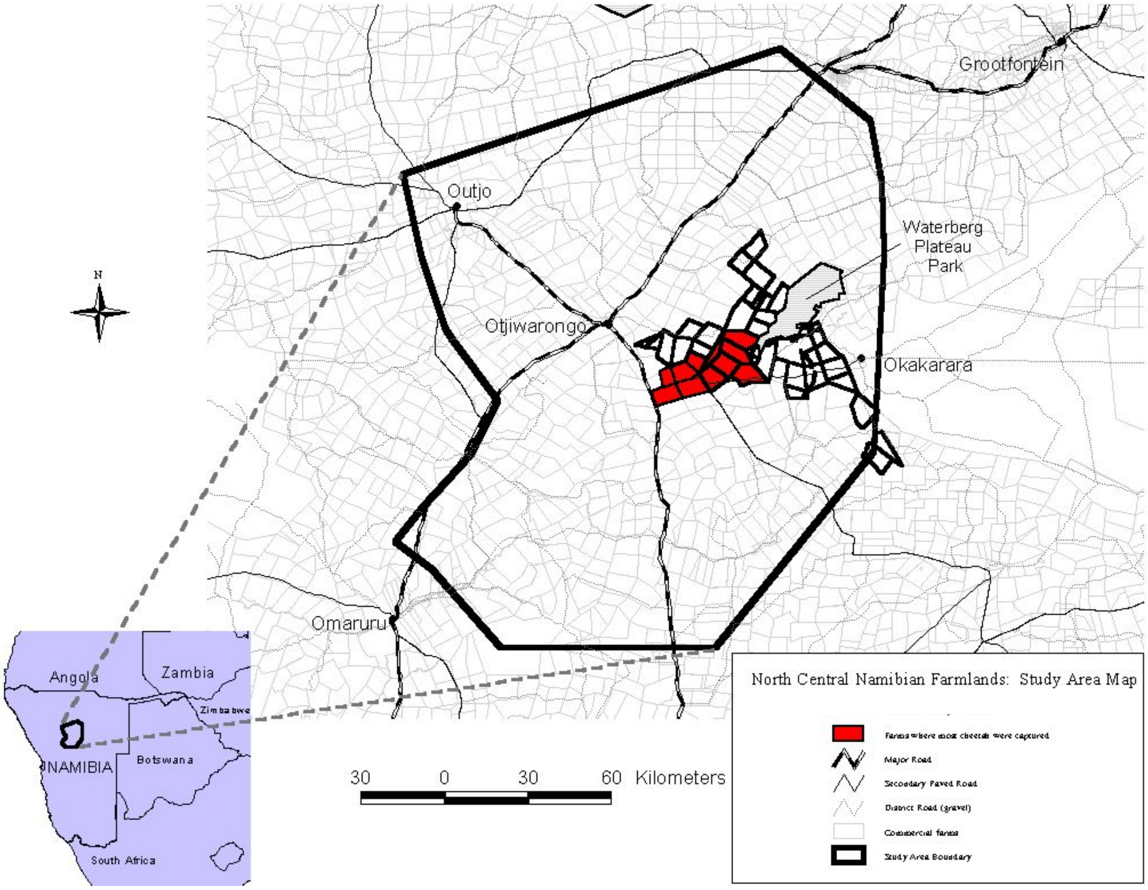


Figure 2.5 The Waterberg Conservancy, an area within the north-central farmlands, is the centre of the radio-tracking study area. Farms where over 50% of the cheetahs were captured for radio-tracking studies are highlighted. Waterberg Conservancy farms border the south-west boundary of the Waterberg Plateau Park.

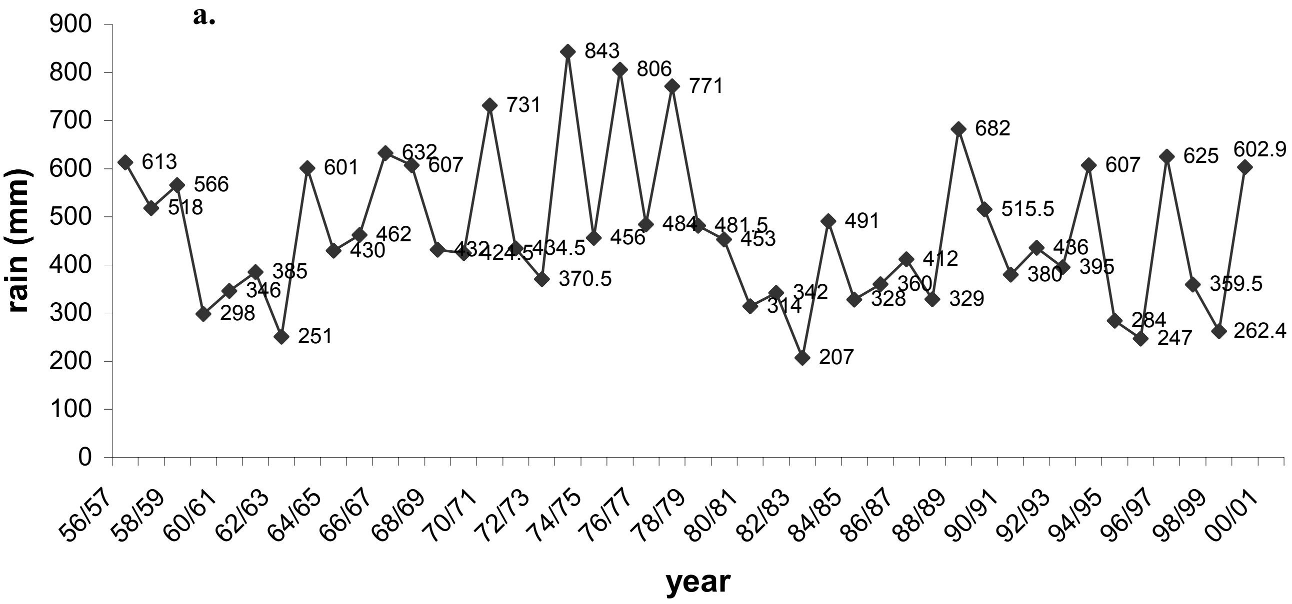
The Waterberg Plateau is a remnant of a much larger plateau that extended southwards some 100km. When 'Gondwanaland' broke up, some 150 million years ago, it caused an upwelling of lava covering huge area and compacting underlying sediments into rock and started an erosion cycle (Schneider 1993). The Waterberg Plateau is still at an elevation of 1,800m above sea level and the farms surrounding the Plateau close to 1,500 use meters above sea level.

The sediments that make up the plateau and surrounding lands are of the Karoo sequence laid down 290-120 million years ago, and consist of the Omingonde Formation (Schneider 1993). The Omingonde Formation consists of a mix of sandstone, conglomerated, mudstones, and siltstones. A 100m thick layer of dune sandstone was deposited over earlier sediments and is known as the Etjo formation (Schneider 1993).

The area in which the Waterberg Conservancy is situated is mixed bushveld savannah with a mean annual rainfall of 467.6mm (± 156.3, Figure 2.6a). Figure 2.6a shows the annual rainfall for a 43-year period, from 1957 through 2000, in the Waterberg

Conservancy. The mean rainfall per month averaged over the years 1957 – 2000 in the Waterberg Conservancy area is presented in Figure 2.6b. The mean rainfall for the hot, dry season (also referred to as the intermediate season, season 3) for the 40-year period of time was 123.37mm and for the hot wet (season 1) 348.60mm.

a.



b.

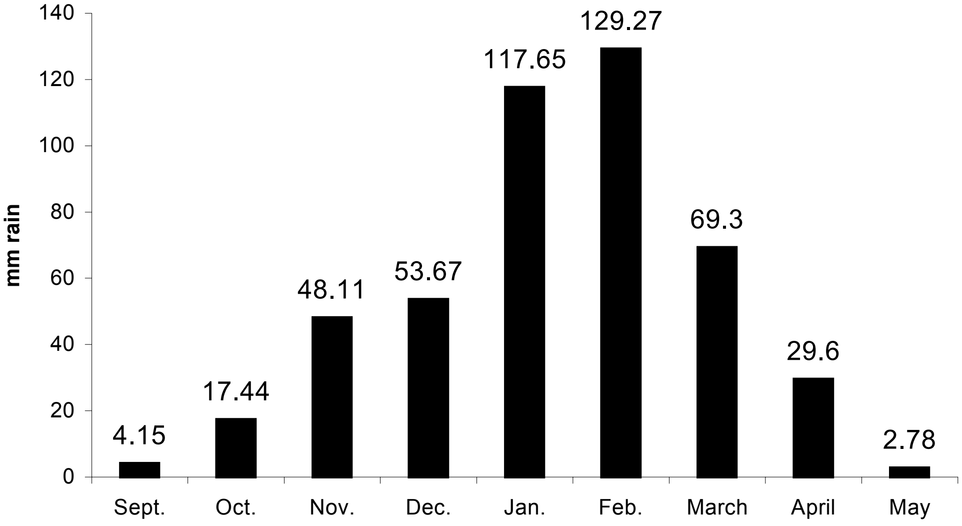


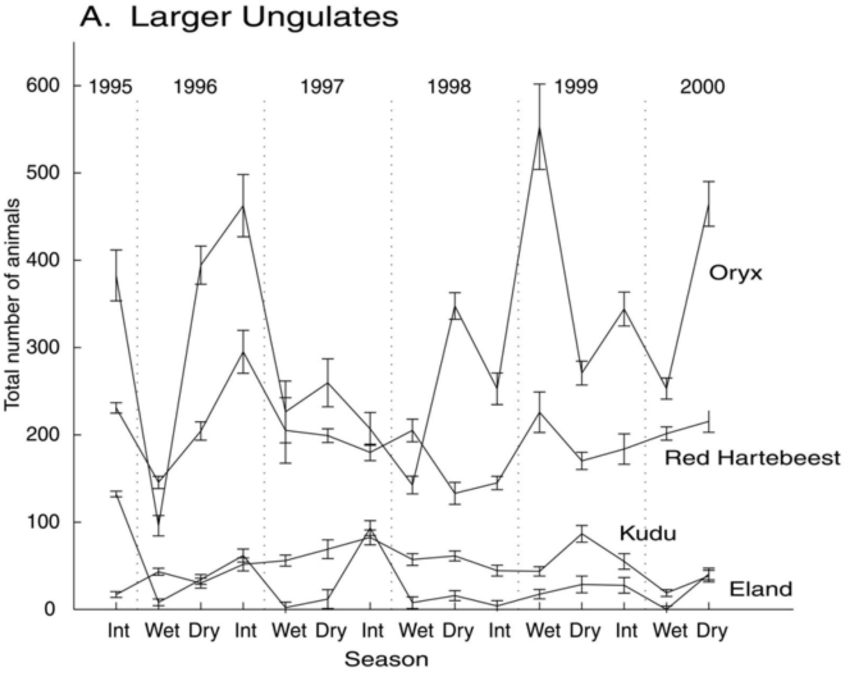
Figure 2.6a Annual rainfall in Waterberg Conservancy cheetah research study area (1957 – 2000). These data show the fluctuating rainfall over this 43-year period.

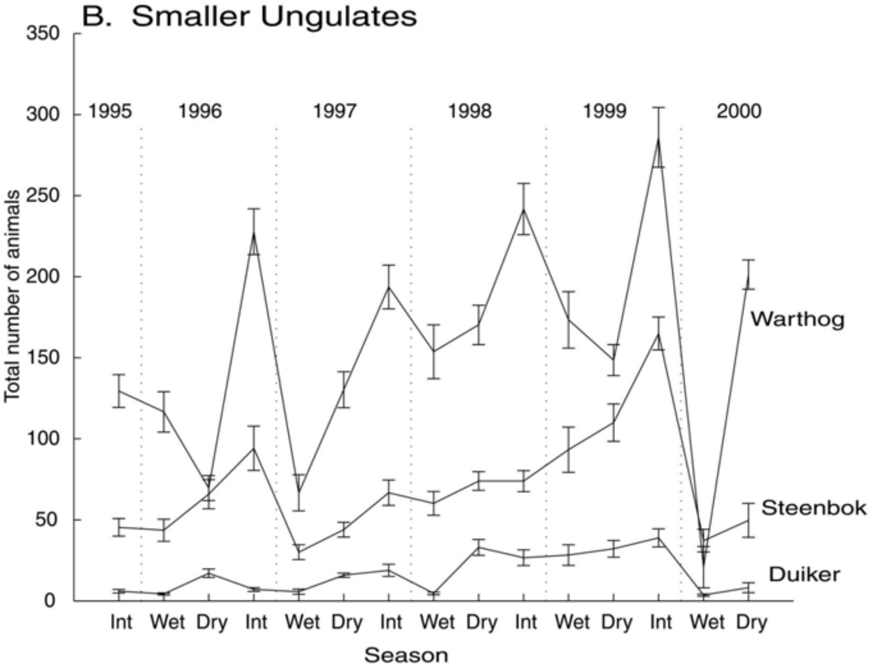
Figure 2.6b Mean rainfall per month (averaged from 1957 - 2000) in Waterberg Conservancy research study area.

2.4.1 Game densities in the Waterberg Conservancy

The Waterberg Conservancy supports a large number of species and game animals that are managed using a common game management plan. Conservancies are discussed in more detail in Section 2.6.2. The free-ranging game in the Waterberg Conservancy is representative of the game throughout the radio-tracking study area. To follow trends in game densities and habitat preference, a 4½-year study was conducted on the Cheetah Conservation Fund's research farm within the Waterberg Conservancy. Relative abundance of common ungulate species were examined in the different bush density habitats that are common in the study area (Muroua et al. submitted, Appendix III).

Road strip counts were used to document the seasonal density of kudu, oryx, eland, red hartebeest, warthog, steenbok, and common bush duiker. Figures 2.7a & 2.7b present numbers of each species counted during the three seasons from 1995 to 2000 and Table 2.4 present the density of the different game species in relation to different vegetation types (see Appendix III for complete methods for calculating game densities). This data shows that there are large fluctuations in game numbers during different seasons and years as well as in different habitat types. Game density and distribution in this study are discussed in relation to cheetah home range use in Chapter 11.





Figures 2.7a & 2.7b Numbers of individuals of seven game species counted 1995-2000.

Table 2.4 Game densities (animals/km^2) and estimated biomass (kg/km^2) by habitat type (sparse, medium, thick) using bush canopy.

	Game Density by Habitat (animals / km^2)				Estimated Biomass (kg/km^2)		
	Sparse Bush < 30% canopy	Medium Bush 30 to 75% canopy	Thick Bush > 75% canopy	Average weight	Sparse Bush < 30% canopy	Medium Bush 30 to 75% canopy	Thick Bush > 75% canopy
Oryx	2.34	0.77	0.99	150	351.4	115.9	148.6
Kudu	0.56	0.74	0.77	136	76.0	101.0	104.8
Red Hartebeest	0.49	0.06	0.18	125	61.5	7.2	22.9
Eland	0.34	0.06	0.10	340	114.5	20.6	35.2
Duiker	0.08	0.12	0.02	18	1.5	2.1	0.4
Steenbok	0.27	0.30	0.12	11	3.0	3.3	1.3
Warthog	0.26	0.22	0.21	45	11.5	9.7	9.6
		TOTAL BIOMASS BY HABITAT			619.4	260.0	322.8
		MEAN BIOMASS			**400.7**		

2.5 Social and economic features of Namibia

Namibia, known as South West Africa until its independence in 1990, is a huge country with a small human population (1.6 million people) (Barnard 1998). As a newly democratic country, gaining independence in 1990, it has a bitter sociopolitical history, which has affected people's attitudes towards each other and towards natural resource management.

Pre-history of Namibia dates the pastoral cattle-owning peoples from east-central Africa, the ancestors of today's Herero and Owambo-speaking Namibians, to the 16th and 17th centuries (Angula 1988). Well-established kingdoms, with structured economies, existed long before the arrival of the Europeans in Namibia (Barnard 1998). In 1884, Namibia was proclaimed a German protectorate, allowing Germans to expand into the productive rangelands for the development of a cattle-farming industry (E.U. 1995, Hamutenya 1988). After World War I, Namibia was placed as a protectorate of South

Africa and administered under their laws. Although German Namibians owned most of the country's businesses and farms until that time, South Africans began immigrating into the country as government administrators and were provided with livestock farms by the government. Today, seventy percent of Namibia's population is directly or indirectly dependent on agriculture as a livelihood (Schneider 1994, van Schalkwyk 1995), and extensive livestock farming is considered the backbone of the country's agriculture. The farmlands are divided into what are referred to as commercial and communal lands, each representing approximately 40% of the agriculture lands, of which 51% are cattle farms and 33% are small stock farms (Schneider 1994, van Schalkwyk 1995).

During the 1940s, as a result of the apartheid laws, re-settlement areas known as communal areas were formed for the individual native tribes (Katzoa et al. 1993). This re-settlement placed the people onto marginal agriculture land, which deteriorated through the communal farming system (Katzoa et al. 1993). The communal land has undergone various management practices primarily resulting from the sharing of land by the people and their cultural influences. These areas are known for the high density of farmers occupying the land, which is overgrazed and, in most areas, denuded of wildlife.

There are 6,000 commercial farms and approximately 4,400 commercial farmers in Namibia. The majority of the commercial farms range in size from 5,000 to 20,000 hectares (average 8,000 ha, Table 2.1) and are primarily bushveld with grasslands suitable for livestock or game (Marker-Kraus et al. 1996). In addition, 90% of the county's cheetah's habitat and range (Morsbach 1987) are on privately-held commercial farms.

Commercial livestock farming directly contributed approximately 10.7% to the GDP in the 1980s (Barnard 1998) and beef products contribute 87% of the country's gross agricultural income (van Schalkwyk 1995). Namibia's commercial farming sector is geared towards maximising the returns for high quality meat products with other products (i.e. hides or game) being of secondary importance (Barnard 1998).

Most farms practice mixed farming with both livestock and free-ranging game as an estimated 70% of Namibia's huntable game species (Joubert and Mostert 1975) are on privately-held commercial farms. Additionally, game farming, where fenced farms keep game inside, contributes a large amount of foreign currency to Namibia, the majority from trophy hunting.

Trophy hunting is also conducted on the mixed livestock and wildlife farms with free-ranging game, where farmers are allowed to utilise their game and conduct shoot to sell and hunting for biltong as a part of their commercial farming practices. In a recent report from the Ministry of Environment and Tourism (M.E.T. 1999) it was estimated that in 1998 that more than US$ 42 million (N$ 250 million) was contributed to the Namibian GDP from wildlife production and utilisation, with the value from trophy hunting at US$ 4.7 million (N$ 28 million). The total derived from trophy hunting was US$ 26.7 million (N$ 160 million). Around 2,000 to 3,000 tourist hunters visit Namibia each year and approximately 1.3% of the country's population are directly employed in the hunting industry.

A 20- year survey (1972-1992) showed that the economic value of wildlife as a percentage of the total value of land use increased from 5% to 11%, the number of game species on privately owned land increased by 49%, and the abundance of wildlife on private land increased by 80% (M.E.T. 1999). They estimated that the national population of large mammals included 32 species, 700,000 animals with a nominal value of wildlife populations at an average of US$ 167 (N$ 1,000)/animal or US$ 117 million (N$ 700 million). The percentage (number) of total commercially and economically valuable wildlife animals includes: 21% (150,000) of on Protected Areas, 71% (500,000) on commercial farmland, 7% (50,000) on Conservancies & state land (M.E.T. 1999). Annual off take of large mammals includes: 6-10,000 in live export, 6-10,000 trophy-hunted, and 80-88,000 hunted for meat, biltong, and personal use (M.E.T. 1999).

2.6 Development of Namibia's commercial livestock farming

The first European settlers colonised Namibia in 1884 and started the large commercial livestock farms that are still in production today (Schneider 1994). Since the beginning of farming in Namibia, farmers' interests conflicted with the existence of large predators such as lion, hyaena, wild dog and leopard. Close monitoring or protection of livestock was impractical due to the large size of farms, which were necessary to sustain livestock because of limited access to water. Elimination of predators became the accepted practice and lion, hyaena and wild dog were eradicated from the vast majority of the farmlands by 1950. Cheetahs were a rare sight on farmlands prior to the 1950s, possibly due to the presence of these larger predators (Gaerdes 1974a, Gaerdes 1974b).

The most important change to the environment was caused by the sudden abundance of readily accessible water for livestock, when farmers began sinking boreholes wherever water could be found. Prior to this, wildlife migrated throughout the country locating water and grazing sources. With the development of waterholes, wildlife became resident on the farmlands and, because they competed with livestock for water and food, they were culled to reduce competition. As a result, for example, kudu, oryx and springbok populations decreased by approximately 15% between 1955 and 1960 (Table 2.5). Farms were listed for sale in the 1960s as 'free of wildlife' (von Wietersheim 1988).

Table 2.5 Population estimates for three major game species in Namibia[a]

Species	1955	1960	1973	1980	1983
Kudu	72 500	60 800	111 900	200 000	83 700
Oryx	26 900	24 500	40 600	45 000	20 600
Springbok	45 700	37 300	141 900	250 000	91 700
TOTAL	145 100	122 600	294 400	495 000	196 000

[a]Namibia's Ministry of Environment and Tourism (Joubert 1985).

Over the 30-year period from 1960-1990, Namibia saw a 47% reduction in cattle numbers (2,077,511 to 1,107,082) on commercial farmlands, as thick bush has replaced the majority of open grazing land. This is a process known as bush encroachment (Schneider 1994). Bush has encroached over 14 million hectares of good farmland, primarily since the 1980 drought (Marker-Kraus et al. 1996). As a result, nearly one-third of Namibia's livestock farmlands have significantly decreased productivity and severe reduction of grazing lands. This has been exacerbated by farmland mismanagement. Research has recently shown that bush encroachment has affected this northern area by an estimated 8 to 10 million ha, and has reduced beef production on the affected land by up to 30% or 34,000 tons per year, which is worth about N$102 million (US$25 million) (Quan et al. 1994).

2.6.1 Drought, disease and game farming

Drought and disease in the 1960s increased the strain on the ecosystem already caused by the shift from diverse wildlife populations to high numbers of grazing livestock. In July 1961, a foot and mouth disease (FMD) outbreak devastated livestock production. Cattle were quarantined, preventing the common practice of moving cattle to areas of better grazing during drought. This resulted in high cattle mortality, as well as further degradation of the farmland (Schneider 1994). In 1961, the first veterinary cordon fences (2.8 m high game fences) were erected to prevent movement of wildlife and the spread of disease (Schneider 1994). A national vaccination campaign halted the spread of FMD, but the 1961 outbreak and animal confinement left grasses depleted and wildlife migrations disrupted.

Due to declining wildlife numbers, a 1967 Nature Conservation Ordinance transferred utilisation rights of huntable game species to the landowners, an economical method of encouraging landowners to conserve wildlife. Kudu, oryx and springbok populations then increased by 60% from 1960 to 1973 (Table 2.5) (Joubert and Morsbach 1982).

The good rains during the early 1970s produced good grasses. Farmers stocked heavily, with two to three times the recommended capacity of one large stock unit per 20 hectares (Berry 1990). The populations of three game species (kudu, oryx, springbok) increased by 40% between 1973 and 1980 (see Table 5). Cheetah numbers also increased during this time due to the reduction of larger predators, improved water development, and returning resident wildlife populations.

However, in 1979, the first indication of what was to become the country's worst drought of the century appeared (Schneider 1994), and the degenerative effects of overstocking began to show on the land. Grasses began to disappear, and in many areas of the country, as much as 60- 90% of the open grassland became heavy bush (Bester 1996). Farmers began to reduce livestock numbers on commercial farmlands during the 1980s, but the reduction was not rapid enough to prevent degradation of the entire farming system. Bush encroachment accelerated on the overgrazed savannah. Because the drought limited grazing, many farmers resorted to catching the migratory free-ranging game in order to protect their pastures for domestic stock use. Between 1981 and 1983 the game populations in the country declined by 50% (Table 2.5), due to the effects of the drought and game cropping (Joubert 1985).

In addition, at the end of the 1970s and into the 1980s, a rabies epidemic resulted in the mortality of nearly 80% of the kudu population (Hassel 1984). Although it is difficult to estimate the exact number of kudu that died during the epidemic, a conservative estimate places the loss at 30,000 to 50,000 (Hassel 1984) and contributed to the 58% decline in the kudu population decline between 1980 and 1983 (Table 2.5).

In the 1980s, with grass cover low from the drought and populations of kudu and other prey species reduced, cheetahs were more prone to predating upon livestock. The conflict between farmers and cheetah peaked (Table 2.6).

Table 2.6 Utilisation of cheetah in Namibia 1980 - 1991[a]

Method	1980	‘81	‘82	‘83	‘84	‘85	‘86	‘87	‘88	‘89	‘90	‘91	TOTAL
Shot[b]	623	669	850	721	646	537	318	317	272	271	301	145	5 670
Trophy Hunted	0	0	0	12	7	21	17	12	20	32	29	40	190
Live Exports	139	58	40	124	61	113	67	87	82	67	69	51	958
TOTAL	762	727	890	857	714	671	402	416	374	370	399	236	6 818

[a] Information derived from (CITES 1992). [b] For protection of livestock.

At the same time, the lack of suitable grazing land and lack of water prompted many livestock farmers to seek alternative revenue sources. Many farmers began confining game inside fences to propagate it for profit. In areas where game was abundant, farmers erected high game fences (2.6 m high and consisting of 21 strands of wire) on portions of their farms for utilisation of wildlife and trophy hunting. Most game farms were developed in the northern central regions of the country where diverse game populations were plentiful (von Wietersheim 1988).

2.6.2 Development of land conservancies for sustainable utilisation

In early 1990, shortly after Namibia's independence, many farmers were concerned about the increasing pressure exerted on wildlife due to varying methods of land utilisation and misuse of wild-game resources for personal gain. The concept of group-controlled, group-regulated land areas for conservation of wildlife was envisioned, and the conservancy movement was born. The first conservancy was established in Namibia in 1992 (Marker-Kraus et al. 1996).

A conservancy consists of a group of commercial or communal (tribal) farms on which landowners or land occupiers have pooled their resources for the purpose of conservation. Conservation for this purpose is described as 'the management of human use of organisms or ecosystems to ensure such use is of a sustainable nature... besides sustainable use, conservation includes protection, maintenance, rehabilitation, restoration and the enhancement of populations within ecosystems' (Marker-Kraus et al. 1996).

Namibia's commercial farmers were given conditional ownership over certain game species through the 1967 SWA Wildlife Ordinance (Ordinance 31), thus allowing private utilisation of game. However, game occurring in communal areas (state-owned tribal lands) stayed in possession of the government, as land occupied by 'indigenous' populations was, and still is, state-owned.

Due to this political disparity, people who lived on communal land were not granted the same conditional-use rights of certain game species as their commercial counterparts. After the establishment of the conservancy idea in Namibia, the Ministry of Environment and Tourism realised that conservancies on communal lands were a solution to this situation. Through regulations stipulated by an Act of Government, it is now possible for communal peoples to share in the wealth of sustainable game utilisation through the creation of conservancies on communal lands. Currently, there are 19 established and emerging communal conservancies, compared to 24 on commercial farmlands, of which some are using their land for hunting as well as for tourist activities (LM pers. obs). Local inhabitants who previously could not share in the benefit that proper game utilisation generated are now direct beneficiaries through the conservancy concept.

To streamline the conservancy movement in Namibia, an umbrella body, CANAM (Conservancies Association of Namibia), was established in 1994 to coordinate conservancy efforts and to act as a lobby group in the interest of conservancies and conservation. Conservancies are important for free-movement of wild game species and the tolerance provided for predator species as a part of the ecosystem. Today, the land conservancy concept is a growing movement throughout all of southern Africa.

2.7 Namibia's wildlife and environmental laws: a synopsis

Records from the 1760s show that early explorers to Namibia/South West Africa were impressed with the abundance of game throughout the country (Shortridge 1934). This natural resource was unregulated until German colonisation in 1884, when legislation was enacted and game became the property of the state, thus giving government control over hunting on private farmlands. Despite this legislation, farmers continued to remove wildlife to provide more grazing land for livestock.

In response to declining wildlife numbers, the Nature Conservation Ordinance 31 of 1967 placed utilisation rights of huntable game (excluding protected and specially protected species) under the care of the landowner on whose property the game was present. Thus, wildlife rights resided with the landowner. The rationale for this ordinance was that landowners would protect and manage wildlife if they owned it, because they would economically benefit from its existence on their land. With legalised ownership, it was surmised that owners would see game as an asset instead of a burden. However, some game species migrate and therefore continually 'change' ownership somewhat nullifying the concept of game as the property of a specific landowner or lessee. Although problems arose when individual farmers irresponsibly overutilised this mutual resource, this ordinance is directly responsible for the increase of game (Table 2.6) (von Wietersheim 1988).

Because of the decline of cheetah populations internationally, in 1970 the United States placed the cheetah on its Endangered Species List. In 1975 international endangered species laws placed the cheetah on Appendix I of CITES, and on the vulnerable or endangered list of IUCN. This classified the cheetah as an endangered species, which prohibited the sale of live cheetah or skins on the international market. Namibian farmers were confused by this classification, as they thought cheetah an abundant commodity.

Furthermore, a Namibian Nature Conservation Ordinance in (1975) classified the cheetah as a 'protected animal'. However, the same ordinance permitted shooting cheetah in the interest of protecting life or property. The ordinance specifies that cheetah removal through catching or shooting must be reported within 10 days to the state police or the present Ministry of Environment and Tourism.

The 1990 Namibian Constitution, Section 95, includes clauses supporting both sustainable utilisation of wildlife and protection of the environment and invites the private sector to cooperate, stating that it is the responsibility of every Namibian citizen (Namibian Government 1990). Sustainable utilisation can be achieved only through sound management practices backed by research and vigorously upheld by the active participation of people utilising the resource.

2.8 Trophy hunting of cheetahs

Namibia has a well-developed trophy hunting industry. Since 1992, CITES has allowed a limited trade quota of 150 Namibian cheetahs annually under a special exception in the Treaty. This quota is based on population estimates of 2,500 animals, made in 1986 (Marker-Kraus et al. 1996, Morsbach 1987). This limited trade includes legal trophy hunting as well as live export to internationally recognised zoological facilities. The quota was permitted in an attempt to reduce indiscriminate removal of cheetah. However, not every country has accepted the quota; the United States for example, lists the cheetah as an endangered species and will not downlist the Namibian population of cheetahs until scientific data provides reliable population estimations.

Since its inception, the annual quota of 150 animals has never been met (Marker and Schumann 1998). The number of cheetahs removed under the CITES however, are not a complete measure of the number of cheetah killed during these years, as additional cheetahs are killed annually to protect livestock or are indiscriminately removed.

In 1994, in an effort to support long-term conservation strategies for the cheetah, the Namibian Professional Hunters Association (NAPHA) developed a special committee called RASPECO (Rare Species Committee). This committee developed guidelines and programmes that support sustainable utilisation of rare species, such as the cheetah, for the enhancement of the species (NAPHA 1995). It was envisioned that through the development of this programme the indiscriminate catching and killing of cheetahs would stop, thus securing a future for the animal in Namibia and as such a committee was developed to define ethical hunting guidelines and produce a brochure for hunting cheetahs in Namibia (NAPHA 1995).

As part of this program, NAPHA members were asked to participate by signing a 'COMPACT for the Management of Cheetah' on their farms. The committee believed it was important for all involved to activate the hunters and farmers toward long-term cheetah conservation, as they are the people responsible for ensuring that all trade in cheetahs is sustainable and legal and that hunting quotas are enforced.

NAPHA members represent about 15% of the 3,000 plus landholders in Namibia. As of November 1998, more than 190 hunters had signed, comprising 1.5 million hectares and representing more than 70% of the land where NAPHA members hunt (Register 2000).

CHAPTER 3

ASPECTS OF THE MANAGEMENT OF CHEETAHS TRAPPED ON NAMIBIAN FARMLANDS

This thesis chapter has been submitted as the following paper:

Aspects of the management of cheetahs, *Acinonyx jubatus jubatus*, trapped on Namibian farmlands. L.L. Marker, A.J. Dickman, M.G.L. Mills & D.W. Macdonald. Submitted to *Biological Conservation.*

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CHAPTER 3: ASPECTS OF THE MANAGEMENT OF CHEETAHS TRAPPED ON NAMIBIAN FARMLANDS

ABSTRACT

The Namibian cheetah population has recently undergone serious decline due to human-mediated removals, and investigating the rates and causes of such removals is an important aspect of the future management of cheetah populations outside protected areas. We examined cheetahs that were reported live-trapped or killed on Namibian farmlands between 1991 and 1999. A perceived threat to livestock or game led to the vast majority of live captures and to almost half of the cheetah deaths investigated. Despite this, livestock predation from cheetahs appeared to be minimal, and was usually perpetrated by cheetahs with injuries. Most of the cheetahs were trapped in groups, and cheetahs' relative sociality leads to the easy removal of entire social units. Long-term monitoring must include detailed consideration of these indiscriminate removals, as they involve many cheetahs, fluctuate between years, often go unreported, and are likely to have a serious impact on cheetah populations outside protected areas.

3.1 INTRODUCTION

Intra-guild hostility is emerging as a fundamental element of carnivore communities, with important consequences for distribution and behaviour (Hersteinsson and Macdonald 1996). In the case of the cheetah, it has the practical consequence that their conservation within protected areas is often complicated by conflict with larger predators (Laurenson 1994, Marker 1998, Morsbach 1987, Nowell and Jackson 1996). Because of such competition in areas with, for example, abundant lions or spotted hyaenas, cheetahs are found in greater density on land where these large carnivores have been largely eliminated, as is the case on Namibian farmlands. They therefore occur in areas where they are likely to be in conflict with livestock farmers due both to the development of agriculture and to a reduced wild prey base (Caro 1994, Marker 1998, Marker-Kraus et al. 1996, Nowell and Jackson 1996). Therefore, whereas the conservation of some large carnivores may lie in protected areas, the survival of the cheetah is also likely to rely upon workable conservation strategies being implemented on farmland.

Most (perhaps 90%) of Namibia's approximately 2500 cheetahs are found in a contiguous 275 000 km^2 area of commercial livestock and game farmland (Marker-Kraus et al. 1996). There they kill smallstock and cattle calves up to six months of age, although the magnitude of their depredations is exaggerated (Marker-Kraus et al. 1996). Cheetahs enjoy protected status in Namibia, but an exemption allows them to be shot in the course of protecting life or property. Despite this protection, Namibian farmers have often removed wild cheetahs as a preventative and largely indiscriminate measure, by either shooting on sight or by live-catching them in traps and placing them in captive situations (Marker-

Kraus et al. 1996). The relative sociality of cheetahs enables entire social groups to be removed in one trapping effort, as the calls of one trapped cheetah will attract others in the group into adjoining traps (Marker-Kraus et al. 1996).

Between 1980 and 1991, the Convention for International Trade for Endangered Species (CITES) reported over 6700 cheetahs 'removed' from the Namibian farmland (CITES 1992). Considering their protected status, it is startling that during the 1980s Namibian farmers are believed to have halved the cheetah population from 6000 animals to less than 3000 (Morsbach 1987). This level of culling is clearly a potential threat to the cheetah, and irrespective of ethical considerations, raises the question of whether it is justified economically by reduced stock damage. It is this widespread and indiscriminate capture that is one of the most important factors to understand with relation to managing the cheetah population.

The Cheetah Conservation Fund is a non-profit organisation that was established in Namibia in 1991 in an attempt to understand and work towards reducing conflict between farmers and cheetahs on their land. The extensive contact made by the Cheetah Conservation Fund with Namibian farmers since 1991 provided a valuable opportunity to examine cheetahs that were live-trapped or killed on the farmlands and gain information regarding such removals. This paper examines the level of removals of cheetahs examined by the Cheetah Conservation Fund between 1991 and 1999, the causes for these removals and describes the subsequent fates of the captured cheetahs.

3.2 METHODS

Between 1991 and 1999, we examined cheetahs that were reported to us after being opportunistically live-trapped or killed on the Namibian farmlands. In order to live-trap cheetahs, farmers used capture cages, usually measuring approximately 2m x 0.75m, with trap release doors at each end and a trigger plate in the middle, as shown diagrammatically in Figure 3.1. Cheetahs were examined either in the field where captured or transported in a 2.2m by 0.85m crate up to 500 km to our research centre at Otjiwarongo.

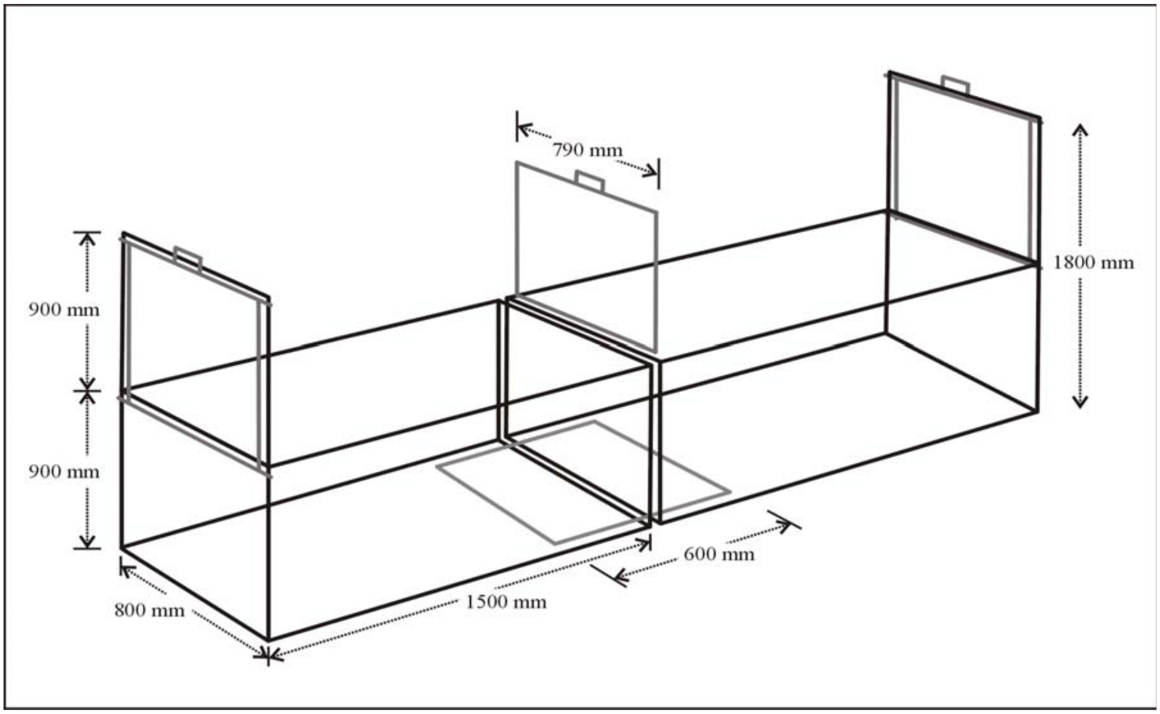

Figure 3.1 Design of a typical capture cage used to live-trap cheetahs on the Namibian farmlands

Age classification was based on the descriptions from previous studies and on personal experience (Blueweiss et al. 1978, Burney 1980, Caro 1994) and took into account weight, tooth wear, gum recession, wear on pads, pelage, scarring, body size, social groupings of animals caught together, and reproductive condition, as described below in Table 3.1.

Table 3.1 Description of the physical factors used to age cheetahs in this study. Information was gained through both personal experience of the authors, and data from other published studies (Burney 1980, Caro 1994). Each individual factor would not be sufficient to age an examined cheetah, but the consideration of numerous factors gives us more confidence in the age class assigned.

Category (class)	Age (months)	Teeth	Haircoat	Approx. weight (kg)		Approx. length (cm)		Approx. chest girth (cm)		General
				M	F	M	F	M	F	
Young cubs (1)	0—6	28-30 days: deciduous canines & incisors erupt, 45-50 days: molars erupt	6-7 wks: leg spots & yellow hair colouring develop; 3-4 m: loss of mantle	≤19	≤18	≤ 96	≤ 92	≤ 54	≤ 54	Eyes open 7-10 days, cubs emerge from den at ~6 weeks
Large cubs (2)	>6—12	~7m: lower incisors lost, ~8mo: adult teeth appear, ~9.5m: last adult molars erupt	Still have long fur on back of the neck, although it is no longer a defined mantle	12—31	12--30	84--120	82--114	42--61	40--57	Lanky appearance until ~9mo, then begin to fill out; acquire 2/3 adult size by 12mo old
Adolescents (3)	>12--18	No tartar or yellowing	Some long fur on back of neck; fur on face and body fuzzy and scruffy rather than smooth	30—38	25--35	110--133	105--125	60--76	56--64	Full height but not adult weight, leggy, still with dam
Young adults (5)	>30--48	Slight tartar and yellowing	Slight mane still, males have scars, females usually pregnant or with cubs	39—56	30--41	115--140	113--126	64--83	64--89	Fully grown but not fully muscled, in prime physical condition
Prime adults (6)	>48--96	Yellowing and tartar; slight gum recession, some gingivitis	Mane on back of neck is gone	37—58	31--52	118--137	115--126	66--80	63--75	Fully muscled, prime physical condition but starting to show signs of ageing
Old adults (7)	>96--144	Yellowing and tartar, gum recession, gingivitis, canines tipped, loss of teeth, esp. incisors	Coat beginning to look ragged, poorly groomed, scarred	-	26--48	-	105--131	-	-	Pads becoming smooth and elongated, sunken face, thinner, loss of muscle tone
Very old adults (8)	>144	Yellowing and tartar, gum recession, gingivitis, canines tipped, loss of teeth, esp. incisors and canines, broken teeth	Ragged, poorly groomed, scarred coat	-	-	-	-	-	-	Pads quite smooth and elongated, sunken face, body delicate and frail

Accuracy of these criteria was found appropriate by comparing these estimated ages with age categories determined from examination of cementum layers of the lower premolars of dead cheetahs (Matson's Laboratory, LLC, Milltown, MT, USA). Cheetahs in the first 3 classes were considered to be dependent upon their dam and were categorised as juveniles.

Cheetahs were classified as to the social group that they were a part of when they were captured or killed. Adult males were either found singly or in coalitions of two to four, while adult females were categorized as either being lone females or females accompanied by dependent cubs. The other social groupings of cheetahs included dependent cubs whose dam was not captured at the same time, and mixed-sex groups of young subadults, which were presumed to be littermate groups. While it was never possible to know without any doubt that all the members of any social group had been captured, the majority of farmers left their traps open for several days after catching a cheetah, and in this way were likely to catch the entire social group. In addition, the ground around a trap was checked for fresh cheetah tracks before a cheetah was taken away, to try to minimize the chances of trapping only part of a social group.

The date, location and reason for capture or killing was recorded, and whether any other individuals were trapped or killed at the same time. Farms were categorized as being either livestock farms, if they were operated using livestock as the primary source of revenue, or game farms, if game provided the major source of income. Some farms did not fit into either category, for instance the Cheetah Conservation Fund farms, which are kept primarily as research areas, and these were categorised as 'other'. In cases where the cheetahs were captured because the farmer perceived them to be a threat to his livestock, evidence was sought regarding whether the cheetahs captured had actually been causing a problem or not. Factors indicating that the cats caught were indeed ‘problem animals’ included capture on a livestock kill, and capture in or near a livestock kraal, especially one near human habitation. Such cheetahs were categorized either as definitely causing a problem, e.g. actually captured on a livestock kill, or likely to be causing a problem, due to more circumstantial evidence such as capture near a livestock kraal.

All the cheetahs were given a physical examination, both to collect morphometric and biomedical data, and to test the hypothesis that factors that may disadvantage the animal’s hunting ability could cause it to seek easier prey such as domestic stock. Such factors included eye injuries and cataracts, injuries to legs and feet, infected wounds, an unusually high parasite load leading to poor body condition, broken canine teeth and mouth injuries. Cases were excluded where the animal was still a dependent cub, had been held captive for over 30 days, or there was uncertainty regarding whether an injury had been sustained in the wild or while in captivity. In addition, where possible, the animal’s history was taken into account as certain behavioural factors may reduce hunting efficiency, e.g. the loss of coalition members or the loss of the mother when cubs were just reaching independence.

Fates of animals after examination included release back into the wild at location of capture, within 100km of the capture location, relocation within the country (defined as release further than 100km from the capture location), translocation out of the country, and being permanently placed in captivity.

Statistical analyses were performed using SPSS version 10.0 software (SPSS Inc. Chicago, USA) and Microsoft Excel 2000 (Microsoft Inc., USA). Means significance testing was carried out using the parametric independent samples t-test, while departures from expected ratios were analysed using a chi-squared test. In addition, the non-parametric Spearman's rank correlation coefficient was used to determine the significance of relationships between variables measured on nominal scales, while Pearson's correlation coefficient was calculated for interval data. All tests were two-tailed unless otherwise stated.

3.3 RESULTS

Overall, from 1991 to 1999, we performed 376 examinations on cheetahs that had been reported to us after being opportunistically live-trapped on Namibian farmland. Twenty-eight cheetahs were recaptured at least once during the study, including seven that were recaptured twice and two that were recaptured three times, totalling 37 recapture events in all. In addition, 32 necropsies were performed on cheetahs that were killed or found dead in the wild.

Table 3.2 presents yearly information about capture events, examinations and fates of cheetahs handled. The sex ratio of live captures differed significantly from an expected 1:1 ratio ($X^2 = 35.8$, $df = 1$, $p < 0.001$), with a strong bias towards males.

Table 3.2 Breakdown of capture events, necropsies and fates of examined cheetahs.

	Pre 91		1991		1992		1993			1994			1995		1996			1997		1998		1999		Total			Overall total
	M	F	M	F	M	F	M	F	U	M	F	U	M	F	M	F	U	M	F	M	F	M	F	M	F	U	
Original captures	11	2	7	1	19	14	31	21	0	26	9	0	24	11	12	13	0	40	16	33	23	10	10	213	120	0	333
First examinations	0	0	2	0	17	10	42	22	0	27	14	0	23	10	15	12	0	32	17	40	25	15	10	213	120	0	333
Necropsies	0	0	0	0	1	0	3	2	1	1	4	2	1	1	3	1	1	0	1	2	1	5	2	16	12	4	32
Recaptures	0	0	0	0	0	0	10	0	0	5	2	0	9	0	0	0	0	1	0	1	3	4	2	30	7	0	37
Releases within presumed home range	0	0	0	0	1	1	25	5	0	10	0	0	16	2	3	2	0	4	4	20	11	12	7	91	32	0	123
Releases outside presumed home range	0	0	0	0	0	0	8	4	0	8	7	0	0	2	4	1	0	8	1	3	3	0	1	31	19	0	50
Wild into captivity	1	0	2	0	13	8	10	12	0	3	3	0	4	3	1	1	0	22	12	16	10	2	3	74	52	0	126
Translocations	0	0	0	0	1	0	0	0	0	6	0	0	7	2	4	7	0	0	0	0	0	0	0	18	9	0	27

The length of time that had elapsed between capture and our examination ranged from 1 to over 100 days, with a mode of 2 days. The majority of cheetahs were examined within ten days of capture (Figure 3.2).

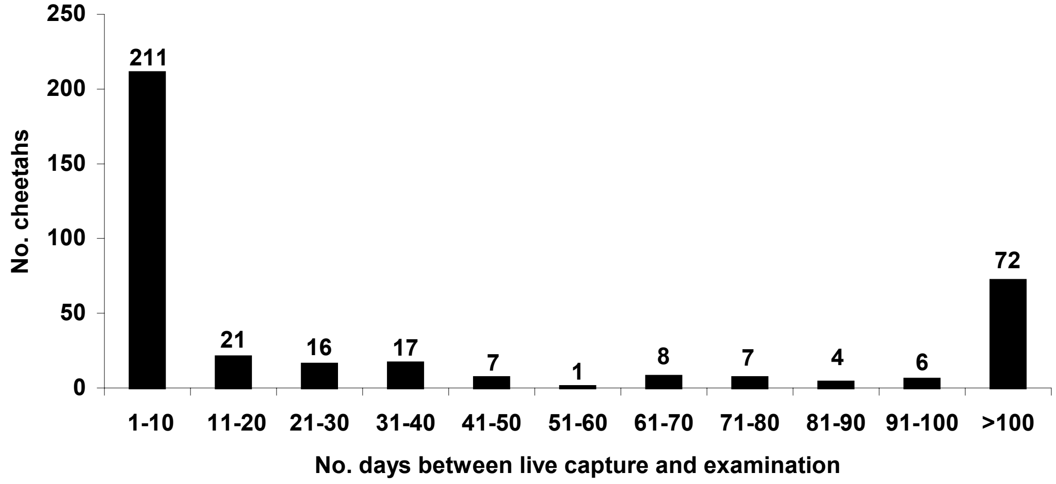

Figure 3.2 Number of days between reported date of capture and date of examination.

3.3.1 Dates of capture

There was a mean of 40.3 capture events reported annually to CCF between 1991 and 1999, ranging from eight in 1991 to 62 in 1993 (Table 3.2). There was highly significant variation in the numbers of capture events reported annually ($X^2 = 66.3$, $p < 0.001$). The number of groups of cheetahs captured each year from 1991-1999 also varied significantly ($X^2 = 31.6$, $p < 0.001$), ranging from 4 in 1991 to 32 in 1993, with a mean of 21.7 groups per year from 1991-1999 (Table 3.3). Both the number of individual cheetahs and the number of social groups reported captured showed a slight increase through the course of the study, although neither trend was significant (individuals: $r = 0.47$, $p = 0.169$; groups: $r = 0.51$, $p = 0.137$).

Table 3.3 Number of social groups captured and reported each year.

Year	Pre-1991	1991	1992	1993	1994	1995	1996	1997	1998	1999	Total
No. social groups captured	9	4	19	32	25	24	12	31	29	19	204

Month of capture was known for 370 of the 376 capture events and is shown in Figure 3.3. There was a significant variation in the number of cheetahs reported captured by month ($X^2 = 40.7$, $p < 0.001$), ranging from 13 to 47 with a mean of 30.8. The main peaks for captures were October, December - January and May - June.

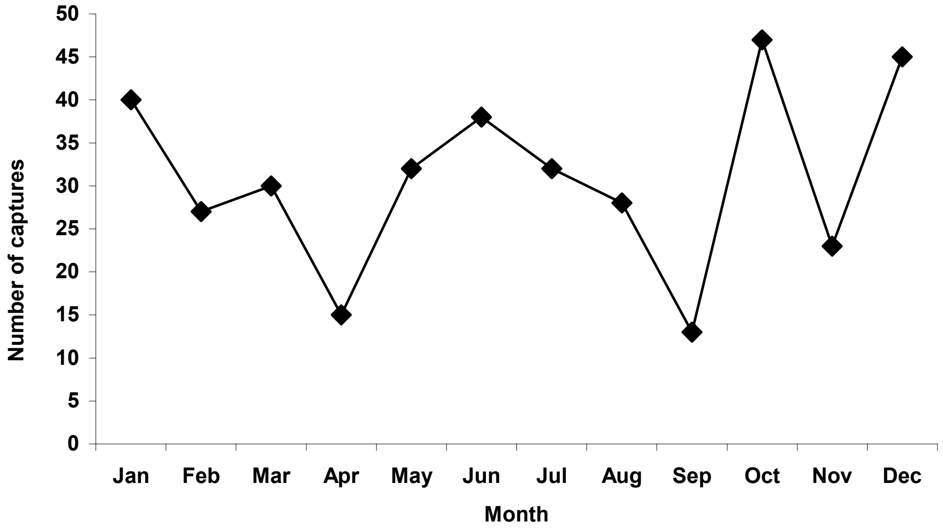

Figure 3.3 Reported month of capture for all cheetahs examined.

3.3.2 Reasons for live captures

The reasons for capture for all 376 live-trapped cheetahs are presented in Figure 3.4. The vast majority of cheetahs, 92.2% (*n* = 343), were trapped due to farmers perceiving them as a threat to either game or livestock. Livestock farmers comprised the significant majority of the 91 farmers that reported trapping cheetahs for this reason (χ^2 = 22.3, $p < 0.001$). Overall, therefore, significantly more cheetahs (57.7%) were reported captured in response to a perceived threat to livestock than to game (χ^2 = 8.2, $p = 0.004$).

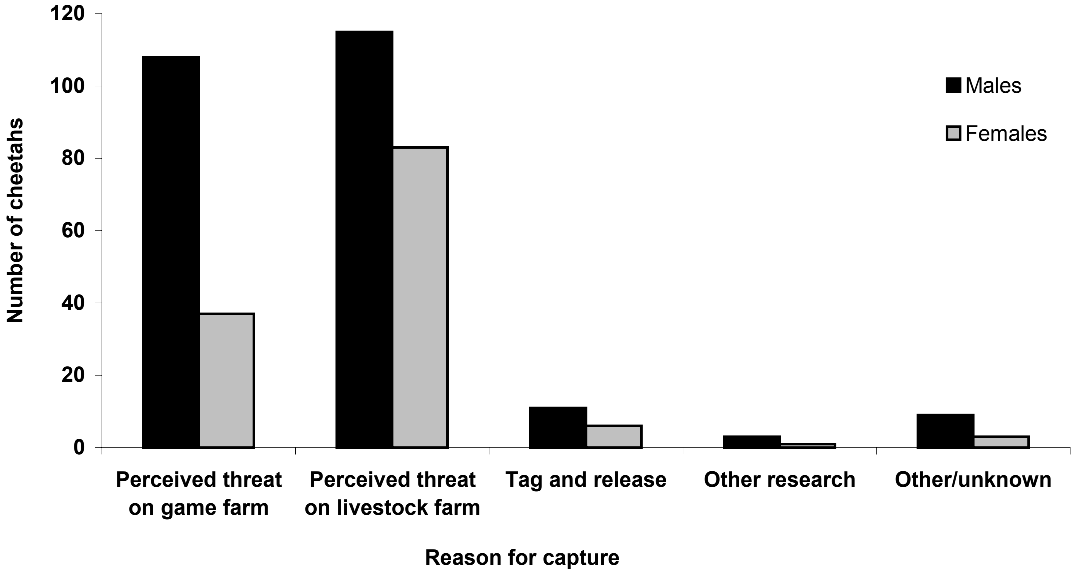

Figure 3.4 Reported reasons for capture of cheetahs examined.

Table 3.4 presents information regarding the number and social groups of cheetahs captured on different farm types. This indicates that although cheetahs may be perceived as a problem more frequently on livestock farms, game farmers capture proportionally more cheetahs when a problem is perceived ($\chi^2 = 51.8$, $p < 0.001$). This did not appear to be an effect of different farm sizes: size was known for 71 of the 91 farms reporting captures, and there was no significant difference in size between game and livestock farms ($t = 0.83$, $p = 0.410$).

Table 3.4 Demographic composition of cheetahs captured and examined (SM = single males; C = coalition groups, CM = coalition males, CS = coalition size.

							No. cubs with dam			No. cubs without dam				No. LM						
Farm type	**SM**	**No. C**	**No. CM**	**Mean CS**	**SF**	**Females with cubs**	**M**	**F**	**Total**	**M**	**F**	**Total**	**No. litters without dam**	**M**	**F**	**Total**	**No. litters**	**Mean LM group size**	**No. animals**	**No. groups**
Game farm	31	21	50	2.4	12	7	16	6	22	8	10	18	13	3	2	5	2	2.5	145	86
Livestock farm	22	15	35	2.3	13	17	25	25	50	28	21	49	24	5	7	12	5	2.4	198	96
Other	11	3	6	2.0	5	2	3	3	6	3	0	3	1	0	0	0	0	-	33	22
Total	**64**	**36**	**85**	**2.2**	**30**	**26**	**44**	**34**	**78**	**39**	**31**	**70**	**38**	**14**	**9**	**23**	**10**	**2.5**	**376**	**204**

Table 3.5 shows the social composition of the cheetahs caught on different farm types, as well as the results of statistical comparisons. Of the cheetahs captured as a perceived threat to livestock or game, significantly more coalition males were trapped on game farms given the ratio of farm types involved, while significantly more unaccompanied cubs were captured on livestock farms. There were no statistically significant differences for any of the other social groups, although slightly more females with cubs were trapped on livestock farms. When group sizes were examined between the different farm types, the group size of cubs trapped without a dam was greater on livestock farms, which accounts for the higher capture rate. There were no statistically significant differences for any of the other social groups.

Table 3.5 Demographic breakdown of cheetahs examined, separated by farm type.

Social group	No. captured on game farms	No. expected on game farms	No. captured on livestock farms	No. expected on livestock farms	Test statistic (A)	df	p	Mean group size on game farm	Mean group size on livestock farm	Test statistic (B)	Df	p
Single males	31	25.1	22	27.9	2.65	1	0.103	-	-	-	-	-
Male coalitions	50	40.2	35	44.8	4.53	1	0.033*	2.4	2.3	0.217	34	0.829
Single females	12	11.8	13	13.2	0.01	1	0.944	-	-	-	-	-
Females with cubs	7	11.4	17	12.6	3.17	1	0.075	3.1	2.8	0.699	22	0.492
Unaccompanied cubs	18	31.7	49	35.3	12.22	1	0.001**	1.4	2	-2.06	35	0.047*
Littermate groups	5	8	12	9	2.18	1	0.140	2.5	2.4	0.205	5	0.846

* = Significant at the $p < 0.05$ level (A) = Chi-squared test
** = Significant at the $p < 0.01$ level (B) = Independent samples t-test

The percentage of cheetahs examined that were captured due to a perceived threat to game or livestock decreased significantly through the course of the study ($r = -0.88$, $p < 0.001$). When this was examined by farm type, there was a decrease in the percentage of cheetahs captured to protect livestock through time ($r = -0.59$, $p = 0.071$) but the percentage trapped to protect game increased ($r = 0.25$, $p = 0.488$), although neither trend was individually significant.

3.3.3 Physical and behavioural condition

Overall, 15.4% ($n = 35$) of the adult cheetahs examined had a physical or behavioural impediment that had the potential to reduce their hunting ability (Table 3.6). There was no significant difference in the frequency of potential problems between the overall sample population and those trapped as being threats, nor any significant difference observed between cheetahs captured as a perceived threat on game farms and those on livestock farms ($\chi^2 = 0.02$, $p = 0.876$). When examined by social group, there were no significant deviations from the frequency of problems seen in the overall population for any group.

Table 3.6 Frequency of physical or behavioural problems observed in cheetahs captured and examined.

	Overall sample population (n=376)	All adults examined (n=227)	Adults trapped as threat on game or livestock farm (n=203)	Adults trapped as threat on game farm (n=105)	Adults trapped as threat on livestock farm (n=98)	Cheetahs probably taking livestock (n=6)	SM (n=64)	CM (n=91)	SF (n=30)	Females with cubs (n=26)	Cubs trapped without dam (n=70)	Litter-mates (n=78)
% healthy cheetahs	88.0	84.6	84.7	82.9	86.7	16.7	85.9	83.5	83.3	84.6	92.9	88.2
% cheetahs with a physical or behavioural problem	12.0	15.4	15.3	17.1	13.3	83.3	14.1	16.5	16.7	15.4	7.1	11.8
Chi-squared statistic	-	2.541	0.003	0.236	0.236	21.371	0.097	0.084	0.041	0.000	1.564	0.163
Df	-	1	1	1	1	1	1	1	1	1	1	1
P	-	0.111	0.954	0.627	0.627	0.000**	0.756	0.771	0.839	1.000	0.211	0.686

** = significant at $p < 0.001$ level

Although 198 cheetahs were captured through the study due to a perceived threat to livestock, there were only six cases (3.0%) where there was at least circumstantial evidence that the cheetah captured was indeed taking livestock. Of these six cats, five had physical or behavioural problems that could hinder their normal hunting technique. Three had injured paws, and one of these also had a respiratory disorder while another had several broken teeth, including a canine. The fourth cheetah causing problems had been part of a coalition but his brother had been shot previously, while the fifth had been released alone back into the wild at a young age and was in very poor condition when recaptured. There was therefore a significant relationship between the occurrence of problems that could impede hunting and the likelihood of preying upon livestock, with cheetahs apparently taking livestock showing a much higher than expected frequency of problems.

3.3.4 Fates after capture

Not all the captured cheetahs were removed, as some farmers were willing to have the cheetahs that they captured marked and then released back onto their land. To gain a better understanding of the level of removal on different farm types, we examined the eventual fates of captured cheetahs.

Of the 369 live cheetahs handled for which fates were recorded, 45.8% (*n* = 169) were held in captivity following examination, including 43 that were in permanent captivity prior to the examination and 126 wild cheetahs that were subsequently placed in captivity. Figure 3.5 presents the reasons for wild cheetahs entering captivity after examination. Nearly half (47%) were cubs captured on their own and were too young for release without a dam, while refusals by game and livestock farmers to allow releases accounted for 45% of wild cheetahs entering captivity.

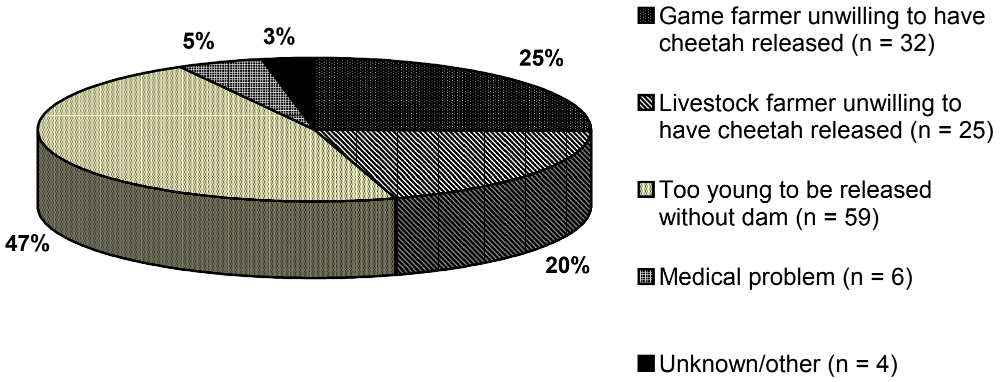

Figure 3.5 Reported reasons for wild cheetahs entering captivity after examination.

Of the 145 cheetahs that were trapped on game farms as a perceived threat, 115 were potentially releasable (i.e. healthy animals of independent age, or cubs that could have been released with their dam). Of these, 29.6% (*n* = 34) were placed in permanent captivity due to the farmer's refusal to allow a release. Similarly, refusal by livestock farmers to release accounted for the captive placement of 30.0% (*n* = 36) of the 120 cats caught for posing a threat to livestock that had potential for release. There was therefore no significant difference between game and livestock farmers regarding the percentage of healthy cheetahs that they decided not to release ($\chi^2 = 0.007$, $p = 0.933$). Both game and livestock farmers showed a decline in the level of refusals through the study, but these trends were not statistically significant (game farmers: $r_s = -0.276$, $p = 0.472$; livestock farmers: $r_s = -0.275$, $p = 0.509$). These trends are shown in Figure 3.6.

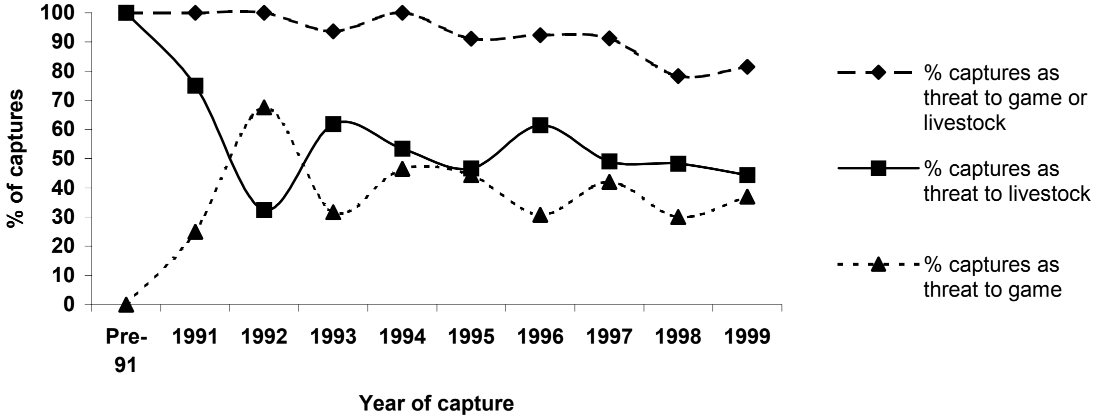

Figure 3.6 Trends in reported captures due to perceived threats towards game and/or livestock.

After examination, 46.9% (*n* = 173) of the 369 cheetahs were released back into the wild in Namibia. The majority of these, 71.1% (*n* = 123) were released either at site of capture or within their presumed home range, and 28.9% (*n* = 50) were relocated elsewhere within the country. Relocation distances varied from 100km to 600km from the site of capture, with a mean of 213km. Of the remaining cheetahs, 7.3% (*n* = 27) were translocated out of the country for re-introduction in other countries; 24 went to South Africa and three to Zambia.

3.3.5 Causes of death

During the study period 63 (40 males, 20 females and 3 of unknown sex) deaths of wild cheetahs were recorded. As with captures, the sex ratio of the reported deaths was significantly biased towards males ($\chi^2 = 6.67$, $p = 0.010$). Figure 3.7 presents the causes of death for the wild cheetahs examined. Human-caused mortality accounted for 79.4% ($n = 50$) of these recorded deaths. Ten were accidental deaths, including five in the wild and five in capture cages, while the remaining 40 were deliberate killings, including five males and two females that were trophy hunted. Although more of these deliberate killings occurred on livestock farms ($n = 25$) than on game farms ($n = 15$), the difference was not significant ($\chi^2 = 2.50$, $p = 0.114$).

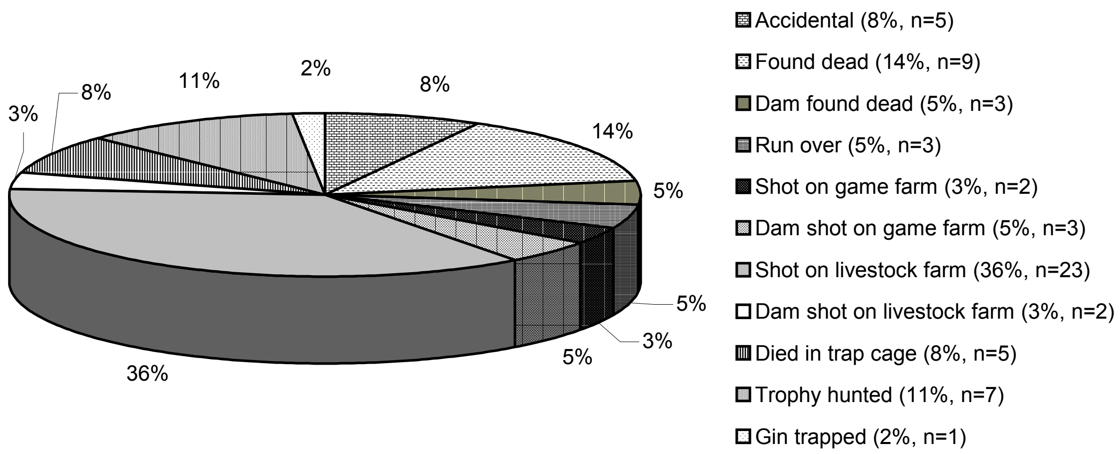

Figure 3.7 Reported causes of death for wild cheetahs.

The main cause of deliberate killings, accounting for 25 cheetahs, was being shot due to being a perceived threat, of which 92.0% were shot on livestock farms and 8.0% on game farms. In addition to these direct deaths from shooting, three cubs were assumed to have died after their dam was shot on a game farm, and two cubs were assumed to have died when their dam was shot on a livestock farm. Overall, therefore, shooting as a protective measure accounted for 47.6% ($n = 30$) of the total reported mortality in the wild. Trophy hunting, by comparison, accounted for only 11% of overall deaths.

3.3.6 Overall removals

Combining the data on human-caused mortality with that regarding wild cheetahs entering captivity and those translocated allows an overview of the number of cheetahs reported to the Cheetah Conservation Fund as removed from the Namibian farmlands each year. In total, 203 of the examined cheetahs (123 males, 78 females and 2 of unknown sex) were removed during the study period, including 126 captive placements, 50 human-caused deaths and 27 translocations. Most ($n = 118$, 58.1%) of these removals were directly attributable to the attitudes of game and livestock farmers. There was no significant difference between game and livestock farmers regarding the overall number of removals ($\chi^2=0.31$, $p = 0.501$).

3.4 DISCUSSION

Determining the rates and causes of removal from a population are vital to understanding the threats to its continued viability and how best it can be managed with regard to long-term, sustainable utilisation. Understanding the causative factors that lead to removals allows future management plans to be focused on the important areas of conflict between humans and cheetahs and to identify possible solutions.

These issues are particularly important with regard to the Namibian cheetah population, the vast majority of which occurs on privately owned land rather than in reserves, leading to a large potential for conflict, and which underwent a dramatic decline in the past (CITES 1992). The indiscriminate removal of cheetahs, which is unstable and fluctuates annually, must be understood both when considering quotas for legal utilization such as trophy hunting, and for formulating management plans. The information presented here can be used in future conservation efforts so that suitable strategies can be implemented that will not threaten the long-term survival of the population.

3.4.1 Dates of capture

The significant variation in the number of captures reported each year shows that indiscriminate removals are likely to fluctuate highly between years, making management of removals and an understanding of their long-term effects more difficult. There was no indication that the number of cheetahs trapped or removed annually had declined through the study period. However, it is difficult to interpret whether a change in the level of reported removals in a given year is a true effect or rather a result of variation in the reporting rate of such removals.

The fact that significantly more cheetahs were trapped in October, December-January and May-July is important as these times correspond with the main calving seasons in Namibia (Marker-Kraus et al. 1996). Farmers tend to increase their trapping effort around these times as a preventative measure against livestock loss. Introducing management techniques such as synchronising calving seasons within and between farms and using calving corrals and guarding animals, however, has been shown to be more effective in reducing losses to predators rather than indiscriminately removing them (Marker-Kraus et al. 1996).

3.4.2 Reasons for capture

During the study, the motivation for trapping 92.2% of cheetahs examined was a perceived threat to livestock or game. Previous studies have shown that actual loss of livestock to cheetahs is far less than is commonly thought (Marker-Kraus et al. 1996). This study supported that, as only 3% of the cheetahs trapped as a perceived threat to livestock were actually likely to have been causing livestock loss. Additionally, predation of game by cheetahs is natural behaviour; therefore, cheetahs captured in game farms should not on these criteria be perceived as 'problem' animals. However, the continued perception of cheetahs as a significant threat to livestock and game is clearly of vital importance with regard to reducing indiscriminate removal and must be addressed. As discussed above, the use of correct livestock management measures are more effective at reducing stock losses than indiscriminate predator removals (Marker-Kraus et al. 1996). Effective game farm management techniques include the exclusion of predators through proper maintenance (e.g. electrification) of perimeter fencing. The formation of conservancies has been effective in reducing farmer-predator conflicts and in improving game management (Marker-Kraus et al. 1996). Previous research has been influential in the formation of new wildlife laws that promote the development of conservancies (Marker 1998), and legislate that game farms cannot be managed in a way that is detrimental to wildlife.

Cheetahs causing livestock losses, but that are suitable for relocation back into the wild, should be considered for relocation to re-establish or supplement populations in protected areas such as national parks where domestic livestock does not occur. This could have an important impact in increasing genetic diversity within existing cheetah populations, as cheetahs have exceptionally low heterozygosity (O'Brien et al. 1983), which could potentially cause problems as populations become further isolated and fragmented. Cheetahs not suitable for re-release should be made available to supply the need for new bloodlines in captivity, taking the pressure off non-problem wild cheetahs. Such movements within Namibia should be monitored through an official body such as the Large Carnivore Management Association.

The trend seen that slightly more females with cubs were trapped on livestock rather than game farms could be taken to indicate that they were more likely to resort to stock-taking due to the pressures of raising a litter. In many cases, however, farmers increase their trapping effort upon seeing the signs of a female with cubs not in response to greater stock loss but rather as a preventative measure.

However, removing cheetahs indiscriminately, particularly if the farmer is not experiencing current problems, may actually create problems rather than preventing them. This might occur either by removing part of a social group and making it harder for the remaining ones to hunt efficiently, or by creating a vacuum that may become occupied by younger, more inexperienced dispersing animals. Under both these situations, the cheetahs left in the territory may not be as well equipped to hunt as before and may resort to taking livestock as easier prey (Marker-Kraus et al. 1996).

3.4.3 Physical and behavioural problems

The unusually high frequency of problems amongst cheetahs likely to be causing livestock loss, compared to the general adult population, indicates that these problems may be causative in making cheetahs prey upon domestic stock, rather than it being usual hunting behavior as is commonly thought by farmers. Although adult males are more prone to intra-specific aggression and there is a greater likelihood of them sustaining injuries during fights over dominance, mates or territory holding, there was no significant variation in the incidence of physical problems between different social groups.

3.4.4 Fates after examination

After examination, 34% of previously wild cheetahs entered captivity, mainly due to the capture of cheetahs that were too young to be released alone. The capture of young cheetahs without a dam means that those animals are unable to be released back into the wild, and could be made available for captive breeding programs to legitimate national or international zoological facilities to maintain their genetic lines. Live export of cheetahs is permitted by the CITES quota, but during 2000 Namibia stopped all export of cheetahs to zoological facilities, in an attempt to reduce market demand and stop indiscriminate catching (M.E.T. 2000).

Farmers' attitudes accounted for almost all the remaining wild cheetahs that entered captivity. Although the perception of cheetahs posing a significant threat to livestock is a long-standing one, in many cases it is exaggerated in relation to the actual number of cheetahs that cause losses. The predation upon game is a more difficult problem, as it is clearly natural behaviour, and in many cases game can only be protected through the exclusion of predators such as cheetahs. This study showed that the proportion of cheetahs captured as perceived threats declined through time, however, and that the proportion of healthy cheetahs that were refused release also decreased. This may be an indication of changing attitudes due to ongoing extension work with farmers regarding better livestock and game management techniques, and education about the cheetah's threatened international status despite its relative abundance on Namibian farmlands.

Nearly half of the cheetahs examined were released back into the wild; the majority (71.1%) back into their own territory. Initial analysis from a companion study at the Cheetah Conservation Fund has shown that relocation of cheetahs is a viable option in cases where the farmers are unwilling to have them released nearby. Further analysis of data gathered through radio-tracking these cheetahs will reveal the tendency to move back towards their original capture site, which is a common concern amongst farmers allowing relocation.

It is important to realize, though, that most of the releases reported here occurred as a direct result of long-term contact and work with farmers on a relatively small percentage of Namibia's farmlands. For the rest of the country, further from the core study area, releases are probably less likely and the number of trapped cheetahs alone may give the best indication of the level of removal on farms nationwide.

The translocations that occurred during this study were important in the successful re-establishment of the cheetah population in the Hluhluhwe-Umfolozi Park, which took place over a two-year period of time. In addition, the translocations helped to establish a cheetah population in Phinda, and were experimental in Zambia. These translocations stopped in 1996 after farmers began to allow more tag and release or radio-collaring of cheetahs within Namibia. Despite having been removed from the Namibian population, these translocations have played an important role in developing schemes for the cooperative management of cheetahs between different range states. In the future, such cooperative management will become an increasingly important component of cheetah conservation, and has been identified as a component of a Global Cheetah Masterplan (Grisham 2000).

3.4.5 Causes of death

The most common reported cause of death in the wild was shooting by livestock farmers, accounting for over a third of all deaths, and human-caused mortality appeared to outweigh natural causes of death. The number of removals, both live-trapping and deaths, in this study show that the Namibian cheetah population still undergoes a substantial offtake on an annual basis, especially as previous research shows that these numbers are likely to be only a small fraction of the actual total removals (Marker-Kraus et al. 1996).

Of the cheetahs that underwent necropsies, only seven were trophy hunted animals. The limited number of cheetahs trophy hunted can be of only minimal consequence to the population, especially when compared to the large numbers of cheetahs killed indiscriminately. However, the utilization of female cheetahs should be limited (Berry et al. 1996), and they are not recommended as trophy animals (M.E.T. 1999, NAPHA 1995).

3.5 CONCLUSIONS

Cheetahs actively seek to avoid larger predators such as lions and spotted hyaenas, instead dispersing into areas with low densities of these competitors (Durant 1998). The Namibian farmlands provide an excellent refuge from larger carnivores but provoke a conflict instead with the farmers who consider them a threat to their livestock and game. This results in widespread trapping, often performed as a preventative measure rather than in response to an actual problem, and leads to the removal of many cheetahs on an annual basis.

The most important step towards reducing such removals is continued extension work with farmers on livestock and game management techniques to decrease losses to predators and diminish the perception of cheetahs as pests. The same issues are relevant in other range countries, and are being addressed through collaborations between farmers and conservationists, e.g. the National Cheetah Management Program in South Africa and the Cheetah Working Group in Zimbabwe. In addition, well-regulated trophy hunting and community-based ecotourism are both viable options for giving cheetahs increased economic value on the farmlands and providing an incentive to reduce indiscriminate removals.

Where the removal of cheetahs is unavoidable, relocation is a viable alternative to killing them, as is the translocation into suitable areas with a viable prey base in other countries to supplement their cheetah populations. These movements involve complex issues, however, and must be done with thorough planning and adequate monitoring to be effective. If release is not possible, then moving the cheetah into a recognized national or international captive breeding facility should be an option in order to maintain genetic diversity and provide educational and conservation benefits. Meanwhile, continued monitoring of removals from the Namibian cheetah population will provide additional data, which can be used alongside those presented here in formulating future management plans and population models for effective conservation efforts.

CHAPTER 4

MORPHOLOGY, PHYSICAL CONDITION AND GROWTH OF THE NAMIBIAN CHEETAH

This thesis chapter has been submitted as the following paper:

Morphology, physical condition and growth of the Namibian cheetah, *Acinonyx jubatus jubatus*. Marker, L. L. and A. J. Dickman. Submitted to the *South African Journal of Wildlife Research.*

Chapter 4: Table of Contents

CHAPTER 4: MORPHOLOGY, PHYSICAL CONDITION AND GROWTH OF THE CHEETAH

ABSTRACT

Information regarding the morphology and growth of wild cheetahs is scant, and even where data exist they were rarely collected using a standardised methodology, making comparisons very difficult. We used a consistent technique to examine 241 Namibian cheetahs in order to study the morphology, growth rates and physical condition of wild cheetahs, and to investigate how these data compared to previous studies, both within Namibia and elsewhere. Cheetahs were examined between 1991 and 1999 in order to gather information on 20 different body measurements, investigate sexual dimorphism and determine growth rates. Significant sexual dimorphism, with the males being larger, was evident for all measurements. The majority of cheetahs were in excellent condition at the time of examination, although old animals and those that had been held in captivity for greater than a month were in significantly poorer condition. Cheetahs in excellent physical condition had a significantly higher weight to length ratio, but there was no significant difference between those in fair and poor condition. Both male and female cheetahs reached adult body mass at age group 6 (49-96 months old). Results from this study show significant differences when compared to those from cheetah populations in East and South Africa, although such differences may be due to variations in collection methodology or differences in morphology. It is therefore vital to standardise and describe morphometric data collection techniques in detail so that the true extent of differences between populations can be more accurately assessed. A suggested standardised collection methodology is presented.

4.1 INTRODUCTION

The cheetah is the world’s fastest land animal, and is highly specialized for speed in terms of anatomy, physiology, and behaviour (Ewer 1973, Gray 1968). Films of cheetahs running show an acceleration from zero to 80km/h in just 3 strides, with the maximum speed of 110km/h being attained in few seconds (Hildebrand 1959, Hildebrand 1961). Such impressive physiological ability is the result of a highly specialised morphology, including a lightweight skeleton, long foot and leg bones, and a small, aerodynamically efficient frame. The skull is small and thin-boned and the face is relatively flat with a reduced muzzle length that allows the large eyes to be positioned for maximum binocular vision (Ewer 1973). To rapidly alleviate the high oxygen debt accumulated through high-speed chases, the nostrils are enlarged and the sinuses are extensive and air-filled (Ewer 1973, Guggisberg 1975). In an evolutionary trade-off, the small skull cannot support a large masseter muscle bulk and the enlarged nasal cavity does not leave room for long root canals, so the jaws are weak and the canine teeth are small compared to those of other large cats. As a consequence, the cheetah is ill equipped to defend either itself or its kills from other large, more powerful predators (Caro 1994).

This uniquely specialised felid once ranged across Asia, India, the Middle East and Africa (Myers 1975), but it now occurs in only a fraction of its historic range (Marker 1998). Today, most taxonomists recognize 5 subspecies, although the extent of morphological differences between subspecies is uncertain and information from genetic studies indicates that cheetahs as a species are exceptionally uniform (Menotti-Raymond and O'Brien 1993, O'Brien et al. 1985, O'Brien et al. 1987, O'Brien et al. 1983).

Detailed information about the morphology of wild *A. j. jubatus* (sp.) is sparse but has shown some regionalised variations. Cheetah morphometrics have been described from several studies in different regions of Africa including East Africa (Caro 1994, Caro et al. 1987, McLaughlin 1970), South Africa (Labuschagne 1979, McLaughlin 1970) and Namibia (du Preez 1976), but only one of these studies (Caro 1994, Caro et al. 1987) provided a large data set. We collected morphometric data for almost 250 cheetahs from across Namibia over an eight-year period, making this the most comprehensive study of wild cheetah morphology to date.

We present data on the morphology of Namibian cheetahs and compare our results to those from other studies in southern and East Africa in order to examine the extent of morphological differences between cheetahs measured herein and elsewhere. Growth curves for wild cheetahs are presented, and the physical condition, growth, and morphology are all investigated in relation to age and sex. In addition, comprehensive measurement guidelines are defined that can be used in future studies. Our use of this standard measurement protocol on a large sample size should provide valuable information regarding the morphology, sexual dimorphism, physical condition and growth of wild cheetahs, and provide a solid base for comparisons with other studies.

4.2 METHODS

Cheetahs that were live-trapped or killed on Namibian farmlands between 1991 and 1999 were examined, using the capture protocol described in Chapter 3. Live cheetahs were immobilised either in the capture cage or in our squeeze/transport crate using either a hand syringe or blowpipe. Animals in a holding compound were darted using an air-pump dart gun (Telinject, Germany) or blowpipe (Telinject, Germany). In all immobilizing procedures, anaesthesia was administered intramuscularly in the hindquarters with Telazol (tiletamine-HCI and zolazepam HCI, Warner Lambert, Ann Arbor, MI, USA) 100 mg/ml with a normal dose of 4 mg/kg. The animals showed signs of sedation within four to six minutes and were recumbent within eight to 10 minutes. Dead cheetahs were collected and brought to CCF, where they were examined and the skeletons kept in storage. Cheetahs were assigned to one of eight age class categories using the criteria described in Chapter 3.

In many cases, cheetahs were held captive for some time before CCF was contacted, so the number of days that animals were in captivity prior to examination was recorded. For this study, only measurements and masses recorded from animals held <30 days in captivity were used, as they were hypothesized to be representative of the wild situation. Measurements for adult animals were included only when the individual had been caught as an adult (defined as >30 months old) in order to give a more accurate indication of the normal measurements for wild cheetahs, without influence from development in a captive situation. Data were not included if the age group was not known.

During anaesthesia, a thorough physical examination was performed and each cheetah was placed in 1 of the following 3 categories depending on condition, musculature, body fat, injuries, and external parasites: 1) excellent – robust, healthy coat, includes minor capture cage trauma; 2) fair – not robust, poor hair coat; 3) poor – sores, moderate to severe medical problems. Superficial wounds sustained in the capture cage were not considered while allocating categories, as they were not considered to be natural.

Morphometric data were collected on 20 variables using the protocol shown in Appendix IV. For variables measured on both sides of the body, such as tooth, leg, foot and testicle measurements, the mean was used for analyses. There was some variation in sample size for each parameter measured, as it was not always possible to measure every variable on every cheetah examined due to factors such as rapid recovery from anaesthesia or injury to a particular body part. Some cheetahs were examined multiple times due to treatment for injuries etc., but measurements were only recorded from the 1st examination for each adult cheetah unless additional data were obtained through subsequent examinations that had not initially been possible.

Vernier calipers were used to record skull length, skull width, muzzle length, tooth lengths, and foot measurements, and allowed measurements to be recorded to 0.1 cm. All other measurements aside from body mass were taken using a 200 cm measuring tape, and were recorded to the nearest 1.0 cm. Body mass was recorded to the nearest kilogram. Leg measurements were taken while the legs were positioned as if the cheetah was taking a normal step.

Rates of growth were estimated from measuring cubs of different ages, and from multiple examinations of individual cubs as they aged. As the rate of development in a captive situation may not be parallel to that in the wild, data were used only from cheetah cubs that had been held captive for <30 days in captivity prior to examination.

To investigate whether there were any spatial differences in cheetah morphology, we compared the cheetahs captured in different regions of the country. We used accepted National regions as designated by the Ministry of Agriculture (Schneider 1994). Temporal differences also were investigated by analysing results collected across seasons and years. Data were analysed using SPSS PC version 10.0.5 for Windows 95/98 and NT (SPSS Inc., Chicago, Illinois). Assumptions of normality were tested using the Kolmogorov-Smirnov and Shapiro-Wilk statistical tests, and in cases where the data deviated significantly from a normal distribution, parametric tests were replaced with non-parametric equivalents. Statistical techniques used included single-factor analysis of variance (ANOVA), Student's *t*-tests, independent samples *t*-tests using Levene's test for equality of variances, and the non-parametric Mann-Whitney and Kruskal-Wallis tests. Additionally, a regression analysis was used to describe the relationship between body weight and chest girth, following Currier (1979). Results were considered significant at $P < 0.05$, and all tests were 2-tailed unless otherwise stated.

4.3 RESULTS

Samples were categorized by sex and age group (Table 4.1).

Table 4.1 The numbers of male and female cheetahs examined, categorized by age group, during the study period. This included both 'wild' (captive < 30 days) and 'captive' animals (held for ≥ 30 days before examination). Percentages refer to the proportion of the total sample population that was contributed by each age group.

Age group	Male	Female	Total	%
0--6 mo	10	10	20	8.3
>6--12 mo	20	21	41	17.0
>12—18 mo	13	7	20	8.3
>18—30 mo	17	6	23	9.5
>30—48 mo	46	9	55	22.8
> 48—96 mo	47	24	71	29.5
>96—144 mo	5	5	10	4.1
>144 mo	1	0	1	0.4
Total	159	82	241	-

4.3.1 Sexual dimorphism

Significant sexual dimorphism, with males being larger, was evident for all measurements recorded, and is summarized in Table 4.2. There was a significant difference between the mean weights of male cheetahs between years ($F = 2.880$, *d.f.* = 8, $P = 0.007$) but not for females ($F = 1.136$, *d.f.* = 8, $P = 0.368$).

Table 4.2 Morphometric data for the wild adult cheetahs (aged over 30 m at capture, and held in captivity for <30 days), collected using the protocol shown in Appendix IV. All measurements are in centimetres (cm), apart from body mass, which is measured in kilograms (kg). Statistical tests were conducted between the measurements for adult males and females to ascertain the degree of sexual dimorphism exhibited for each parameter. *Test 1 = independent samples t-test, with equal variances assumed (test statistic = t), and test 2 = Mann-Whitney U test (test statistic = z).

Measurement	Adult male				Adult female				% dimorphism	Test*	Statistic	df	*P*
	Mean	Range	SD	*n*	Mean	Range	SD	*n*					
Body mass	45.6	31—64	5.99	99	37.2	26—51	5.14	38	22.7	1	-7.67	135	0.000
Upper canine length	2.2	1.6--2.6	0.20	87	1.1	1.7--2.3	0.16	37	5.3	2	-2.93	-	0.003
Lower canine length	1.6	1.0--1.1	0.23	86	1.4	1.0--2.0	0.22	35	9.5	2	-3.27	-	0.001
Skull length	15.7	11.1--18.0	1.04	85	15.0	12.0--17.0	1.06	38	5.3	2	-4.03	-	0.000
Skull width	14.6	12.4--17.2	0.86	84	13.3	10.8--14.7	0.75	37	10.2	1	-8.30	119	0.000
Muzzle length	7.7	5.6--11.5	1.15	86	6.8	4.9—8.6	0.80	37	12.3	2	-4.08	-	0.000
Muzzle girth	28.0	16—33	1.14	83	26.1	23—30	1.51	36	6.9	2	-5.19	-	0.000
Chest girth	71.7	64—83	3.86	90	67.3	56—75	3.76	38	6.5	2	-5.28	-	0.000
Abdomen girth	59.4	46—81	5.67	89	54.0	44—68	5.01	38	10.0	1	-5.10	125	0.000
Body length	125.5	108—152	7.03	94	120.1	105—135	5.91	38	4.5	1	-4.14	130	0.000
Tail length	76.7	51—87	5.17	94	72.5	57—79	4.83	39	5.9	2	-4.79	-	0.000
Total length	202.2	167—226	9.38	94	192.4	162—214	9.53	38	5.1	2	-5.28	-	0.000
Total foreleg length	77.0	71—86	3.07	85	73.6	62—80	3.58	38	4.6	1	-5.34	121	0.000
Total hindleg length	81.1	73—89	3.21	86	77.8	69—83	2.80	38	4.2	2	-5.12	-	0.000
Front foot length	8.2	6.8--9.8	0.47	87	7.8	6.8—9.0	0.46	38	4.7	2	-4.29	-	0.000
Front foot width	6.1	5.2--7.2	0.40	87	5.7	4.9—6.6	0.40	38	7.1	1	-5.25	123	0.000
Hind foot length	9.2	8.0--10.3	0.49	86	8.8	7.0—9.7	0.51	38	3.8	2	-3.40	-	0.001
Hind foot width	6.2	4.9--8.0	0.46	86	5.9	4.9—7.0	0.48	38	5.3	1	-3.41	122	0.001
Testicle length	2.8	1.9--3.8	0.49	81	-	-	-	-	-	-	-	-	-
Testicle width	2.0	1.5--2.6	0.23	83	-	-	-	-	-	-	-	-	-

4.3.2 Regional variation

Cheetahs were captured in seven different geographical regions (*n* ranged from 6-80 cheetahs) and there were no significant differences in adult body mass between cheetahs, either male or female, between regions (males: $F = 1.51$, *d.f.* = 9, $P = 0.165$; females: $F = 1.63$, *d.f.* = 6, $P = 0.173$). There was no significant effect of seasonality on body mass for adult males or females (males: $F = 1.715$, *d.f.* = 2, $P = 0.185$; females: $F = 0.273$, *d.f.* = 2, $P = 0.763$). Those cheetahs considered 'captive' at the time of examination, i.e. those that had been captive for ≥30 days, weighed less than the 'wild' cheetahs, although the difference was not statistically significant for either sex (males: $F = 3.034$, *d.f.* = 1, $P = 0.084$; females: $F = 0.294$, *d.f.* = *1*, $P = 0.591$).

4.3.3 Physical condition

Physical condition scores were assigned to 240 animals (99.6%), of which 63% (n = 151) were in excellent condition, 22.9% (n = 55) were in fair condition, and 14.2% (n = 34) were in poor condition. Overall there was no significant relationship between physical condition and any of the following factors: sex (z = -0.76, P = 0.449), season ($\chi^2 = 1.213$, d.f. = 2, P = 0.545), or region ($\chi^2 = 8.803$, d.f. = 9, P = 0.456). There also was no overall relationship between age group at exam and physical condition ($\chi^2 = 9.326$, d.f. = 7, P =0.230), although old and very old adults (those >96 months) were found to be in significantly poorer condition than other cheetahs (z = -2.96, P = 0.003). Cheetahs that had been held captive for ≥30 days were in significantly poorer physical condition (z = -2.40, P = 0.016).

The ratio of weight to total body length varied significantly between physical condition groups for adult wild cheetahs ($\chi^2 = 16.248$, *d.f.* = 2, $P < 0.000$), with cheetahs in excellent physical condition having significantly higher ratios than those in other conditions ($z = -4.00$, $P = 0.000$). This ratio (Figure 4.1) was not significant between those in fair versus poor condition ($z = -0.98$, $P = 0.328$).

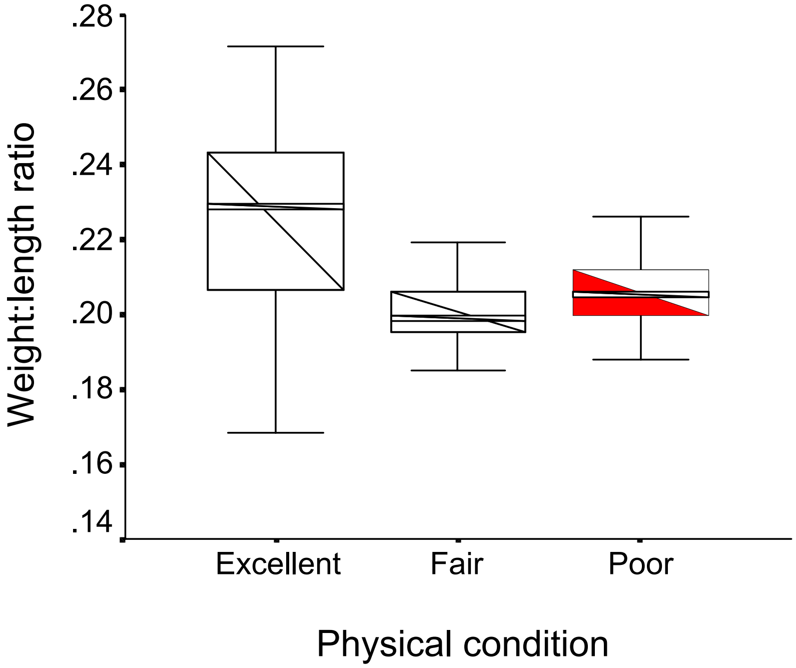

Figure 4.1 Ratios of weight to length for adult cheetahs in excellent, fair and poor physical conditions. Data were restricted to cheetahs that were captured when already adult (> 30 months old), and also to those that were considered to be wild at the time of examination, i.e. had been held in captivity for <30 days, to reduce the influence of captivity.

4.3.4 Growth curves

Full adult body mass was not achieved until age group 6 (49-96 months old) in our sample population, for both sexes (Figure 4.2).

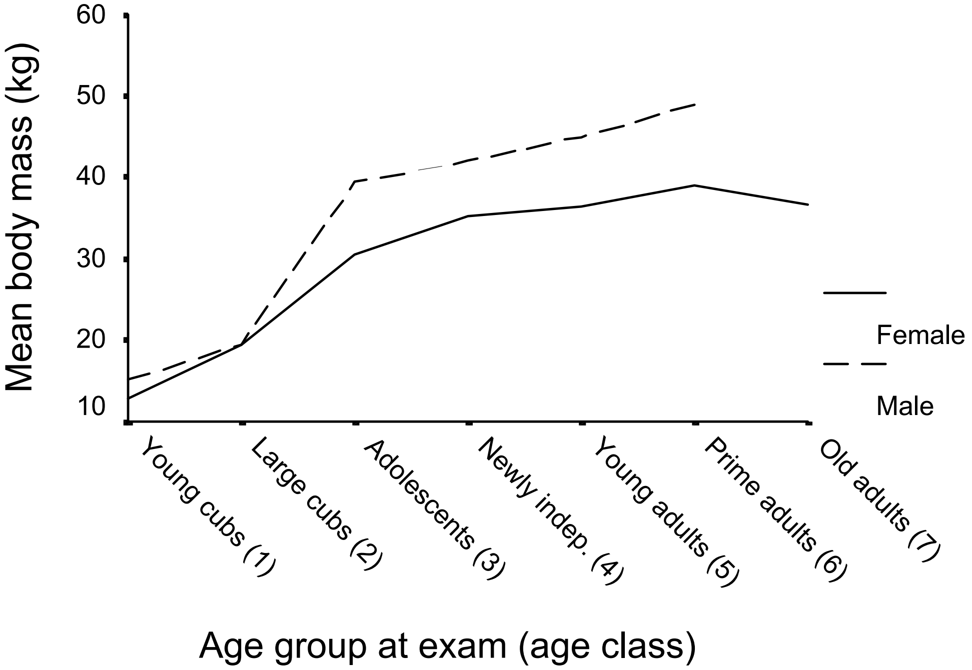

Figure 4.2 Mean body mass of Namibian cheetahs examined in different age groups, separated by sex. Data were restricted to wild animals, i.e. those that had been held in captivity for <30 days.

Growth curves, for both body mass and body length, are presented in Figure 4.3 using data from cubs (≤12 months old) that had been held captive for <30 days (range 1-13 days captive, mean 4.3 days for males, and range 0-14 days captive, mean 4.6 days for females). There was no significant difference in the length of time that male and female cubs had been held in captivity ($t = 0.345$, *d.f.* = 51, $P = 0.732$). Using a power equation, where y = body weight (kg) and x = chest girth (cm), a close correlation was found between these 2 variables ($y = 0.727x + 38.5$, $R^2 = 0.89$).

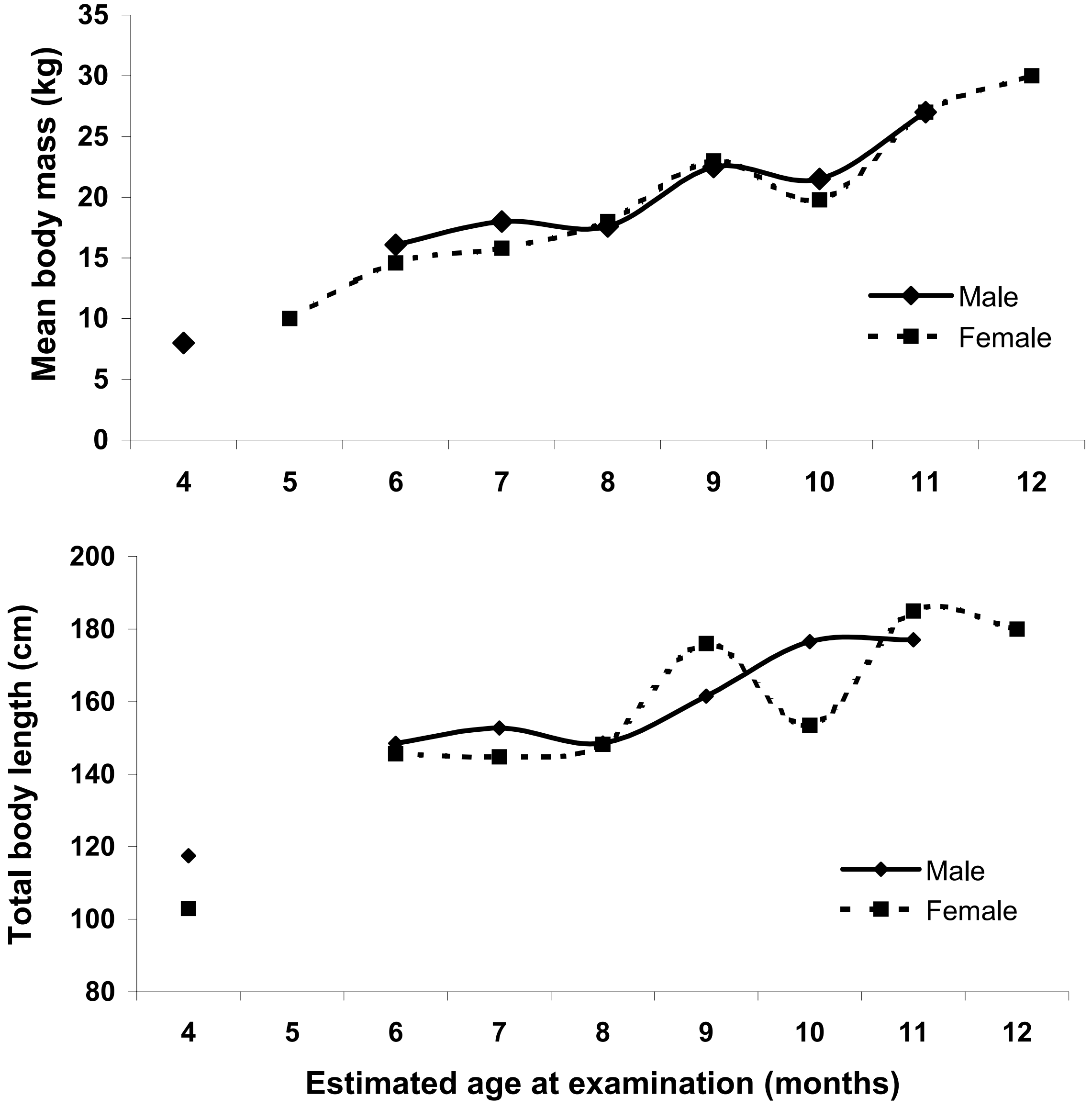

Figure 4.3 Growth curves for a) body mass and b) body length of wild Namibian cheetah cubs (those held in captivity for < 30 days by the time of examination), separated by sex.

4.3.5 Comparisons with other studies

The results from this study were compared to those found in other morphometric studies of cheetahs (Caro 1994, du Preez 1976, Labuschagne 1979, McLaughlin 1970). There were significant variations between studies for every parameter measured apart from female shoulder height (Appendix V) even when examining cheetahs of the same subspecies, suggesting that it may be the measuring protocols as much as actual body measurements that differ significantly between studies.

Compared to the South African population of *A. j. jubatus* (McLaughlin 1970), the Namibian cheetahs were smaller in some categories, for instance in body mass for both sexes, but larger for other parameters such as female chest girth. Sample sizes in the South African study were often small, however, and this may be a source of bias.

When the measurements obtained here were compared to those gathered from East African (*A. j. raineyii*) cheetahs in the Serengeti (Caro 1994), Namibian cheetahs were larger every time there was a significant difference. The data from the Serengeti cheetahs was strikingly different, however, from the East African data recorded by McLaughlin in 1970, despite both studies being performed on *A. j. raineyii*. The East African cheetahs examined by McLaughlin were significantly larger than those measured by Caro for all parameters apart from female chest girth, and generally were very large, with mean masses of 61kg for males and 52kg for females, compared to a mean across all the other studies of 48kg for males and 40kg for females. When the CCF data were compared to McLaughlin's results, the East African cheetahs appeared to be longer and heavier than the Namibian ones, although they had a smaller female chest girth.

McLaughlin (1970) studied both East and South African cheetahs, and there were no significant differences between the two subspecies for all measurements taken, apart from total length for males, where the East African males were longer. The McLaughlin (1970) data may be compromised, however, by the fact that it relies upon very small sample sizes of 1-6 animals, while the Caro data is more comprehensive, with sample sizes ranging from 12-24 animals, and the data in this study relying on larger samples still. Because of the larger sample sizes, we feel that Caro's results are more likely to be representative of the normal measurements of *A. j. raineyii*.

Both sexes of cheetahs measured in this study were significantly heavier than the measurements recorded for captive cheetahs in North American zoos (Wildt et al. 1993) (captive males: mean mass = 40.2 kg: $t = 9.05$, *d.f.* = 98, $P = 0.000$; captive females: mean mass = 35.0 kg: $t = 2.65$, *d.f.* = 37, $P = 0.012$). This followed the trend seen through the study, where cheetahs held captive for a month or more were lighter than their wilder counterparts, although the difference was not statistically significant.

4.4 DISCUSSION

The large home ranges of Namibian cheetahs (Marker 2000) and the homogeneity of the semi-arid farmland environment mean that the Namibian population is exposed to similar habitats and prey across different geographic regions. There would therefore appear to be no selective pressure for varying physical condition or body mass between seasons or regions of the country, and this was supported by the results of this study.

4.4.1 Physical condition

Physical condition did not vary between age groups except for older cheetahs (>96 months), and cheetahs held in captivity for an extended time (≥30 days). Older animals, both male and female, were in significantly poorer physical condition, which for females may be a result of the increased physiological stresses from rearing young, similar to that reported in mountain lion studies (Charlton et al. 1998, Roelke et al. 1985), and for males may be a result of territorial fighting over the years. Additionally, many of the older cheetahs examined were found to have suffered broken teeth, which could contribute to poorer physical condition in both males and females.

As a specialised sprinter and hunter, the cheetah's physiological makeup may need a certain amount of regular exercise to maintain optimum physical health. Studies conducted on captive cheetahs have shown a variety of health problems and stress related diseases that may be linked to low levels of exercise (Caro 1994, Caro et al. 1987, Munson 1993, Munson et al. 1999, Terio 2000). Although our study only presents physical condition scores rather than an in-depth analysis, wild cheetahs held in captivity for extended lengths of time (≥30 days) were in significantly poorer physical condition than others, and this could potentially predispose them to disease problems in the future (Munson and Marker-Kraus 1997).

4.4.2 Growth curves

Our growth curves indicate that cheetah continue to grow until they reach >49 months of age. This growth is comparable to the age when both female and male cheetahs are in their prime, are fully developed and muscled, and when males are able to hold and defend territories (Caro and Collins 1987). Quantifying relationships between body size and various other parameters has been presented for a number of species, to help predict certain ecological and physiological characteristics (Bailey 1968, Blueweiss et al. 1978, Charlton et al. 1998, Robinson 1960). In our study, assessment of physical condition scores of individual animals corresponded well with body weight to body length ratios.

Currier (1979) presented a useful correlation between chest girth and body weight of pumas that could be used in field conditions where scales are not available. This correlation has also been used in other species (Beger and Peacock 1988, Charlton et al. 1998, Durner and Amstrup 1996, Millspaugh and Brundige 1996) and showed a good correlation for cheetahs in our study, indicating that chest girth could be used to estimate weight fairly accurately in the field.

4.4.3 Comparisons with other studies

The cheetahs examined herein showed significant sexual dimorphism for all parameters measured, which differed from the Serengeti cats that exhibited dimorphism only in body mass, chest girth and tail length (Caro 1994). There also were significant differences in most of the variables measured between all the published studies (Caro 1994, du Preez 1976, Labuschagne 1979, McLaughlin 1970). These differences may reflect local adaptations to environmental conditions, e.g. climate, latitude, prey type and availability, but also may reflect differences in measurement protocols.

The Namibian cheetahs measured in this study were larger than the Serengeti cheetahs, but generally were smaller than the East African cheetahs measured by McLaughlin in 1970, despite both McLaughlin and Caro studying *A. j. raineyii*. Because of such discrepancies, it is difficult to make any conclusions about the extent of morphometric variations between the different subspecies. The fact that McLaughlin's results show very little variation between East and South African subspecies, presumably using the same measurement techniques, again suggests that differences in results between studies could be due as much to variation in measurement protocols as to actual subspecific variation.

McLaughlin's data are hampered by small sample sizes, however, and because of this, we consider Caro's study to be more representative of the normal measurements of *A. j. raineyii.*

Various authors have hypothesized about the possible causes of size variation within species, with factors such as climate, prey base and competition from other predators being of probable importance (James 1970). An in-depth discussion of potential mechanisms goes beyond the scope of this paper, however, and for further discussion interested readers should consult (Gay and Best 1996).

A study by O'Brien et al. (1987) revealed that the two subspecies *A. j. jubatus* and *A. j. raineyii* are genetically very similar, being separated by a Nei genetic distance of only 0.004. This extreme uniformity questions the validity of classifying them as separate subspecies based on genetic data, and it is difficult to establish the degree of morphological variation without using a standardised methodology. It is important to standardize techniques for gathering morphometric data, and for authors to clearly state how their data were collected, so that the extent of differences can be ascertained. This study presents a clear methodology used for measuring cheetahs, which, if adopted as a standard in future research, would make it easier to directly compare morphological variation between different populations.

CHAPTER 5

PATTERNS OF MOLECULAR GENETIC VARIATION IN NAMIBIAN CHEETAHS

This thesis chapter is in preparation as the following paper:

Population genetics of Namibian cheetahs (*Acinonyx jubatus*). Marker, L.L., A.J. Wilkerson, R.J. Sarno, J. Martenson, S.J. O'Brien & W.E. Johnson.

Chapter 5: Table of Contents

CHAPTER 5: PATTERNS OF MOLECULAR GENETIC VARIATION IN NAMIBIAN CHEETAHS

ABSTRACT

The Namibian cheetah population is the largest population of free-ranging cheetahs. The extent and phylogeographic patterns of molecular genetic diversity were addressed in a survey of 313 Namibian cheetahs from throughout their range. Size variation among 38 polymorphic microsatellite loci was assessed between 89 unrelated cheetahs from seven regions of the country, and an additional 224 individuals were assessed to investigate questions of paternity, gene flow, geographical patterns of genetic variation, and questions relating to cheetah behavioural ecology. Differences in microsatellite size variation showed limited regional differentiation supporting the notion of a panmictic population. Small F_{st} values were indicative of high recent gene flow between populations, and may be extenuated in Namibia due to the extensive removals (killing and trapping) of cheetahs by farmers over the past 30 years. Phylogenetic analyses revealed some population structure, with populations from the same geographic regions tending to cluster together. Measures of genetic variation were similar among all regions and were comparable to cheetah populations in Eastern Africa. Relatedness values (*R*) were calculated among unrelated individuals and among individuals in offspring and sibling groups of known individuals. Most of the previously hypothesized family groups were confirmed by paternity analyses, and 45 new potential sire/dam offspring and 7 sibling groups were identified, which provided information on cheetah social behaviour including dispersal and the success of translocation within the country through reproduction. Radio-collared female cheetahs were more closely related to the population of cheetahs in the study area than males, an indication that males

disperse from their natal home range. The long-term maintenance of current patterns of genetic variation will depend upon retaining habitat characteristics promoting natural dispersal and gene flow of cheetahs.

5.1 INTRODUCTION

In the early 1900s cheetahs were found in areas of suitable habitats throughout the Sahel area of Africa, and from the Middle East and the Arabian Peninsula to India and the southern provinces of the former Soviet Union (Myers 1975, Nowell and Jackson 1996). Today, cheetahs have been extirpated from a large portion of this area. Asian populations are nearly extinct, with the largest confirmed population (of less than 50 animals) inhabiting central Iran (UNDP 2001). In Africa, there are an estimated 15,000 cheetahs remaining, with the largest populations existing in Namibia, Botswana, and Zimbabwe in southern Africa, Kenya and Tanzania in East Africa (Marker and Schumann 1998), and smaller, more isolated African populations remaining in perhaps 23 other African countries (Marker 1998). The majority of these populations are threatened by high levels of intraguild competition within protected areas, habitat loss, poaching and widespread killing to protect livestock outside protected areas (Marker and Schumann 1998, Nowell and Jackson 1996).

One of the largest remaining cheetah populations exists across portions of north-central Namibia (Marker-Kraus et al. 1996, Nowell and Jackson 1996). As in other parts of Africa, these populations have historically been persecuted. In Namibia, the cheetah population halved in the 1980s, as over 6,700 individuals were trapped and killed as pests (CITES 1992). However, over the last decade management practices have been undergoing gradual changes (Marker and Schumann 1998, Marker-Kraus et al. 1996). Landowners are increasingly changing their preconceptions about cheetahs and allowing some degree of coexistence (see Chapter 12). However, farmers still trap cheetahs as a precautionary measure to reduce livestock loss. In the past these cheetahs were mostly killed. Due to changing attitudes, many trapped cheetahs today, if not directly caught killing livestock are allowed by the landowners to be released either on their own property or translocated to areas where farmers are more tolerant of cheetahs. There are an estimated 2,500 to 3,000 cheetahs in Namibia, over 90% of which inhabit unprotected areas on privately owned commercial livestock or game farms (Marker-Kraus et al. 1996, Morsbach 1987, Nowell and Jackson 1996). These farms generally have no lions or spotted hyenas and support over 70% of the country's huntable game animals (Joubert and Mostert 1975, Richardson 1998).

Namibian cheetahs are found in a variety of social groups, including coalitions of adult males, single adult males, single adult females, and family groups (females accompanied by dependent cubs, or groups of siblings that have recently reached independence), (Marker-Kraus et al. 1996). Male coalitions, which range from 2-4 animals (mean = 2.3), have average yearly home ranges of 910.4 km^2 (± 903.4 km^2) and females 1226.5 km^2 (± 618.6 km^2) (see Chapter 11). Cheetahs in Namibia have also been recorded as occasionally forming unusually large social groups (Marker-Kraus et al. 1996, McVittie 1979), suggesting perhaps that there might be more opportunity and perhaps less social resistance to individuals overlapping in similar home ranges (see Chapter 11).

Various aspects of cheetah molecular genetics have been well studied and have been the focus of much discussion and attention (Driscoll et al. 2002, May 1995, Menotti-Raymond and O'Brien 1993, O'Brien et al. 1985, O'Brien et al. 1983). The cheetah evolved from a common ancestor with the puma (*Puma concolor*) and jaguarundi (*Herpailurus yaguaroundi*), presumably in North America, in the late Miocene (5-8 million years before the present) (Janczewski et al. 1995, Johnson and O'Brien 1997, Pecon-Slattery and O'Brien 1998, van Valkenburgh et al. 1990) and predecessors of modern day cheetahs were once distributed across North America and

Europe (Adams 1979). However, by the end of the last glacial period, the cheetah had disappeared from most of its prior distribution, and the few surviving cheetahs experienced at least one severe demographic bottleneck that significantly reduced levels of molecular genetic variation as measured by several methods, including mtDNA sequence variation (Menotti-Raymond & O'Brien 1993), allozyme size variation (O'Brien et al. 1985, O'Brien et al. 1987, O'Brien et al. 1983, Roelke et al. 1993, Wildt et al. 1987), variation in the Major Histocompatibility Complex (MHC-RFLP) (O'Brien et al. 1985, Yuhki and O'Brien 1990) minisatellite variation (Gilbert et al. 1991, Menotti-Raymond and O'Brien 1993, Roelke et al. 1993) and microsatellite size variation (Driscoll et al. 2002). The bottleneck and associated loss of genetic variation has also been linked to several important life history characteristics of cheetahs, including increased fluctuating asymmetry in metric skull measurement (Wayne et al. 1986), relatively low levels of normal spermatozoa in males (Wildt et al. 1983, Wildt et al. 1987), immunologically accepted reciprocal skin graphs between unrelated individuals (O'Brien et al. 1985), and an increased susceptibility to infectious disease agents (Brown et al. 1993, Evermann et al. 1988, Heeney et al. 1990, Munson 1993, Munson and Marker-Kraus 1997, O'Brien et al. 1985).

During the 12,000 years since this bottleneck, cheetah populations have been reconstituting genetic variation, to the point where current levels of cheetah microsatellite variation approach those of several other outbred populations of felids (Culver et al. 2000, Driscoll et al. 2002, Uphyrkina et al. 2001). However, the heterozygosity observed using microsatellites may reflect the proposed late Pleistocene homogenization of allele variation that was followed by maximal reconstitution of microsatellite heterozygosity but incomplete size expansion (allele size breadth or MV), which requires a longer period for saturation (Driscoll et al. 2002, Goldstein and Pollock 1997). Therefore, the new polymorphic alleles observed in the populations today would have developed by new mutations in the elapsed interval. By an infinite allele model of evolution, the number of generations would be on the order of the reciprocal of the mutation rate (Driscoll et al. 2002, Nei and Li 1979, Nei et al. 1975). Additionally, there can be variation in mutation rates among microsatellite loci that depends of the repeat structure (Brinkman et al. 1998, Ellegren 2000, Wierdl et al. 1997). Using two estimated mutation rates, Driscoll et al. (2002) placed the mutation time from 488 – 1786 generations, or a minimum of between 2,928 and 10,716 years to generate the present microsatellite variation in cheetahs. The cheetah microsatellite variation shows a pattern of a recently and ongoing expanding population (Driscoll et al. 2002).

The goals of this study were to utilize the variation at 38 microsatellite loci to: 1) characterise patterns of molecular genetic variation across the Namibian cheetah population to determine if there were any major barriers to gene flow or recognizable substructure; 2) compare levels of molecular genetic variation among geographic regions in the country; and 3) utilize the microsatellite to address aspects of the social behaviour of Namibian cheetahs by looking at relatedness within known social groups including male coalitions, females with young and sibling groups.

5.2 METHODS

5.2.1 Sample collection and DNA extraction

Samples collected were from wild-caught cheetahs live-trapped in cages or wild-born captive animals using capture and anaesthesia methodology described in Chapter 3 from 1991 to 2000 throughout the range of the cheetah within Namibia (Appendix VI, Figure 5.1). The Otjiwarongo district contained the core population of cheetahs for this study; however, high numbers of cheetahs were also sampled from the Okahandja and the Omaruru district (Figure 5.1). From the core areas, forty-two individuals were fitted with radio-telemetry collars and their activities and movements were monitored for an average 19.4 (± 13) months (see Chapter 11). Cheetahs were classified into one of 5 social groups: single males, male coalitions, single females, mother with cubs, and independent siblings without a dam (see Chapter 3) and were categorised according to the social group with which they were caught, including dams (D) with offspring (off) and sibling (sib) groups and are labeled according to groups for relatedness tests (Appendix VI).

Total genomic DNA from 313 individual cheetahs was extracted from frozen leukocytes and blood stored in a concentrated salt solution (100mM Tris, 100mM EDTA, 2% SDS). DNA was extracted following one of two standard extraction techniques: phenol-chloroform (Modi et al. 1987, Sambrook et al. 1989) or salt precipitation (Montgomery and Sise 1990).

Figure 5.1 Map of regions where cheetahs originated.

5.2.2 Microsatellite markers

Nineteen microsatellite loci (FCA8, FCA26, FCA51, FCA85, FCA96, FCA97, FCA117, FCA126, FCA133, FCA169, FCA187, FCA212, FCA214, FCA224, FCA247, FCA290, FCA298, FCA310, FCA344) were characterised in 313 cheetahs (Figure 5.1, Appendix VI) to address questions of behavioural ecology. An additional 19 microsatellites (FCA14, FCA69, FCA75, FCA78, FCA80, FCA88, FCA94, FCA105, FCA113, FCA161, FCA166, FCA171, FCA192, FCA208, FCA225, FCA230, FCA327, FCA559, FCA42) were characterised in 89 presumed 'unrelated' cheetahs from throughout Namibia (Figure 5.1). Cheetahs were defined as 'unrelated' if they had not been captured or observed together, and were chosen when possible to ensure male and female representatives for all capture areas. The unrelated animals were then selected if they had more than 21 loci represented.

These microsatellites were amplified following previously described PCR amplification conditions (Menotti-Raymond et al. 1999, Menotti-Raymond et al. 1997). All microsatellites were dinucleotide repeats except Fca559 and Fca42, which had tetra-nucleotide repeats. These 38 microsatellites were from 11 of the 19 domestic cat chromosomes. Of the 38 loci, 23 were unlinked or at least 20 cM (centimorgams, a unit of distance between genes on chromosomes) apart in the domestic cat and are therefore assumed to be unlinked in cheetah (Driscoll et al. 2002, Menotti-Raymond et al. 1999). Five pairs of loci were linked at distances of 12 cM (Fca85/Fca96), 9cM (Fca075 and Fca096), 6 cM (Fca212/Fca126), 4 cM (Fca224 and Fca161), and 1 cM (Fca171/Fca161). The dye-labelled PCR products of the microsatellite primer sets were pooled and diluted together based on size range and fluorescent dye so that 3-6 loci could be multiplexed and electrophoresed and subsequently analysed in an ABI 377 automated sequencer. Microsatellite allele sizes were estimated by comparison with a GS350 TAMRA (ABI) internal size standard. Data were collected and analysed using the ABI programs GENESCAN (version 1.2.2-1) and GENOTYPER (version 1.1). PCR product length was used as a surrogate for actual repeat length (Ellegren et al. 1995).

Cheetahs were divided into seven geographic regions that in general lacked recognizable physical borders, but coincided with magisterial districts that defined the perimeters of large farms within the districts (Figure 5.1). Estimates of microsatellite size variation such as average expected heterozygosity, average variance, number of unique alleles and average number of repeats were derived from the program MICROSAT (version 1.5) (Minch et al. 1995) for different geographic regions. These estimates of cheetah microsatellite diversity may be biased relative to estimates from other felid populations since only polymorphic loci were used in the present study. Fisher exact test for deviations from Hardy-Weinberg equilibrium (Guo and Thompson 1992) and genotypic linkage disequilibrium between pairs of loci (Garnier-Gere and Dillman 1992, Garnier-Gere and Dillman 1992) were calculated using GENEPOP version 3.2 (Raymond and Rousset 1995) and provided p values for each population pair across all loci. With the same software package we estimated pair-wise genotypic and genic differentiation between populations (Goudet et al. 1996). F-statistic was calculated according to (Weir and Cockerham 1984) using FSTAT, version 1.2 (Goudet 1995) and ARLEQUIN (Schneider et al. 2000) to assess possible geographic structure and levels of gene flow among the geographic regions. F_{st} is a measure of the variation within the subpopulations relative to the total population and is the most inclusive measure of population substructure (Hartl and Clark 1997). Standard deviations for F_{st} and F_{is} values were estimated by jackknifing over all loci as implemented in FSTAT. If required, we corrected type 1 error levels for multiple testing according sequential Bonferroni procedure (Rice 1989). All computed p-values are 2-tailed.

Pairwise genetic distances among all individuals and among individuals from the same area were estimated from composite microsatellite genotypes using the proportion of shared alleles (Dps) algorithm with a (1-M) correction as implemented in the program MICROSAT (version 1.5, (Minch et al. 1995). A phylogenetic tree was constructed from the Dps distance matrix using the NEIGHBOR option of the program PHYLIP (version 3.572) (Felsenstein 1993) and was drawn using the program TREEVIEW (version 1.5) (Page 1996). Bootstrap values reflecting support for the estimated relationships among areas were estimated from 100 iterations using the routines of the program PHYLIP. GENETIX (4.01) (Belkhir 2000) was used to construct a Principal Component Analysis and produce a population cluster matrix.

The probability that proposed mothers were in fact the biological mothers was estimated using the program CERVUS (version 2.0) (Marshall et al. 1998). All individuals were compared against all others, as potential parents, to identify possible parents or situations where the individual had inadvertently been sampled more than once. We investigated the average relatedness between mothers and offspring, between siblings, and between unrelated animals by region. We also examined whether females were ever captured with cubs that were not their own offspring, and whether males captured in coalitions were more related to each other than to males randomly sampled from the population.

In order to infer the nature of the relationships between cheetahs, likelihood ratio tests were preformed to compare the probability of obtaining the pair of multi-locus genotypes of two individuals. In order to calculate these probabilities, baseline gene frequencies of unrelated individuals were required. The average pairwise relatedness among categories of cheetahs was estimated using the program RELATEDNESS 5.0.5 (Queller and Goodnight 1989). Based on these results we categorized cheetah pairs into either related ($R > 0.2$) or unrelated ($R < 0.2$) groups. The relatedness of 37 (24 males and 13 females) radio-collared cheetahs in our study was compared to each other, as well as to 89 (65 males and 24 females) of 120 cheetahs that were marked within the radio tracking study area.

To determine whether estimated degree of relatedness within the population might play a role in the social ecology of cheetah, the relatedness of cheetahs within the radio-tracking study area with R values > 0.2 to the radio-collared cheetahs was analyzed using a Mann Whitney U.

5.3 RESULTS

5.3.1 Genetic variability of microsatellite loci

A total of 248 alleles were observed for the 38 microsatellites analysed in 89 animals. The number of alleles per locus ranged from 3 (Fca 344) to 10 (Fca 096, Fca 097 and Fca 133) (see Appendix VII). The mean expected heterozygosity (H_e) was roughly similar for the seven geographic regions within Namibia (Table 5.1), ranging from 0.640 – 0.708 (Figure 5.2a), whereas values observed in the Serengeti cheetah population were comparable, however slightly lower (H_e 0.599, with an average of 4.08 alleles per locus) (Appendix VII). The mean number of alleles per locus was slightly higher in the region 5otj ($n = 4.6$) (Table 5.1), which is at the center of the Namibian cheetah's distribution area, and lowest in 6out region ($n = 3.7$) which is the western most area of their Namibian range (Figure 5.2b).

The number of group specific alleles varied from 0-6 (Table 5.1, Appendix VII). With the exception of the 7win region, all populations had at least one locus that deviated from Hardy-Weinberg expectations and showed significant ($p < 0.05$) deficiencies in heterozygosity (Table 5.1). After correcting for multiple testing none of the loci deviated from the Hardy Weinberg equilibrium.

Table 5.1 Heterozygosity and number of alleles by district

	DISTRICTS														
	1gob (n = 11)		2gro (n = 11)		3oka (n = 18)		4oma (n = 15)		5otj (n = 21)		6out (n = 7)		7win (n = 6)		(n = 89)
Loci	H_E	A	H_E	A	H_E	A	H_E	A	H_E	A	H_E	A	H_E	A	AT
Fca 8	0.718	4	0.764	5	0.667	4	0.65*	5	0.763	6	0.643	4	0.8	4	6
Fca 26	0.727	6	0.611	3	0.577	4	0.544	3	0.707	6	0.762	4	0.767	4	6
Fca 51	0.573	4	0.364	2	0.343	4	0.295	3	0.138	3	0.433	3	0.533	3	5
Fca 85	0.714	6	0.805	6	0.387	4	0.66	5	0.518	7	0.69	4	0.375	3	7
Fca 96	0.836	7	0.791	6	0.813	7	0.764	6	0.785	7	0.75	5	0.833	5	10
Fca 97	0.833	4	0.875	5	0.726	5	0.8	5	0.695	4	1	3	0.75	4	9
Fca 117	0.75	4	0.727	6	0.783	6	0.85	7	0.862	7	0.821	6	0.817	5	7
Fca 126	0.709	5	0.695	4	0.644	5	0.702**	5	0.55	3	0.607	3	0.583	3	7
Fca 133	0.659	5	0.65*	5	0.715	5	0.703	5	0.64	4	0.595	4	0.917	7	10
++ *Fca 169*	0.667	3	NA	2	0.75	3	0.5	2	0.683	4	NA	NA	0.917	4	4
Fca 187	0.445	3	0.632	3	0.556	3	0.59**	3	0.53	3	0.536	3	0.533	3	3
Fca 212	0.783	5	0.689	4	0.557	4	0.777	5	0.662*	7	0.786*	5	0.7	3	8
Fca 214	0.745	6	0.701	5	0.835**	7	0.786*	6	0.758	7	0.381	3	0.733	4	8
Fca 224	0.686	4	0.736	5	0.733	5	0.667	4	0.721*	5	0.619	3	0.767	4	6
Fca 247	0.677	3	0.732	4	0.699	4	0.673	5	0.765	7	0.65	5	0.825	4	7
Fca 290	0.618	4	0.741	5	0.668	6	0.558	4	0.651	4	0.774	5	0.7	4	7
Fca 298	0.255	2	0.464	2	0.488	2	0.514	2	0.42	3	0.143^{+}	2	0.55	3	3
Fca 310	0.709	4	0.786	6	0.651	4	0.721	4	0.638	4	0.702	4	0.75	4	6
Fca 344	0.491	2	0.509	2	0.472	3	0.51	2	0.498	2	0.548	2	0.4	2	3
Fca 14	0.764	5	0.755*	5	0.771	5	0.66	5	0.669	5	0.702	4	0.8	5	6
Fca 69	0.732	4	0.778	4	0.703	4	0.743*	4	0.741	4	0.738	5	0.733	3	5
Fca 75	0.691	5	0.814*	7	0.639*	5	0.84	7	0.627	5	0.762*	4	0.733	4	8
Fca 78	0.823	6	0.756	5	0.608***	6	0.75	6	0.779	7	0.675	3	0.75	5	9
Fca 80	0.6	4	0.573	4	0.619	3	0.47	3	0.621	4	0.607	3	0.6	3	4
Fca 88	0.727	5	0.7	6	0.694	4	0.705	5	0.623	4	0.631	4	0.817	5	6
Fca 94	0.636	3	0.723	5	0.678*	3	0.733	4	0.684**	3	0.762	4	0.683	3	6
Fca 105	0.741*	4	0.782	5	0.667	6	0.757	5	0.699	5	0.702	4	0.717	4	6
Fca 113	0.572	3	0.556	3	0.572	4	0.561	4	0.591	4	0.262	2	0.717	3	6
Fca 161	0.795	5	0.709	4	0.7	4	0.686	5	0.631	5	0.69	4	0.65	3	5
Fca 166	0.75	5	0.705	5	0.714	5	0.423	4	0.569	5	0.81**	4	0.7	4	5
Fca 171	0.85	8	0.8	5	0.741	6	0.821	6	0.787	5	0.464	3	0.833	5	8
Fca 192	0.673	5	0.644*	4	0.629	4	0.654	5	0.574	4	0.6	3	0.5	3	5
Fca 208	0.783	5	0.709	5	0.544	4	0.724*	5	0.751	5	0.683	4	0.7	3	5
Fca 225	0.736	5	0.655	3	0.709	5	0.712	4	0.641	4	0.488	3	0.767	4	5
Fca 230	0.823	6	0.768	4	0.765	5	0.827	6	0.764*	5	0.75	3	0.85	5	7
Fca 327	0.6	4	0.7	4	0.75	4	0.753	4	0.725	5	0.583	3	0.783	4	5
++ *Fca 559*	0.75	3	0.75	3	0.833	4	0.833	4	0.8	4	NA	NA	NA	NA	4
++ *Fca 042*	1	4	1	3	NA	1	0.75	3	NA	1	NA	NA	NA	2	5
Ave	0.700	4.5	0.701	4.3	0.655	4.4	0.671	4.5	0.642	4.6	0.640	3.7	0.708	3.8	6.1
Sd	0.130	1.3	0.121	1.3	0.118	1.3	0.136	1.3	0.137	1.5	0.144	1.0	0.130	1.0	1.8
FIS (mean)	-0.045		0.040		-0.029		-.0.003		0.099		-0.040		0.038		
FIS (sd)	0.255		0.244		0.181		0.272		0.187		0.187		0.235		

* = significant at < 0.05, ** = significant at < 0.01, *** = significant at < 0.001 (Hardy-Wienberg probability test)

$^{+}$ = sample size not adequate for Hardy-Weinberg probability test

++ = excluded from future analysis due to insufficient data

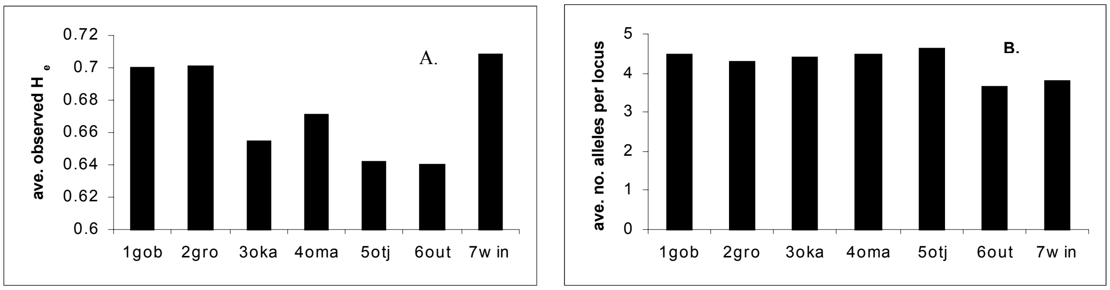

Figure 5.2a & 5.2b. Distribution of alleles (a) and allele frequencies (b) of selected microsatellites in the 7 regional populations.

5.3.2 Genetic relationship between regional groups

Three loci Fca 169, Fca 559 and Fca 42 were excluded from phylogeographic analyses because of insufficient data (Table 5.1). Both the neighbour-joining tree, constructed from a distance matrix based on the proportion of shared alleles (Dps) (Figure 5.3) and the population cluster graph (Figure 5.4), showed some substructure among the seven populations in Namibia. Both methods clustered populations in accordance with geographic location between the central/west (4oka and 5otj), the south/east (1gob and 7win) and the north (2gro and 6out) of the country. In

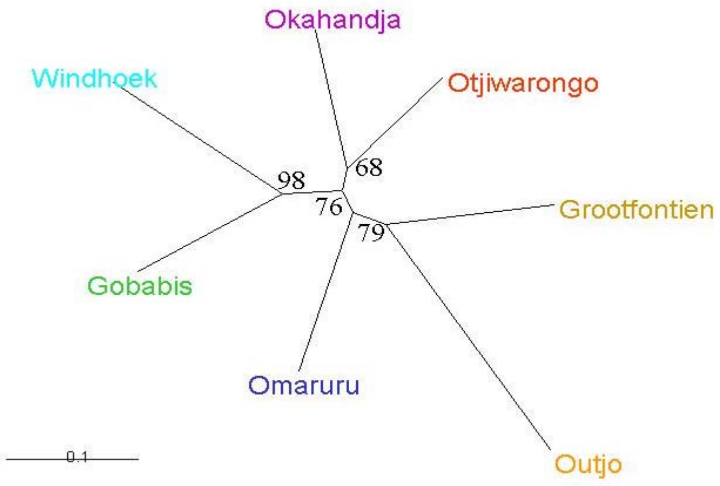

Figure 5.3 Phylogenetic depiction of relationships among 7 subpopulations in Namibia, constructed using proportion of shared alleles distances and the neighbour-joining algorithm.

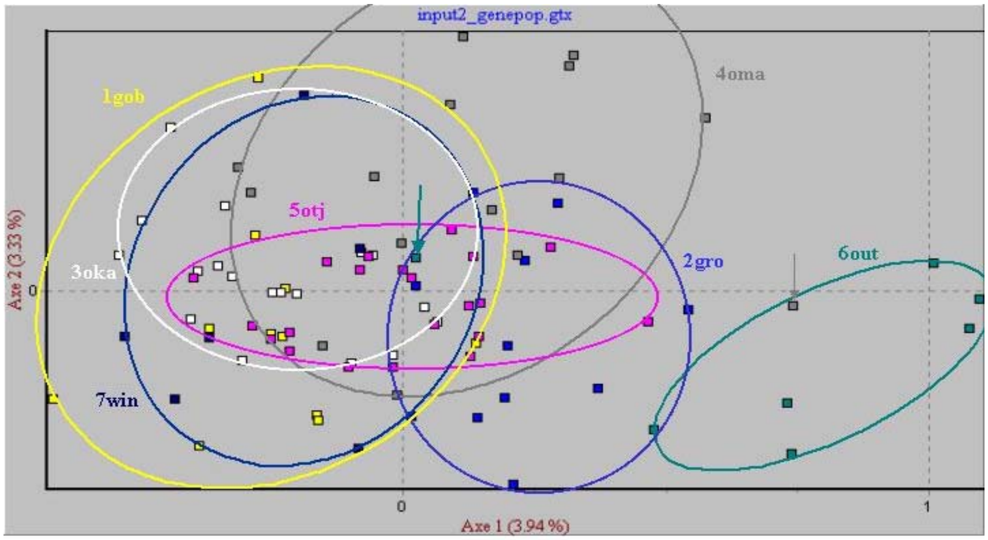

Figure 5.4 Population cluster graph from principal component analysis, showing subpopulation structures.

the population cluster graph (Figure 5.4), the pattern of distribution was consistent with the gene flow seen in Figure 5.3. In regard to the distribution of alleles, all populations were significantly different from each other (Fisher's exact test, all $P < 0.05$) with the exception of 1gob and 7win ($P = 0.80$), which are neighbouring subpopulations (see also Figure 5.5).

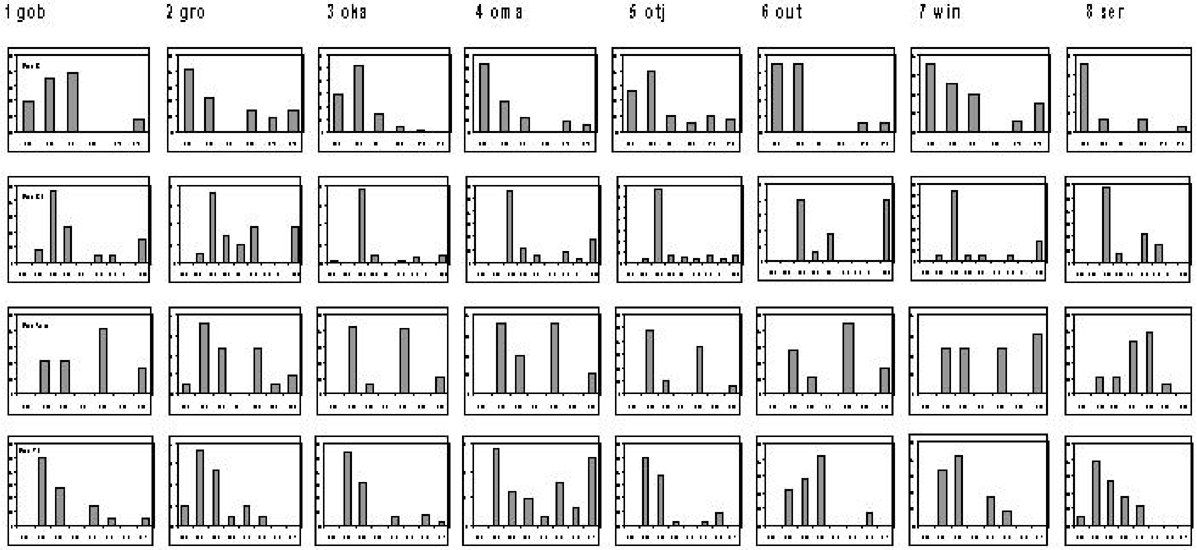

Figure 5.5 Allele distribution of representative microsatellite loci in the 7 regional groups and the Serengeti population (8ser).

The relationships among individual cheetahs were examined in a phylogenetic analysis of composite microsatellite genotypes of the 89 unrelated individuals (Figure 5.6) using the proportion of shared allele distances. There was no apparent structure, with individuals from different regions being intermixed.

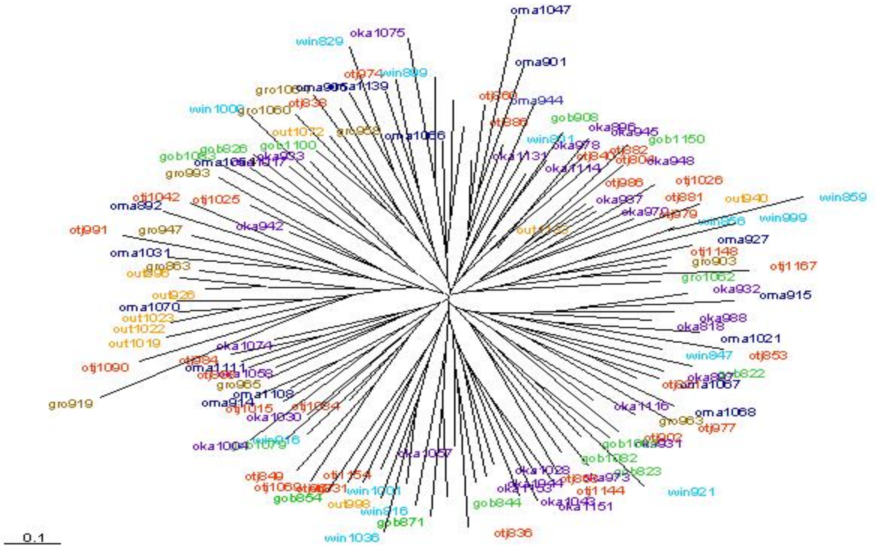

Figure 5.6 Phylogenetic depiction of relationships among individual cheetahs. Colours are coordinated as to regional relatedness.

Pairwise population differentiation among the seven regions was tested using an AMOVA approach with F_{st} and R_{st} statistics, with a mean F_{st} value of 0.021 (± 0.02) (Table 5.2). F_{st} values showed very little genetic differentiation between most of the groups of cheetahs. Only groups 3oka and 6out showed moderate differentiation according to the range (Wright 1978) for F_{st} significance (range 0.05 to 0.15; (Hartl and Clark 1997). Analysis between F_{st} and R_{st} pairwise values (given in Table 5.2) revealed the two matrices to be significantly correlated ($r_s = .853$, $n = 21$, $p < 0.001$, $r^2 = 0.7273$).

Table 5.2 Population pairwise F_{st} and R_{st} estimates using the combined data from the regions. There was little genetic differentiation between most groups of cheetahs with good correlation between the two matrices, although there was moderate F_{st} differentiation between groups 3oka and 6out.

	1gob	2gro	3oka	4oma	5otj	6out	7win
1gob		0.012 (± 0.089)	-0.002 (± 0.062)	0.017 (± 0.090)	0.016 (± 0.073)	0.020 (± 0.013)	- 0.014 (± 0.099)
2gro	0.022 (± 0.054)		0.025 (± 0.071)	0.016 (± 0.090)	0.012 (± 0.063)	0.017 (± 0.127)	0.016 (± 0.132)
3oka	0.023 (± 0.047)	0.025 (± 0.049)		0.027 (± 0.082)	0.015 (± 0.040)	0.086 (± 0.142)	0.003 (± 0.094)
4oma	0.039 (± 0.059)	0.005 (± 0.041)	0.029 (± 0.051)		0.025 (± 0.081)	0.032 (± 0.113)	0.022 (± 0.102)
5otj	0.027 (± 0.048)	0.004 (± 0.036)	0.011 (± 0.030)	0.024 (± 0.045)		0.066 (± 0.130)	- 0.003 (± 0.092)
6out	0.022 (± 0.054)	0.023 (± 0.073)	0.074 (± 0.096)	0.044 (± 0.098)	0.052 (± 0.088)		0.056 (± 0.160)
7win	-0.011 (± 0.049)	0.012 (± 0.079)	0.008 (± 0.064)	0.027 (± 0.055)	0.003 (± 0.058)	0.060 (± 0.102)	

Below diagonal F_{st} above R_{st}

5.3.3 Relatedness

Average relatedness among individuals was -0.0067 (± 0.177, n = 7470 pairwise comparisions) (Figure 5.7). First-order relatives (mother-offspring) had a mean *R* value close to the expected value of 0.5 (0.481, ± 0.141, n = 62). Average relatedness among siblings (136 pairwise comparisons) was *R* = 0.391 (+ 0.167) (Figure 5.7), similar to the theoretical expectation of 0.25.

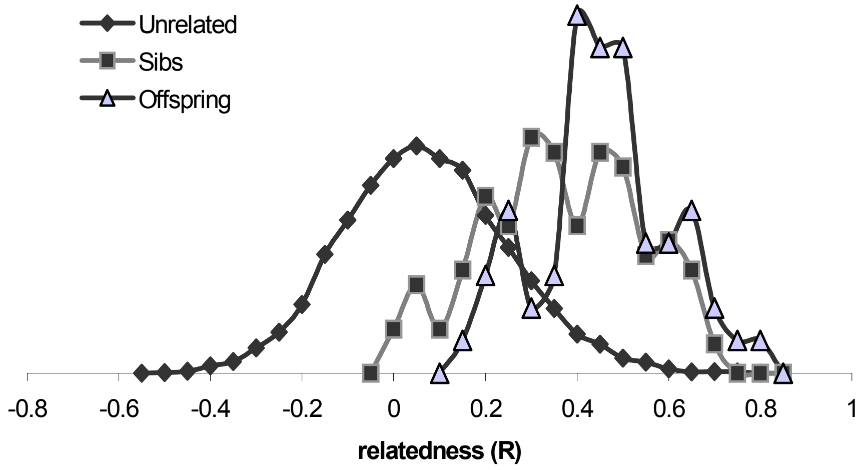

Figure 5.7 Relatedness (*R*) curve depicting degree of relatedness among animals of known relatedness, sibling (sibs) and offspring groups, compared with a curve of degree of relatedness among animals of unknown origin.

Parent/offspring analyses provided strong support that most adult females from family groups selected in Appendix VI were the biological mothers (Appendix VIII). Although the LOD probabilities scores provided a perfect match only 52% of the time (Figure 5.8), there was a 91% match (Appendix VIII) and the high *R* values provided evidence that 100% of the dam and offspring groups were indeed biological families.

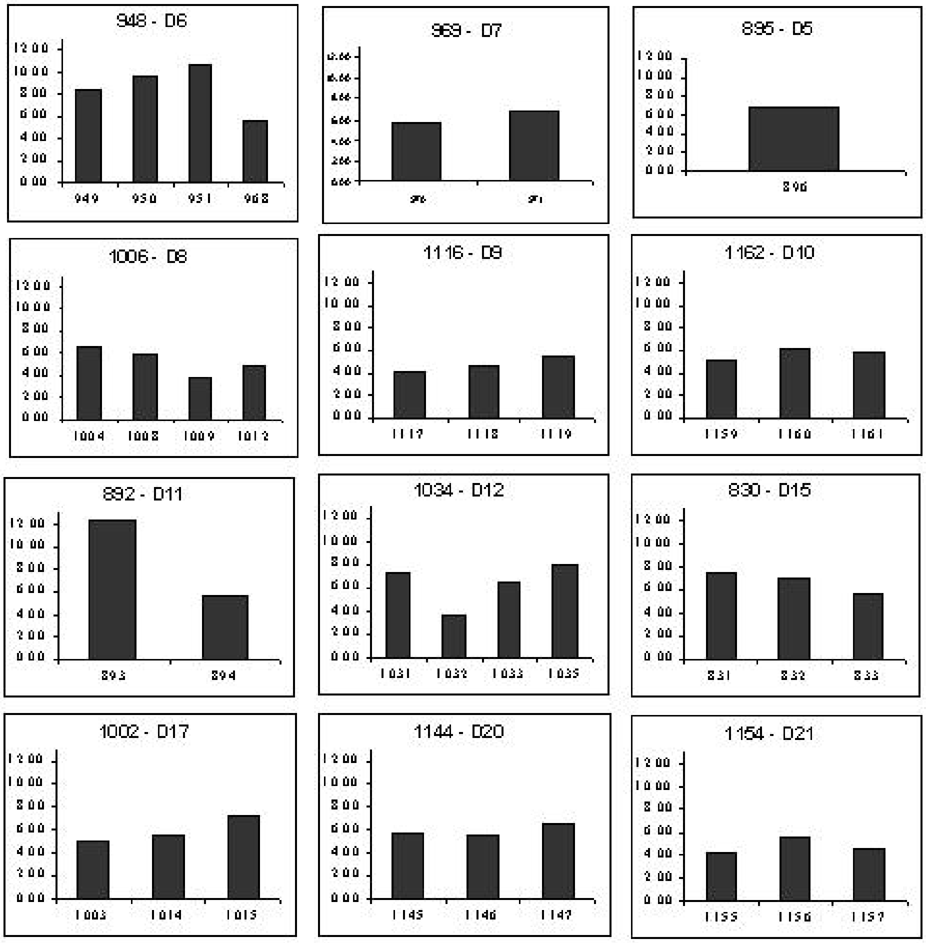

Figure 5.8 Probability (LOD scores) of putative dams of offspring in family groups where there was a 100% probability of agreement.

Analysis of the relatedness between 26 sibling groups, with no dam (Appendix VI), provided evidence to our relatedness questions and found that 19.2% (n = 5) were actually not related to each other. In addition, *R* values for 26 male coalition male groups were compared to each other and showed that 88.5% of the groups were siblings and the 3 groups that were not related supported our behavioral observations. These analyses also identified several previously unrecognised potentially related animals within the population. Table 5.3 shows the probable new related groups, which were selected from over 70 potentially related pairings. Based on the knowledge of the capture location and the age of individuals 15 dam/offspring groups, 30 sire/offspring relationships, and 7 sibling groups were identified. These individuals were caught in the same region or on the same farms and provided greater numbers of related groups than was expected. The genetic relationship of these cheetahs provides insight into the social behaviour of Namibian cheetahs.

Table 5.3 Relatedness value used to identify possible sire/dam and sibling relationships within research population of cheetahs.

***R* values**	**Aju#**	**possible relationship**	**Aju#**	**possible relationship**	***R* values**	**Aju#**	**Possible relationship**	**Aju#**	**Possible relationship**
5	871	dam	846	daughter	3.6	842	sire	1057	daughter
7.8	871	dam	844	daughter	6.5	858	sire	1144	son
6.7	878 RC 112*	dam	1162	daughter	3.15	868 RC 293 ***	sire	1085	son
4.3	1002	dam	1084	daughter	2.19	868 RC 293 ***	sire	1086	son
5	871	dam	846	daughter	2.97	868 RC 293 ***	sire	1088	son
8.8	1067	dam	837	Son	4.2	1128	sire	1142	son
3.6	1025	dam	1167	Son	3.9	842	sire	977	son
5.7	820	dam	1072	Son	4	932 852	sire	988	son
10.2	926	dam	863	Son	4.9	934	sire	1139	son
4.69	986 RC 661**	dam	985 RC 987	Son	7.5	881	sire	985	son
4.6	901	dam	1095	Son	6.5	988 989	sire	1029	son
4	1006	dam	1163	Son	4	932 RC 085	sire	1003	son
5	1168	dam	1075	Son	4	1123	sire	1018	son
10	926	dam	863	Son	4.6	946	sire	1059	son
4	892	dam	990	son	5.7	820	sire	1072	son
5.9	882	sire	895	daughter	6.1	947	sire	1096	son
11.80	881	sire	1026	daughter	6.1	947	sire	1097	son
7.55	989/988	sire	1029	daughter	4.2	1128	sire	1142	son
4.8	1071	sire	1157	daughter	4.6	826	sire	1076	son
6.5	868 RC 293	sire	1144	daughter	5.5	1170	sibs	902	sibs
5.2	832	sire	1092	daughter	5.5	1103	sibs	1040	sibs
4.6	890	sire	902	daughter	6.8	1054	sibs	1076	sibs
4.6	1095	sire	901	daughter	7.1	866****	sibs	919	sibs
6.5	932 RC852 *	sire	1014	daughter	6	860 861	sibs	884 885	sibs
6	947	sire	1096	daughter	5.9	863	sibs	1139	sibs
6.5	988 989	sire	1119	daughter	4.2	864	sibs	1123	sibs

* offspring of relocated cheetahs

** relatedness of cheetahs caught together at playtree

*** identification of sire with known dam

**** dispersal of male from natal home range

The following provide examples of interesting relationships that were identified and include: AJU #s 878 to 1162 dam/daughter, an example of reproduction after translocation of dam; AJU #'s 932 to1014 sire/dam, an example of reproduction after translocation of male into new home range; AJU #'s 985 to 986 dam/son example of relationship of animals caught at playtree together and dispersal distance of son to dam; AJU #s 688 to 1085 – 1088 sire to male coalition group; and 866 to 919, example of dispersing male sibling to female sibling in natal home range (Table 5.3).

Percentage relatedness of individual radio-collared cheetahs at > 0.2 (*R*) to other radio collared (RC) cheetahs and to the wild-marked (W) cheetahs in the Otjiwarongo region are presented in Figure 5.9a & 5.9b. One young female cheetah (Aju # 1084) is not included in Figure 5.9a, as the relatedness values were higher than any of the other cheetahs identified, with an average relatedness to the wild population of 84% and to the radio-tracking population by 25%, suggesting that multiple generations can be identified through long-term sampling of the population. Marked females cheetahs (Figure 5.9a) in the Otjiwarongo region were related at >0.2 18.9% (± 12.9%), and marked males (Figure 5.9b) by 14.5% (± 7.2%). Radio collared males and females were related to other radio-collared cheetahs similarly (10.1%, ± 6.0% for males and 11.6%, ± 7.6% for females) (Figure 5.10). However, there was a significant difference between the relatedness of male and female radio collared cheetahs to the whole population at levels of ≥ 0.40 relatedness (considered to be half-sibs, (Blouin et al. 1996) ($z = - 2.43$, $p = 0.015$, Mann Whitney U), showing that on average, females in the general population were more related to radio-collared individuals than were males.

a.

Relatedn

b.

Figures 5.9a & 5.9b Relatedness values of radio collared females (a) and males (b) are presented as individual animals relatedness to other wild-marked (W) cheetahs (n=89) in the Otjiwarongo region and to the other radio collared (RC) cheetahs (n = 23).

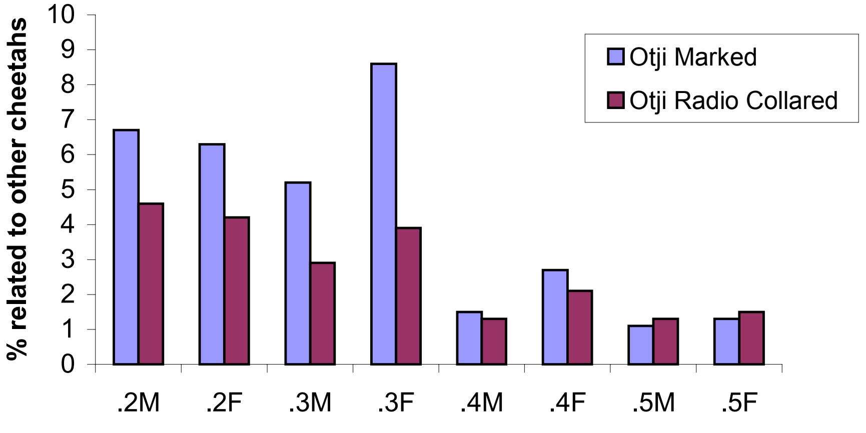

Figure 5.10 Percentage relatedness (0.2, 0.03, 0.3, 0.4) of radio-collared male (M) and female (F) cheetahs to other radio-collared cheetahs in the Otjiwarongo district as well as other marked cheetahs in the Otjiwarongo district.

5.4 DISCUSSION

5.4.1 Relatedness within the Namibian cheetah population

In previous studies, the cheetah has been shown to have extremely low levels of diversity at both the allozome and MCH loci compared to other mammalian species (O'Brien et al. 1985, O'Brien et al. 1987). However, indices of variation derived from the more rapidly evolving microsatellites showed that the Namibian cheetah population was comparable to other recently studied felid populations (Culver et al. 2000, Eizirik et al. 2000, Uphyrkina et al. 2001).

Groups of cheetahs from regions in the central part of the country have the highest average number of alleles per locus (3oka and 5otj) (Table 5.1), perhaps due to gene flow from cheetahs from the other regions of the country. The F_{st} values, a measure of the overall level of genetic divergence among groups, were relatively low. Small F_{st} values, as seen in the Namibian cheetah population, can be indicative of high recent gene flow between populations and can be caused by populations sharing recent common relatives (Wright 1969). Gene flow in Namibia may be induced, in part, due to the extensive removals (killing and trapping) of cheetahs by farmers over the past 30 years or more (CITES 1992, Marker-Kraus et al. 1996), as exploited populations may have higher dispersal levels (Johnson et al. 2001).

5.4.2 Relatedness within known groups

The genetic analysis provided answers to the social behavior questions that were posed at the beginning of the study and provided insights into the relatedness for multiple groups of previously unknown related cheetahs that allowed for the pairing of potential family groups (parent/offspring and siblings). Our data showed that 100% of the family groups that we assumed to be related were. Addition questions as to relatedness of sibling groups showed that 80.8% of the groups were siblings. Of interest, our analysis showed that the 5 sibling groups that were not related were sampled at captive holding facilities, where there was no identification system in place. One of these groups was one of a few that were sampled at a game dealer's facility and is perhaps an artefact of captivity, as the game dealers may have misidentified the correct family groups.

We questioned the relatedness of coalition male groups caught together on farms. Of 26 coalition male groups there were 3 groups found in these that were not related and corresponded with our conclusions based on behavioural information we observed during collections. The male assumed not to be related to the other coalition members was radio-collared as well as one of the members of the assumed coalition group. Our radio-tracking data also supported our hypothesis that these males were not coalition members, but had perhaps been defending their territory when captured. And, as the common practice in Namibia, captured cheetahs are held at the capture-site as a lure to capture other cheetahs. These results show that unlike male coalition groups in the Serengeti, where Caro (1994) found that unrelated males often formed coalitions, coalition male groups in Namibia are made up of related individuals.

5.4.3 Relatedness between unknown groups

The ability to estimate genetic relatedness among individuals from a wild population is useful in several areas of research, particularly to provide insight into the social ecology of the species. From this analysis we revealed that female cheetahs are significantly more related to the cheetahs in our study area than are male cheetahs, thus indicating that males cheetahs disperse from their natal areas. This was reinforced by the genetic findings of individuals such as AJU # 985 and AJU # 866 that showed dispersal from natal home ranges. In addition, several questions were answered about the relatedness between individual animals that provided greater insight into the social behaviour of Namibia cheetahs for instance identifying the relationship of offspring to breeding pairs of radio-tracked cheetahs (AJUs 868 and 1084; Table 5.4).

Male cheetahs frequent and mark 'playtrees' with urine and faeces as a part of their territorial display (Marker-Kraus and Kraus 1995, Marker-Kraus et al. 1996), however, little is known about the female cheetah's behaviour at these marking trees. The relationship of an assumed breeding pair of cheetahs (AJUs 985 and 986; Table 5.4) caught at a playtree together showed that these animals were instead a dam and son. Through the use of radio-telemetry, we discovered that the female had traveled nearly 100km into this area where she was trapped. Both cheetahs were released and the male stayed in the trapping area, whereas the female moved nearly 100km away, and both had clearly defined home ranges.

Both radiotelemetry data and tag and release have shown that cheetahs regularly travel distances greater than 100km (Marker-Kraus et al. 1996, Morsbach 1986). However it is unknown whether these movements led to gene flow. Our genetic data suggest that long distance movements are probably common and result in high levels of gene flow. Individual relatedness scores were insightful to understanding the dispersal of young male cheetahs. For example, the analysis provided interesting information on one of our radio-collared males (AJU 866; Table 5.4), which we discovered was a sibling to female (AJU 919; Table 5.4) captured in 2gro region when still with her dam. This male however was trapped and sampled in region 5otj, over 200km south of the range of his sister, showing dispersal from his natal home range. Whereas another female cheetah (AJU 1162, Table 5.4) was found to be the daughter of a relocated female (AJU 878, Table 5.4) caught in the dam's new home range.

These genetic finding support our tag and release and radio-tracking studies that cheetahs migrate into different regions of the country, have large home ranges, and that dispersal of young male cheetahs can move from one region into the next in a few days from their natal home range (Marker 2000, Marker-Kraus et al. 1996, Morsbach 1985, Morsbach 1986). In addition, genetic information on cheetah AJU #1084 provides insight as to the relatedness of a young cheetah to that of the Otjiwarongo marked population, showing that long-term stuidies can provide information regarding relationships over several generations.

As numerous cheetahs have been translocated throughout Namibia in the past decade, the genetic analysis of unknown individual animals also provided insight into the success of translocated cheetahs. The successful translocation of one of the male cheetahs (AJU 932) and that of a female (AJU 878) (Table 5.4) in this study included their ability to eventually produce offspring in their new home ranges suggesting that translocations can be successful (see Chapter 11). These examples are of but a few of the answers that genetic analysis provided to our questions of relatedness within the Namibian cheetah population.

5.5 CONSERVATION IMPLICATIONS

These results imply that cheetahs from the different regions in Namibia do not need to be managed separately, and that persistence in Namibia depends on dispersal from regions throughout the country; therefore efforts of connectivity throughout the country should continue. In addition, our data imply that animals can be translocated within Namibia without significantly altering historic patterns of gene flow. Genetic information provided here, accompanied with ecological and ecosystem approaches, will be useful in developing management strategies and setting priorities for cheetah conservation in Namibia.

CHAPTER 6

A SEROSURVEY OF ANTIBODIES TO VIRAL DISEASES IN WILD NAMIBIAN CHEETAHS

This thesis chapter has been submitted as the following paper:

A Serosurvey of Viral Infections in Wild Namibian Cheetahs *(Acinonyx jubatus)*. L. Munson, L. Marker, E. Dubovi, J.A. Spencer, J.F. Evermann & S.J. O'Brien. Submitted to the *Journal of Wildlife Diseases.*

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CHAPTER 6: A SEROSURVEY OF VIRAL INFECTIONS IN WILD NAMIBIAN CHEETAHS

ABSTRACT

Cheetahs in captivity have unusually severe inflammatory responses to common feline viruses, a trait that may be attributable in part to their lack of genetic heterogeneity and the immunomodulating effects of chronic stress. The largest remaining wild population of cheetahs resides on Namibian farmlands where they share habitat with domestic dogs and cats, which have viruses that could threaten the health of wild cheetahs. To assess the extent wild cheetahs are exposed to these viruses, sera from 81 wild cheetahs sampled between 1992 and 1998 were evaluated for antibodies against canine distemper virus (CDV), feline corona virus (feline infectious peritonitis virus; FCoV/FIP), feline herpesvirus 1 (FHV1), feline panleukopenia virus (FPV), feline immunodeficiency virus (FIV), and feline calicivirus (FCV) and for feline leukemia virus (FeLV) antigens. CDV, FCoV/FIP, FHV1, FPV, and FCV antibodies were detected in 24%, 29%, 12%, 48%, and 65% of the wild population, respectively, although no evidence of viral disease was present at the time of sample collection. Neither FIV antibodies nor FeLV antigens were present in any cheetah tested. Temporal variation in FCoV/FIP seroprevalance during the study period suggests that this virus is not endemic in the wild population. CDV antibodies were detected in cheetahs of all ages sampled between 1995-1998, suggesting the occurrence of an epidemic in Namibia during the time when CDV swept through other parts of sub-Saharan Africa. This survey revealed that wild Namibian cheetahs have been infected with feline and canine viruses that are known to cause serious clinical disease in captive cheetahs. Future translocations should aim to minimise further viral exposure by isolating wild

cheetahs from domestic pets. Also cheetahs with FCoV/FIP, FHV1, or FPV antibodies should be quarantined because these animals may chronically shed viruses.

6.1 INTRODUCTION

The cheetah is globally endangered with the remaining wild populations located principally in southern and eastern Africa. The largest free-ranging population of cheetahs resides in the farmlands of north central Namibia where contact with domestic pets and feral animals is likely (Marker-Kraus et al. 1996). Common viruses, such as feline corona virus (FCoV), which causes feline infectious peritonitis (FIP), feline herpesvirus 1 (FHV1), and feline panleukopenia virus (FPV) or canine parvovirus (CPV) cause unusually severe or persistent clinical diseases in captive cheetahs (Evermann et al. 1988, Junge et al. 1991, Marker-Kraus et al. 1996, Munson 1993). Whether wild cheetahs are similarly affected by these viruses has not been investigated. Wild cheetah populations share ancestry with captive cheetahs, and both populations lack the genetic variability typical of most species, including heterogeneity of major histocompatibility genes (MHC), which determine, in part, the host response to viral infections. (Munson et al. 1993, O'Brien et al. 1985, O'Brien et al. 1983). Therefore, exposure of wild populations to viral diseases of domestic pets is a cause for concern.

In captive cheetahs, some viruses appear to be highly pathogenic and cause persistent viral infections that affect the management of healthy captive populations. FIP occurs more commonly in FCoV-infected cheetahs than in FCoV-infected domestic cats, and FIP epidemics with high morbidity and mortality have occurred in captive cheetahs worldwide (August 1984, Evermann et al. 1988, Heeney et al. 1990, Van Rensburg and Silkstone 1984). FCoV infected cheetahs also persistently shed virus in their faeces despite the presence of circulating antibodies (Kennedy et al. 2001). Feline herpesvirus infections also tend to be persistent and unusually pathogenic in cheetahs. In contrast to the mild upper respiratory disease cause by FHV 1 infection in domestic cats, some FHV1- infected cheetahs develop a severe debilitating ulcerative and eosinophilic dermatitis concurrent with upper respiratory signs (Junge et al. 1991). CPV and FPV infections also are unusually persistent in cheetahs including vaccinated animals and result in chronic debility from enteritis (Steinel et al. 2000). It is of concern that wild cheetahs held captive for rehabilitation or translocation may also develop these usual disease manifestations.

Other viruses of concern in wild cheetah populations include CDV, feline leukemia virus (FeLV) and feline immunodeficiency virus (FIV). During the 1994 Serengeti CDV epidemic, several cheetahs were observed with myoclonus, a sign associated with permanent neurological damage from CDV infection (Appel 1987, Roelke-Parker et al. 1996). FeLV infection has been linked to fatal leukaemia in one captive cheetah (see Chapter 7), and FIV (Brown et al. 1993) has the potential to affect immune function (Brown et al. 1993), further compromising population health. These actual and potential disease threats should be cause for concern in Namibia where conservation strategies include holding and translocating cheetahs.

Home ranges of Namibian cheetahs are extensive, encompassing several continuous farms and often bordering towns and cities (Marker 2000), most of which have both domesticated and feral cats and dogs. Many domestic dogs and cats in Namibia are unvaccinated, and cases of CDV, FCoV, FPL, CPV, and FHV1 have been reported (Schneider 1994). This close proximity of wild cheetahs to infected carnivores provides ample opportunity for viral exposure. Additionally, wild cheetahs are often trapped by Namibian farmers to protect their livestock, and these cheetahs are held in pens near domestic pets or other wild carnivores, such as leopards (*Panthera pardus*), before being translocated to new regions (Marker-Kraus et al. 1996). These capture cages or holding pens would further facilitate viral concentration and transmission. The act of translocating cheetahs may, in turn, carry pathogens to previously uninfected regions, thereby increasing disease risks to indigenous animals. Transmission of some viruses among wild cheetahs would also be facilitated through the territory-marking behaviour of depositing faeces at play trees throughout the farmlands (Marker-Kraus et al. 1996).

Because trapping and translocating cheetahs is part of the regional conservation plan, knowledge of the prevalence and distribution of viral infections in the Namibian farmland regions is needed in order to assess the health risk of these actions. The aim of this study was to determine the prevalence, spatial distribution, and temporal occurrence of antibodies to feline and canine viruses in wild Namibian cheetahs.

6.2 METHODS

Serum was obtained opportunistically from 81 wild cheetahs that were trapped between 1992 and 1998 by landowners in the north-central farmland regions of Namibia, because of perceived threats to livestock. The number of animals sampled per year were 6,17,13,17,6,10, and 12 for 1992-1998, respectively. Animals were trapped in a region extending from 19°30′ S to 23°30′ S and 16°E to 19° E, including the Magisterial districts of Gobabis, Windhoek, Okahadja, Omaruru, Otjiwarango, and Grootfontein (Fig. 6.1). Only cheetahs held in capture cages for less than 6 days were included in the study to assure that antibodies measured reflected exposure to infectious agents in the wild.

Figure 6.1 Location of farms in Namibia where cheetahs sampled for this study were trapped and farms where viruses were found.

Age classification followed the protocol described in Chapter 3. The age distribution of the study population was six cubs from two litters (2 mo and 3.5mo), 22 juveniles and subadults (6-23 mo old; median age = 8 mo old), and 53 adults (median age = 48 mo). Cubs were included in the study despite the possibility that their antibodies were acquired passively, because these antibodies would reflect maternal infection in that trapping region (Spencer and Burroughs

1992). However, cubs were excluded from prevalence statistics to avoid over-representation of maternal antibody status. The population included 57 males and 24 females. This male bias is the result of the greater tendency for males to be trapped by farmers (Marker-Kraus et al. 1996).

Serum samples were obtained under general anaesthesia (Telazol®; tiletamine-HCl and zolazepam-HCl; Warner Lambert, Ann Arbor, MI, USA; 4 mg/kg) delivered intramuscularly in capture cages or by blow dart in enclosures. Serum was separated from blood cells and then frozen at -70° C until tested. The amount of available serum limited the number of serologic tests that could be conducted; so all tests were not performed on every animal.

Sera from 1992-1993 was tested for FPV, FHV1, and feline calicivirus (FCV) antibodies by indirect immunofluorescent antibody tests at the Department of Virology, MEDUNSA, R.S.A. (Spencer 1991); sera from 1993-1998 were tested by serum neutralization tests (FHV and FCV) or haemagglutination inhibition assays (FPV) at the New York State Veterinary Diagnostic Laboratory, Ithaca, NY, U.S.A. because these tests were no longer available at the laboratory at MEDUNSA. The FPV assays used in this study also detect antibodies against CPV2. All sera were tested for CDV neutralizing antibodies against the Onderstepoort stain of CDV at the New York State Veterinary Diagnostic Laboratory, Ithaca, NY, U.S.A. Feline immunodeficiency viral (FIV) antibodies were measured by Western blot at the National Cancer Institute, Frederick, MD, U.S.A., using a FIV antigen isolated from a domestic cat (Olmstead et al. 1992). Feline coronavirus antibodies were detected by indirect immunofluorescence, and FeLV antigens were detected by ELISA at the Washington Animal Disease Diagnostic Laboratory in Pullman, WA, U.S.A (Evermann et al. 1988). These laboratories were selected because they are the labs used by the American Zoo and Aquarium Association Cheetah Species Survival Plan to test captive US cheetahs.

6.3 RESULTS

The overall prevalence of viral antibodies in juvenile and adult cheetahs and prevalence by age group and sex are presented in Table 6.1.

Table 6.1 Prevalence of antibodies to selected feline and canine viruses in free-ranging Namibian cheetahs sampled between 1992-1998.

Virus	Juvenile Males	Juvenile Females	Adult Males	Adult Females	Total
FCoV[a] (FIP)	5/14[b] (36%)	0/8 (0%)	13/37 (35%)	3/13 (23%)	21/72 (29%)
FHV1[c]	1/14 (7%)	1/8(13 %)	7/38 (18%)	0/14 (0%)	9/74 (12%)
FPV (CPV)[d]	4/11 (36%)	2/6 (33%)	14/23 (61%)	4/10 (40%)	24/50 (48%)
FCV[e]	8/11 (72%)	5/6 (83 %)	10/22 (45%)	9/10 (90%)	32/49 (65%)
CDV[f]	8/14 (57 %)	4/8 (50 %)	3/34 (9 %)	2/14 (14 %)	17/70 (24 %)
FeLV[g]	0/14 (0%)	0/8 (0%)	0/34 (0%)	0/13 (0%)	0/69 (0%)
FIV[h]	0/6 (0%)	0/4 (0%)	0/22 (0%)	0/7 (0%)	0/39 (0%)

[a] Feline corona virus (feline infectious peritonitis virus)
[b] Number positive/number of samples tested
[c] Feline herpes virus 1
[d] Feline panleukopenia virus (this test also detects canine parvovirus)
[e] Feline calici virus
[f] Canine distemper virus
[g] Feline leukemia virus
[h] Feline immunodeficiency virus

The temporal pattern of CDV seropositivity is depicted in Fig. 6.2a. The first CDV-seropositive animal was a 4 yr old male sampled in January 1993; however, the test was categorised as suspicious and may not have been a true positive. This was the only positive animal until December 1995. Thirteen of the 17 CDV positive animals sampled between 1995-

1998 were cubs or juveniles, including six 7-8 mo old animals sampled in January and February 1997.

Geographic distribution of CDV positive animals is depicted in Fig 6.1.

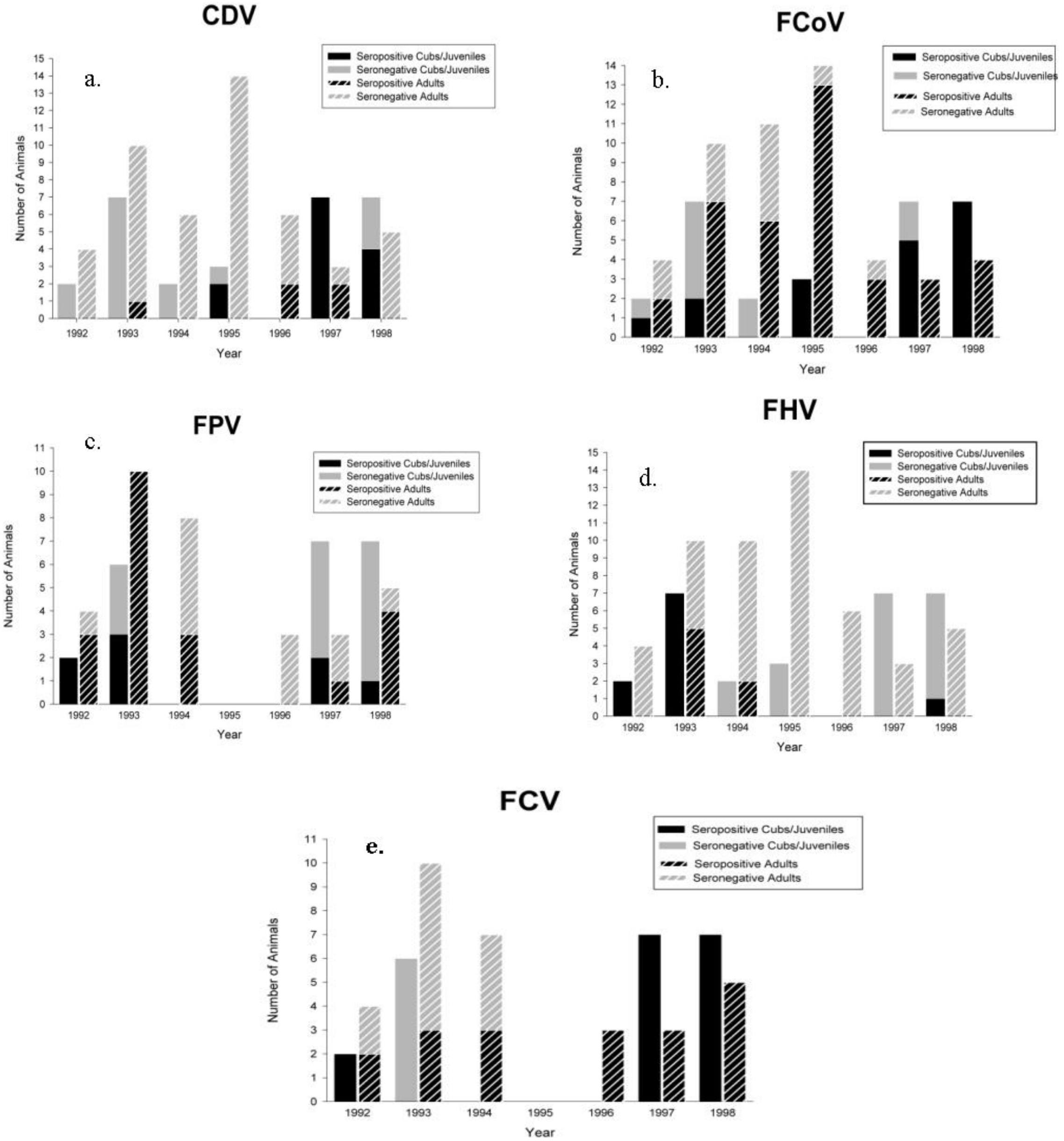

Figure 6.2 a-e. Temporal patterns of seropositivity in 99 wild Namibian cheetahs. a. Canine distemper virus (CDV), b. feline corona virus (FCoV; also known as feline infectious peritonitis virus, FIPV), c) feline panleukopenia virus (FPV; the test also detects canine parvovirus), d) feline herpes virus (FHV1), and e) feline calici virus (FCV).

The temporal and geographic distribution of FCoV/FIPV seropositive animals are depicted in Fig. 6.1 and 6.2b. The youngest animal with antibodies to FCoV was 6 mo old. None of the five cubs and juveniles sampled between 1994-1996 had FCoV antibodies, suggesting this virus may be epidemic and not endemic.

Temporal and geographic distribution of FPV, FHV, and FCV seropositive animals are depicted in Figs. 6.1 and 6.2c-e. Serum from juveniles or cubs was not available to test for FPV or FCV between 1994-1996, so it cannot be determined if these viruses are endemic. None of the 39 wild cheetahs tested had FIV antibodies, and none of the 78 wild cheetahs tested for FeLV had antigen. Of six cubs tested for CDV, FHV and FCoV, one cub had CDV antibodies, one cub had FHV antibodies, and no cub had FCoV antibodies. Of the 5 cubs tested for FPV and FCV, two littermates had FPV antibodies and three littermates had FCV antibodies.

6.4 DISCUSSION

This study disclosed widespread exposure of free-ranging Namibian farmland cheetahs to common feline and canine viruses (or antigenically similar viruses) that are known to cause serious clinical disease in captive cheetahs. Detection of seropositive animals varied both temporally and geographically, although conclusions drawn from these patterns should consider the opportunistic design of this study (all age groups were not sampled in all years or in all districts). However, antibody titres in juveniles are a more accurate measure of recent population exposure, and antibodies against FCoV and CDV in this age group also fluctuated temporally, suggesting that these viruses have cyclical patterns of occurrence in these regions. The low prevalence of FHV in the population precludes further assessment of viral patterns in this ecosystem. The patterns of infection for FPV and FCV also could not be assessed because serum was not available for all years. Although FPV often becomes endemic in populations because of environmental contamination (Barker 2001) the dry, hot environment of Namibia may limit viral persistence. Also, viruses such as FCV and FHV that are principally transmitted by direct contact may not survive in a species that is solitary and wide-ranging.

The detection of CDV antibody-positive animals only in late 1995 through 1998 suggests that an epidemic occurred during that time. The single positive CDV test before December 1995 had a low titre and was categorised as ‘suspicious’, so may have been a false positive or single point exposure. This period closely follows the 1994 to 1995 CDV epidemic that occurred in wild felids in the Serengeti ecosystem (Roelke-Parker et al. 1996) and the 1995 CDV epidemic in African wild dogs (*Lycaon pictus*) in Chobe National Park, Botswana (Alexander et al. 1996). This geographic pattern suggests that a CDV pandemic occurred in sub-Saharan Africa in the mid-1990s. Whether CDV has the potential to be as fatal in cheetahs as it was in lions is unknown. Cheetahs with myoclonus were noted after the Serengeti epidemic, but mortalities were not recorded. Many deaths in the social Serengeti lions were attributable to intraspecific trauma within prides as a result of CDV infection. This cause would be less likely to occur in cheetahs that tend to be more solitary.

The seropositive status of Namibian cheetahs indicates that some animals survived CDV infection. However observation of clinical disease or mortalities would have been unlikely, because cheetahs in this region have very large home ranges and avoid human contact (Marker 2000). Regardless, CDV could pose a future threat to the Namibian cheetah population, because most animals are seronegative (and therefore susceptible) and newer strains of CDV appear particularly pathogenic for felids (Carpenter et al. 1998).

More males were included in the study group because traps are placed primarily at play trees, which are visited more frequently by males due to territorial behaviour (Marker-Kraus et al. 1996). Despite this sex bias in the study population, both sexes had similar exposure to most viruses, which likely reflects the equally large home ranges of males and females in Namibia.

Human population densities in Namibia are low, but humans and domestic pets are present on farmlands throughout the study area (Barnard 1998). Moreover, Otjiwarango, Grootfontein, and Omaruru districts contain large population centres (cities or towns) in close apposition to cheetah habitat. Unvaccinated domestic pets and/or feral dogs and cats in these areas of dense human habitation likely serve as reservoir hosts for canine and feline viruses. Although cheetahs seropositive to CDV, FPV and FHV1 appear clustered near major population centres, the extensive home ranges of these animals preclude meaningful spatial analyses to assess risk of infection.

Regional differences in infectious disease exposure should be considered when translocations are planned. Feline herpesvirus, FCoV, FPV and CPV have long, unpredictable periods of viral shedding, even in the presence of serum antibodies. Therefore, translocating antibody-positive cheetahs carries the risk of contaminating new environments, thereby imperilling the indigenous carnivores. Equally important to consider is the risk to immunologically naive cheetahs of becoming infected when translocated into infected environments. Stress from capture, confinement, and transport may increase their susceptibility to viral infections or cause recrudescence in chronically infected animals. Together these risks advocate strict quarantine of cheetahs before translocation. Serologic testing of cheetahs during quarantine and before translocation would be ideal, but in many cases is not feasible. Cheetahs that are seropositive for FCoV, FHV or FPV or from seropositive regions should be isolated during holding, and all pens and cages thoroughly sanitized before housing new cheetahs.

Applying strict quarantine protocols during translocation and restricting the movement of infected animals can minimise further spread of viral infections to wild cheetahs.

Vaccination of wild animals to prevent viral infection should be approached with caution because some vaccines developed for domestic pets cause disease when administered to other species. Cheetahs develop antibody responses to multivalent modified-live vaccines for FPV, FHV and FCV (Spencer 1991), but FHV and FPV infections still occur in vaccinated animals, indicating partial immunity (Steinel et al. 2000). Therefore, quarantine and testing, rather than vaccination of wild cheetahs, are the preferred methods for preventing acquisition of viral diseases during translocation. Vaccinating domestic dogs and cats (barrier vaccination) and minimising contact between domestic pets and wild cheetahs would be better management tools for reducing the risk of infectious disease to this population. Because stress may compromise disease resistance, translocation procedures should aim to limit human exposure and holding time before release. Ongoing surveillance in this region will be used to detect changes in viral exposure in indigenous cheetahs as management of wildlife intensifies and human populations increase.

CHAPTER 7

LYMPHOSARCOMA ASSOCIATED WITH FELINE LEUKAEMIA VIRUS INFECTION IN A CAPTIVE NAMIBIAN CHEETAH

This thesis chapter has been submitted as the following paper:

Lymphosarcoma Associated with Feline Leukemia Virus infection in a Captive Namibian Cheetah (*Acinonyx jubatus*). L. Marker, L. Munson, P.A. Basson, S.P. DeVincent, & S. Quackenbush. Submitted to the *Journal of Wildlife Diseases*.

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CHAPTER 7: LYMPHOSARCOMA ASSOCIATED WITH FELINE LEUKAEMIA VIRUS INFECTION IN A CAPTIVE NAMIBIAN CHEETAH

ABSTRACT

This case report describes the occurrence of multicentric lymphosarcoma in a four- year-old female wild-born captive-held cheetah in Namibia after being housed in an enclosure adjacent to a feline leukaemia virus (FeLV) infected cheetah that had previously been in contact with domestic cats. The year prior to the onset of clinical signs, the wild-born cheetah was FeLV antigen negative. The cheetah subsequently developed lymphosarcoma, was then found to have seroconverted to FeLV, and then rapidly deteriorated and died. At necropsy, the liver, spleen, lymph nodes and multiple other organs were extensively infiltrated with neoplastic T-lymphocytes. FeLV DNA was identified in neoplastic lymphocytes from multiple organs by PCR and Southern blot analysis. Although the outcome of infection in this cheetah resembles that of FeLV infections in domestic cats, the transmission across an enclosure fence was unusual and may indicate a heightened susceptibility to infection in cheetahs. Caution should be exercised in holding and translocating cheetahs where contact could be made with FeLV-infected domestic or feral felids.

7.1 INTRODUCTION

The cheetah population in Namibia principally resides on farmlands and continues to be endangered by human activities. High numbers of cheetahs have been captured and removed by farmers as perceived treats to livestock and game (Marker-Kraus et al. 1996). Trapped cheetahs are often held in groups on farms where infectious agents are easily transmitted and where they may contact unvaccinated domestic and feral cats. Because these cheetahs may be used to stock wildlife reserves in southern Africa or providing new founder animals for captive breeding programs, the acquisition of feline viruses by wild cheetahs during holding and translocation is a cause of concern.

Feline leukaemia virus (FeLV) was first isolated in 1964 from domestic cats with lymphosarcoma or myeloid leukemia and is a common subclinical infection of domestic cats (Cotter 1990). FeLV is typically transmitted through saliva or blood from grooming, fighting or shared environs. FeLV infection has only rarely been reported in non-domestic felids, including one of 21 cheetahs in a captive collection. (Briggs and Ott 1986, Douglass 1979, Effron et al. 1977, Meric 1985, Rusheed and Gardner 1981). However, no clinical disease has been reported in any infected zoo felid to date.

7.2 CASE STUDY

The Cheetah Conservation Fund (CCF) near Otjiwarongo, Namibia, is a non-government organisation with educational, scientific, and conservation programs aimed at preserving a healthy cheetah population in Namibia. CCF often houses wild-caught cheetahs for rehabilitation and translocation and cares for orphan cheetahs. An orphan hand-raised female cheetah (cheetah #1) was housed at CCF from 1991-5 after having been caught in the wild. The cheetah had been housed alone in captivity since

5 wks of age at a facility with no domestic cats, then moved to CCF at 8 mo.-old, where it was housed alone until its death.

In December 1993, a wild-caught, captive-raised 2-yr-old male cheetah (cheetah #2) was confiscated from a private facility by a local authority and placed at CCF. The originating facility also housed a large number of feral domestic cats and two wild-caught cheetahs (cheetah #3 and cheetah #4) that were 18 mo. and 4 yrs-old. Prior to confiscation, cheetah #2 was attacked by cheetah #4 who was housed in an adjacent pen, resulting in deep lacerations and puncture wounds. In February 1994, cheetah #3 became ill, so serum was tested from cheetah #3 and cheetah #4 for FeLV antigens with an antigen detection enzyme-linked immunoabsorbant assay (ELISA) (Golden Vet Lab, Johannesburg, South Africa). Both animals were positive for FeLV antigens. Cheetah #3 subsequently died, but the cause of death was not determined because no necropsy was performed.

After moving to CCF in December 1993, cheetah #2 was housed in a pen adjacent to cheetah #1 with only a single wire-mesh fence separating the enclosures. Although food dishes and water sources were not shared, the cheetahs often had aggressive interactions across the fence line. Because of the positive FeLV tests in cheetahs #3 and #4 and history of fighting between cheetahs #2 and #4, serum was collected in February 1994 at CCF from cheetahs #1 and #2 for FeLV antigen testing (Golden Vet Lab). The ELISA test was positive in cheetah #2 and negative in cheetah #1. The positive tests in cheetahs #2 and #4 were confirmed at the Washington Animal Disease Diagnostic Lab (Waddl); an adequate sample was not available to retest cheetah #3 at this lab.

In January 1995, CCF's 4-yr-old hand raised cheetah (cheetah #1) became lethargic, irritable, anorectic, and appeared to have lost weight. A preliminary physical examination was performed in February 1995, which was done without anaesthesia since CCF staff could handle the cheetah. The cheetah was painful on palpation of the right cervical region, but the only abnormality noted was a large tick embedded in the skin. Two weeks later, the cheetah developed ptyalism, marked bilateral lymphadenopathy in the facial and neck regions, polydypsia and pica. Treatment was initiated with oral tetracycline (625 mg PO TID) (Upjohn, Kalamazoo, Michigan) for suspected rickettsial disease. Two days later treatment was changed to doxycycline (300mg PO SID) (Medpet (Pty), Johannesburg, South Africa) to increase central nervous system penetration and to alleviate the signs of pica that may have been caused by gastrointestinal upset from tetracycline administration. Despite treatment, the cheetah developed bilateral facial swelling in the maxillary region, bilateral ptosis, wheezing, and pulmonary congestion over the next few days.

In March 1995, the cheetah was anaesthetised with Telazol® (tiletamine-HCl and zolazepam-HCl; Warner Lambert, Ann Arbor, MI; 4mg/kg, IM) for evaluation. The cheetah was febrile (105.4^{o} F) with bilateral, symmetrical facial edema. Facial, cervical, prescapular, and popliteal lymph nodes were enlarged and firm, and there was mild splenomegaly. Complete blood count and serum chemistries were performed and no abnormalities were noted. Aspirates of lymph nodes were taken and interpreted as lymphoblastic lymphosarcoma. An ELISA test for FeLV antigens was positive. Despite supportive treatment, the cheetah's condition continued to deteriorate and she died three days later.

At necropsy, there was marked enlargement of all lymph nodes, splenomegaly and hepatomegaly. Histopathological findings included effacement of lymph node architecture by malignant lymphocytes and marked infiltration by malignant lymphocytes of hepatic and splenic sinusoids. Malignant lymphocytes were also present in the interstitium of the kidney, lung, tonsil, salivary gland, thyroid, trachea and bone marrow. Neoplastic lymphocytes had both large and small cell morphology.

Immunohistochemical stains for B and T cell markers were performed on formalin-fixed, paraffin-embedded sections using monoclonal antibodies previously validated for use in cheetahs (Terio 2001). The neoplastic cells were CD3 positive and CD79A and CD45R negative. The final necropsy diagnosis was multicentric T-cell lymphosarcoma.

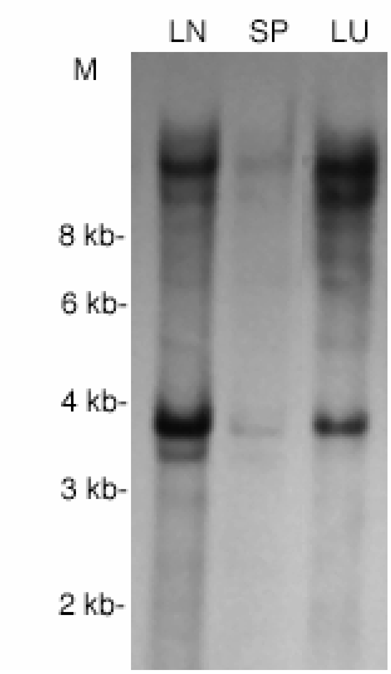

Fig 7.1 Identification of feline leukemia virus in tissues from a cheetah with lymphosarcoma. Total cellular DNA was extracted and analysed by Southern transfer and hybridisation using the FeLV exU3 probe. LN, SP, and LU correspond to lymph node, spleen, and lung, respectively. The relative molecular mass of DNA (M) is shown in kilobase pairs. The FeLV internal virus band migrates at 3.65 kb.

To determine if the neoplastic lymphocytes contained FeLV, DNA was extracted and subjected to PCR using primers that amplify a 155-bp region of the SU gene from exogenous FeLV subgroup A. DNA was isolated from lymph node, liver, spleen, and lung (Figure 7.1), and polymerase chain reaction (PCR) and Southern blot analysis for FeLV were performed as described previously (Quackenbush et al. 1996, Quackenbush et al. 1989). Briefly, 1 μg of DNA was amplified by PCR. The PCR mixture consisted of 20mM Tris-HCl (pH 8.4), 50mM KCl, 2 mM $MgCl_2$, a 125μM concentration of each dNTP, 10 pmol of each primer (TR1- 5'AATGTAAAACACGGGGCA3", Q1- 5'CCCATCTTGTGCCCCTCCA3'), and 2.5 units of *Taq* DNA polymerase (Gibco BRL) in a total volume of 100µl. All samples were denatured at 94°C for 5 min and then each amplification consisted of 30 sec at 94°C, 20 sec at 57°C, 20 sec at 72°C for 35 cycles followed by one cycle at 72°C for 5 min. Fifteen microlitres of the amplified product was separated on a 2% agarose gel. For Southern blot analysis, total cellular DNA (10µg) was digested with *Kpn*I, separated through a 1% agarose gel, and transferred to nitrocellulose. The blot was crosslinked with UV light and hybridized with the exogenous FeLV-specific probe (exU3). The FeLV exU3 probe identifies a 250-bp sequence in the unique region of the long terminal repeat of exogenous feline retroviruses only (Mullins et al. 1980, Mullins et al. 1981).

All neoplastic tissues from cheetah #1 contained the FeLV sequence. DNA isolated from the spleen of the control animals was negative by PCR for FeLV. Southern blot analysis of *Kpn*I digested DNA and hybridization with the exU3 LTR-specific probe demonstrated the presence of an internal virus band of 3.6 kb in all tissues from cheetah #1. A pattern of clonal viral integration was also revealed in these tissues suggesting a clonal proliferation and systemic dissemination of virus-infected cells.

This is the first confirmed case of FeLV-associated lymphosarcoma in a non-domestic felid. The source of FeLV was presumed to be cheetah #2 that was housed in close proximity to cheetah #1 and had been exposed to domestic cats at its previous location. Unfortunately, no confirmatory tests were performed on the domestic cats. The means of transmission from cheetah #2 to cheetah #1 is presumed to have been via saliva through the enclosure fence. Food dishes, direct physical contact, and other traditional means of FeLV transmission were unlikely, because preventative hygiene practices were in use. The animals were housed in adjacent enclosures because the risk of transmission was thought to be low.

It is possible that stress from several recent environmental changes in the management of cheetah #1 led to the exacerbation of disease (Cotter 1990). One month prior to the onset of illness, CCF moved to a new location, which was unfamiliar to cheetah #1, cheetah #2 was removed from the adjacent enclosure, and the rainy season began. However, fecal corticoids were not elevated in cheetah #1 (K. Terio, personal communication). It also is possible that the pathogenicity of FeLV in these animals is attributable to innate low resistance. Cheetahs are thought to be particularly susceptible to some viral infections because of their extremely reduced levels of diversity at allozyme and MHC loci which illustrated extreme genetic uniformity of the species (Heeney et al. 1990, Johnson et al. 2001, O'Brien et al. 1985). Furthermore, cheetahs tend to respond to infectious agents with an abnormally exuberant immune response (August 1984, Evermann et al. 1988, Heeney et al. 1990, Junge et al. 1991, Munson 1993, Van Rensburg and Silkstone 1984), which in this case may have predisposed it to neoplastic transformation of replicating lymphocytes.

Over the past ten years, 69 wild Namibian cheetahs have been tested by CCF for FeLV, and no positive animals have been detected. Additionally, over 100 cheetahs in captivity in Namibia were tested of which only four animals (those in this report) were FeLV antigen-positive. These data indicate that FeLV is not endemic in wild cheetah populations in Namibia, but that cheetahs are susceptible to FeLV infection and its consequences. This case report also provides further evidence that wild populations could be adversely affected by proximity to domestic cats.

CHAPTER 8

THE INCIDENCE OF DENTAL ABNORMALITIES IN WILD-CAUGHT NAMIBIAN CHEETAHS

This thesis chapter has been submitted as the following paper:

The incidence of dental abnormalities in wild-caught Namibian cheetahs, *Acinonyx jubatus jubatus*. L.L. Marker & A.J. Dickman. Submitted to the *Journal of Mammalogy*.

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CHAPTER 8: THE INCIDENCE OF DENTAL ABNORMALITIES IN WILD-CAUGHT NAMIBIAN CHEETAHS

ABSTRACT

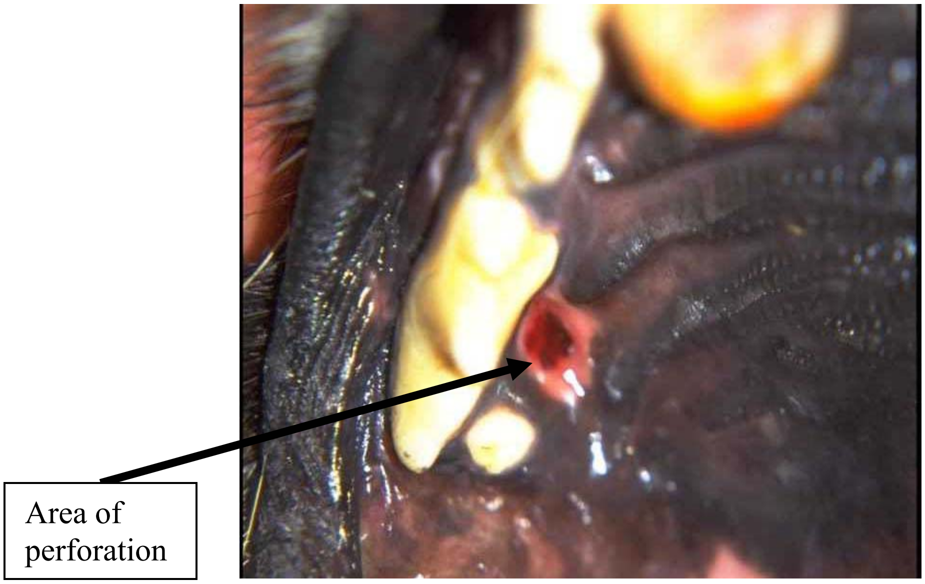
Two hundred and eight cheetahs that were opportunistically live-trapped on Namibian farmlands were examined for signs of dental abnormalities. Three abnormalities were recorded: erosion of the upper palate, possibly a predisposition to focal palatine erosion, where the first lower molar penetrates the palatine mucosa; crowding of the lower incisors; and the absence of one or both upper premolars. Just over 40% of the cheetahs examined showed deep palatine erosion, and 15.3% of these had perforated upper palates. In addition, 31.7% of the cheetahs examined had crowded lower incisors and 20.9% had one or both upper premolars missing. The incidence of focal palatine erosion is of particular interest as it has only been recorded in captive cheetahs, where it was attributed to a 'soft' captive diet, and never before in completely wild individuals. To attempt further understanding of the potential causes of such erosion, the condition was examined in relation to sex, age, region, time in captivity, and the occurrence of other dental abnormalities. No relationship was found between the severity of the condition and time spent in captivity, while juveniles showed more severe erosion than adult cheetahs.

Cheetahs missing either one or both upper premolars showed a higher incidence of deep erosion, and the same was true for cheetahs that exhibited crowded lower incisors. The traditional explanation of focal palatine erosion being an artifact of captivity does not explain its occurrence in this sample population of cheetahs, the majority of which were raised entirely in the wild.

8.1 INTRODUCTION

Focal palatine erosion is a health problem that has been identified in captive cheetahs, in which the first lower molar penetrates the upper palate, medial to the upper first molar (Fitch and Fagan 1982, Phillips et al. 1993). In unaffected cheetahs, there is a slight indentation of the palatine mucosa in this general area, to accommodate the cusp of the tip of the lower first molar.

This erosion is a serious problem that has the potential to cause severe health problems and even fatal disease in individuals, especially when penetration of the hard palate occurs. The pathogenesis of FPE occurs where the lower molar's tip makes regular contact with the palatine mucosa, so the tooth eventually penetrates through the palatine bone itself, causing inflammation. The oral defects observed in affected cheetahs range from sparse cellulitis, the loss of pigmentation and signs of inflammation, to large oral-nasal bony defects extending through the palatine bone into the nasal passage (Fitch and Fagan 1982). Particles of food which lodge in the focal palatine defect result in localised infection and further tissue damage. FPE has been reported in captive cheetahs as early as 10 months of age with a slight, localised cellulitis, although in young cats it may be overlooked as a typical 'teething' disorder (Fitch and Fagan 1982).



Picture 8.1 Focal palatine erosion, where the first lower molar can perforate the upper palate, can lead to fatal infections in affected animals

Although this condition has never previously been reported in cheetahs that were born and raised in the wild, the majority of reported cases have occurred in Namibian wild-caught animals living in captivity and captive-born animals from Namibian founders. When first reported, 86% of the cheetahs with FPE came from one shipment from Namibia in 1970 or their descendants (Fitch and Fagan 1982). This oral defect was attributed to the feeding of soft commercial diets lacking bones on developing cheetahs (Phillips et al. 1993), as well as the possibility of specific family lines, renal disease, suppurative rhinitis, and appears to often accompany, but not always, a maloccluded dentition (Fitch and Fagan 1982).

During examinations of cheetahs handled by the Cheetah Conservation Fund, the opportunity was taken to investigate any dental abnormalities that were observed in wild cheetahs. In addition to focal palatine erosion, other dental abnormalities observed in our sample population were the crowding of the lower incisors, and the absence of one or both upper premolars. The crowding varies from slight crookedness to a severe condition where the incisors are arranged in two parallel rows. In domestic dogs and cats, such problems usually have a genetic basis, although nutritional status, juvenile viral infections, and metabolic disorders are also possible causes (Colmery and Frost 1986, Frost and Williams 1986). The absence of one or more premolars has been recorded in cheetahs before (Ewer 1973), but the objective in this study was to examine this phenomenon in relation to the other abnormalities recorded, particularly the erosion of the upper palate.

Before investigation into the impact, prevalence, and etiology of such dental abnormalities can be undertaken, the anomalies must be properly defined, characterized, and described in literature. The reporting of these conditions, particularly focal palatine erosion, in entirely wild cheetahs is important for other researchers, to encourage further investigation, and to aid in the determination of the ultimate causes of focal palatine erosion and its impact on wild cheetahs.

8.2 METHODS

Cheetahs were examined after being opportunistically live-trapped on Namibian farms, as described in Chapter 3, and had been held in captive situations for varying lengths of time before the Cheetah Conservation Fund was invited to examine them. The region and date of capture was determined whenever possible, and cheetahs that had been held in captivity for 30 days or more by the time of examination were considered to be 'captive' animals. Age classification followed the protocol described in section 3.1, but in order to enable comparisons to be made, we condensed our age classes into the scheme set out in Phillips et al. in (1993), which used four classes for analyses:

(1) Juvenile cheetahs (24 months old or less at the time of exam) that had been captured before adult tooth eruption (before seven months old);

(2) Juvenile cheetahs captured at seven months old or later;

(3) Adult cheetahs (over 24 months old) that had been captured when juvenile (seven to 24 months old) and;

(4) Adult cheetahs that were captured over 24 months old.

Each cheetah was examined for signs focal palatine erosion (FPE) and evidence of other dental abnormalities. A score of 1 was assigned in cases where there was very little or no sign of erosion, a score of 2 indicated a medium erosion, and in cases where erosion had caused a deep depression the condition was scored as a 3. Some of the cases scored as 3 also showed actual focal palatine erosion, signified by perforation of the mucosa, sometimes accompanied by bleeding, inflammation, and signs of foreign matter, and this was recorded as well. Callipers were used to measure particular teeth and inter-oral photographs were taken.

The overall score for analysis was developed as follows:

1 = a score of 1 on both sides of the palate

2 = a score of 1 on one side and 2 on the other

3 = a score of 2 on both sides

4 = a score of 2 on one side and 3 on the other

5 = a score of 3 on both sides.

None of the cheetahs examined had scores that did not fit this scheme, e.g. a score of 1 on one side and 3 on the other. The degree of erosion was considered to be severe if one or both sides of the palate were scored with a 3.

The number of upper premolars was examined for each cheetah, with resulting scores of 0 (no premolar on either side), 1 (one premolar present on one side) and 2 (both premolars present), while the lower incisors were also examined to see whether there was any crowding. Cheetahs were also weighed and their physical condition assessed, looking at factors such as coat condition, musculature, ectoparasite load etc. This excluded injuries that were likely to have been sustained while in the capture cage, to give a better indication of condition in the wild.

Statistical analyses were performed using SPSS version 10.0 software (SPSS Inc. Chicago, USA). Means significance testing was carried out using the parametric independent samples t-test, preceded by Levene's test for equality of variances, and general linear model univariate analyses. Departures from expected ratios were analyzed using Pearson's chi-squared test, while the non-parametric Spearman's rank correlation coefficient was used to determine the significance of relationships between variables measured on ordinal scales. All tests are two-tailed unless otherwise stated.

8.3 RESULTS

Two hundred and eight cheetahs were examined for dental abnormalities between June 1992 and November 1999, and the breakdown of this sample population is shown in Table 8.1. Almost two-thirds (62.5%) of the cheetahs examined were male, while a similar proportion (67.3%) were wild, i.e. had been held captive for under 30 days.

Table 8.1 Sample population of cheetahs examined for dental abnormalities.

		Juv capt under 7m	Juv capt at 7m or older	Adult capt under 24 mo	Adult capt at 24m or older	Unknown	Total
Wild	Male	7	36	0	46	0	89
	Female	4	21	2	23	1	51
Captive	Male	9	2	0	23	7	41
	Female	0	10	5	8	4	27
Total		20	69	7	100	12	208

Precise dates of capture were available for 94.2% (n = 196) of the examined cheetahs and these animals could therefore be assigned to the four age classes described above. Overall, 87 juvenile cheetahs were examined, 12.6% of which (n = 11) were captured before seven months old (Table 8.1).

Although the single most common score assigned was 1, the incidence of deep erosion was relatively high, with 40.9% of the sample population classified as having a deep depression on at least one side of the palate (Table 8.2). Thirteen (15.3%) of these cheetahs (6.3% of the sample population) had perforations in the upper palate as a result of this severe focal palatine erosion.

Table 8.2 Focal palatine erosion scores assigned to captive and wild cheetahs examined of different ages.

		FPE 1	FPE 2	FPE 3	FPE 4	FPE 5	Total
Wild	Juvenile	16	0	17	6	29	68
	Adult	28	3	20	7	13	71
	Unk	0	0	0	1	0	1
Captive	Juvenile	2	2	7	6	2	19
	Adult	18	1	9	3	7	38
	Unk	0	0	0	3	8	11
Total (%)		64 (30.8)	6 (2.9)	53 (25.4)	26 (12.5)	59 (28.4)	208

The frequency of deep erosion amongst cheetahs that had been held captive for 30 days or more was 42.6% (n = 29), while the condition was slightly milder in wild cheetahs, with 40.0% (n = 56) showing severe erosion. There were no significant differences between wild and captive cheetahs, however, regarding overall score ($\chi^2 = 3.573$, $d.f. = 4$, $P = 0.467$), the incidence of severe erosion ($\chi^2 = 0.133$, $d.f. = 1$, $P = 0.716$), or the development of palatine perforation ($\chi^2 = 1.142$, $d.f. = 1$, $P = 0.285$). When just captive cheetahs were examined, there was a slight positive correlation between the score assigned and the length of time spent in captivity, although it was not statistically significant ($r_s = 0.203$, $n = 57$, $P = 0.129$).

Figure 8.1 shows the mean scores by sex for the different age classes. There was no difference between sexes in overall scores ($\chi^2 = 4.980$, $d.f. = 4$, $P = 0.289$), the frequency of severe erosion ($\chi^2 = 2.017$, $d.f. = 1$, $P = 0.156$), or perforated FPE ($\chi^2 = 0.005$, $d.f. = 1$, $P = 0.941$). There was some slight variation, however, in scores between different regions of the country ($F = 2.026$, $d.f. = 8$, $P = 0.045$).

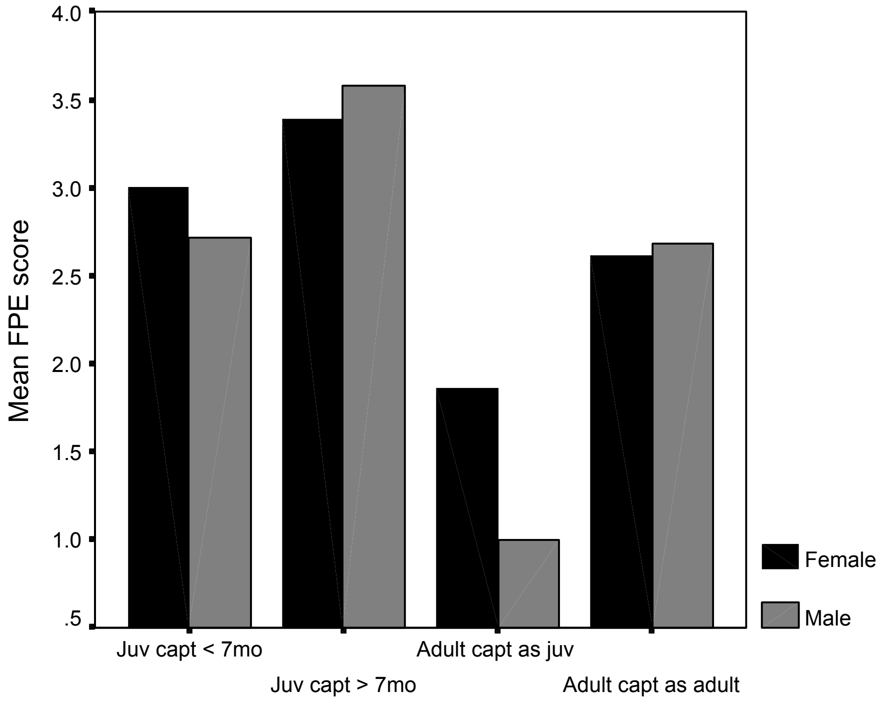


Figure 8.1 Focal palatine erosion scores for adult and juvenile cheetahs of different sexes.

Age did appear to play a significant role in the severity of erosion: juvenile cheetahs had significantly higher overall scores than the adults (χ^2 = 13.645, *d.f.* = 4, *P* = 0.009), were subject to significantly more severe erosion (χ^2 = 9.930, *d.f.* = 1, *P* = 0.002), and were significantly more likely to show perforated erosion (χ^2 = 5.971, *d.f.* = 1, *P* = 0.015). There was no significant difference in the severity of the erosion seen between those juveniles captured before adult tooth eruption and those captured when older (χ^2 = 0.859, *d.f.* = 1, *P* = 0.354). Adult cheetahs captured as juveniles had a lower incidence of severe erosion than those captured when adult already, although the difference was not statistically significant (χ^2 = 3.725, *d.f.* = 1, *P* = 0.054).

Data regarding the number of premolars and the frequency of crowded incisors are shown in Table 8.3 for captive and wild cheetahs examined of different ages.

Table 8.3 Overall frequency of missing premolars, crowded incisors and perforated FPE in the cheetahs examined

		No. premolars			Crowded incisors		Perforated FPE	
		0	1	2	Yes	No	Yes	No
Wild	Juvenile	5	3	60	17	51	2	63
	Adult	10	4	57	25	46	5	69
	Unk	2	3	6	8	3	0	11
Captive	Juvenile	1	2	16	6	13	5	14
	Adult	6	7	25	10	28	1	37
	Unk	0	0	1	0	1	0	1
Total (%)		24 (11.5%)	19 (9.1%)	165 (79.3%)	66 (31.7%)	142 (68.3%)	13 (6.3%)	195 (93.7%)

The number of premolars that a cheetah had was significantly linked to the severity of erosion – those cheetahs that had either one or both upper premolars missing showed a significantly higher frequency of severe erosion than those with both premolars present ($\chi^2 = 7.251$, *d.f.* = 2, $P = 0.027$). The frequency of severe erosion was also significantly higher amongst cheetahs that had crowded lower incisors than those that did not ($\chi^2 = 4.537$, *d.f.* = 1, $P = 0.033$), although there was no significant relationship for perforated FPE ($\chi^2 = 0.290$, *d.f.* = 1, $P = 0.590$).

There was a relationship between the incidence of severe erosion in wild cheetahs and poorer physical condition, as shown in Figure 8.2. Wild cheetahs with severe erosion were significantly less likely to be in excellent condition ($\chi^2 = 11.296$, *d.f.* = 1, $P < 0.001$). While wild cheetahs that had severe erosion were lighter in mass than those without a severe condition, with a mean mass of 33kg compared to 36kg, this difference was not statistically significant ($t = 1.203$, *d.f.* = 135, $P = 0.231$). There was no significant relationship between crowded incisors and either being in excellent physical condition ($\chi^2 = 0.673$, *d.f.* = 1, $P = 0.412$), or body mass ($t = 1.429$, *d.f.* = 135, $P = 0.155$).

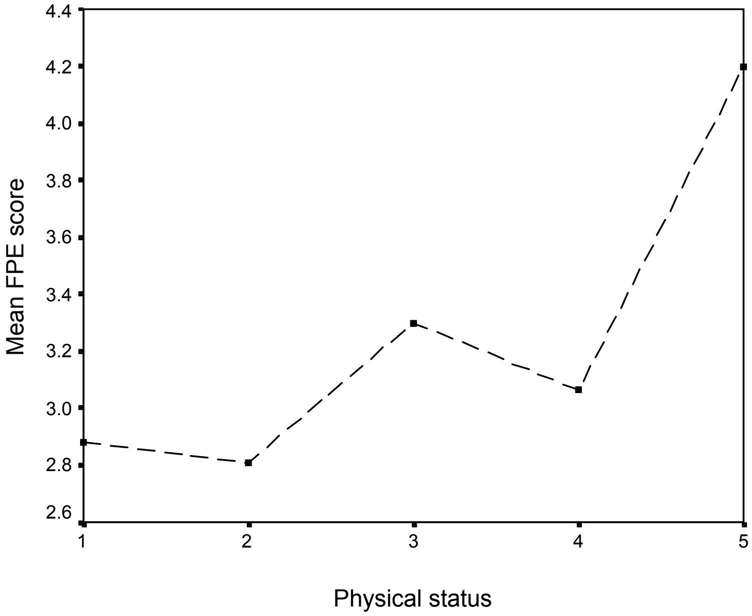


Figure 8.2 Focal palatine erosion scores assigned to cheetahs of different physical status

8.4 DISCUSSION

Although focal palatine erosion was first formally recorded in the captive cheetah population almost 20 years ago, it was believed not to occur in wild cheetahs captured as adults (Fitch and Fagan 1982, Phillips et al. 1993). During this long-term study conducted on Namibian farmlands, however, we found not only evidence of erosion in wild cheetahs that may lead to focal palatine erosion, but also found that it was not uncommon, with 40% of wild cheetahs showing deep erosion on at least one side of the palate. Even more notably, six percent of the cheetahs examined were suffering from perforated palates (the most severe form of focal palatine erosion), including seven animals that had never been held in captivity. This shows that the preconditions for FPE exist in the free-ranging cheetah population throughout Namibia, with slight variations by region.

A common explanation for the development of focal palatine erosion has been that cheetahs brought into a captive situation are fed artificially ‘soft’ diets, which fail to sufficiently wear down the carnassials and hence lead to palate damage (Fitch and Fagan 1982, Phillips et al. 1993). This does not explain, however, the results presented here, which show that cheetahs reared on an entirely natural, wild diet also suffer from the same problem. The effect of diet on tooth wear may indeed be important, and is supported in this study by the evidence that the degree of erosion appears to increase with time spent in captivity, although the trend here was not found to be statistically significant. The fact that the captive cheetahs we examined showed a slightly higher incidence of severe erosion also hints towards some effect of captivity, but we feel that focusing entirely on the issues of diet and captivity as the sole explanation may be misleading.

The juvenile cheetahs examined showed a significantly higher degree of erosion than did the adults, regardless of how old they were when they were captured, and were also more likely to suffer from perforated focal palatine erosion. Although wild cheetahs consume primarily muscle and skin (van Valkenburgh 1996), bone consumption at kills has been recorded to varying extents (Brain 1981, Phillips 1993). It seems likely that the gradual wear from gnawing on tough cartilage and bones will eventually blunt the teeth of adult cheetahs and reduce the extent to which the molar can irritate and penetrate the palatine surface.

In 1982, Fitch and Fagan suggested that malocclusion of the teeth could be a factor in the development of FPE, as FPE often accompanies a maloccluded dentition. If this is the case, it may be reasonable to hypothesize that those cheetahs showing other dental abnormalities, such as crowding of the lower incisors, would suffer from an increased frequency of erosion. Our results suggest that this is indeed the case, with cheetahs that had crowded incisors also showing more severe erosion, although crowding of the incisors did not seem to be linked to actual perforation of the palate. Similarly, more severe erosion was seen in cases where the study animal was missing either one or both upper premolars, indicating that although there may not be a causal relationship, there is some link between the incidences of these different traits.

Although just under a third of cheetahs examined in this study showed some crowding of the incisors, this has not as yet been reported in other studies. It is possible that this is a local phenomenon due to conditions, either genetic or otherwise, specific to the Namibian cheetah population. An alternative possibility is that the defect is the result of generalized inbreeding depression and will be present in most or all cheetah populations throughout the species' range because of the extreme genetic homozygosity. Further research into free-ranging populations elsewhere in Africa is needed.

The cheetah is known to be depauperate in genetic variation (O'Brien et al. 1985, O'Brien et al. 1987, O'Brien et al. 1983), and this has been presented as an underlying explanation for many different problems that the species faces, such as their susceptibility to disease (Evermann et al. 1988, Munson 1993, O'Brien et al. 1985). A high degree of genetic homozygosity is thought to have many effects on the phenotype of a given animal, and such homozygosity carries with it many consequences. Developmental and morphological defects have been reported in highly inbred animals: for instance, dental anomalies similar to those reported here have been observed in the highly inbred populations of captive white tigers (Emily, P., pers. comm.), while other morphological abnormalities have been reported in Florida panthers, which also show very little genetic variability (Johnson et al. 2001, Roelke et al. 1985). The combined allozyme study on Namibian cheetahs and the morphological data suggests a genetic explanation (O'Brien et al. 1983, Wayne et al. 1986). The dental abnormalities as described in this paper may prove to be a genetic condition that predisposes an individual to developing advanced focal palatine erosion. Extensive work has already been done on cheetah genetics (Menotti-Raymond and O'Brien 1993, O'Brien et al. 1985, O'Brien et al. 1987, O'Brien et al. 1983) and protocols exist for both DNA fingerprinting and microsatellite analysis (Gilbert et al. 1991, Menotti-Raymond and O'Brien 1993). Both of these techniques will be used in the near future to examine relatedness of animals with and without these morphological abnormalities.

While the occurrence of focal palatine erosion in wild cheetahs is interesting from a scientific standpoint, the most crucial factor is whether it appears to have a detrimental effect on the cheetahs that exhibit it and on the population overall. Phillips et al. (1993) found with captive animals that even those cheetahs that had FPE were in excellent condition, but we found that in our sample there was a relationship between severe FPE and a loss of physical condition. It is not yet known in what way the dental abnormalities described will impact on the cheetah's ecology, nor what the consequences will be in the long-term. For example, wild cheetahs are known to suffer from kleptoparasitism by larger, more powerful carnivores such as lions and hyaenas (Caro 1994), and if cheetahs with dental abnormalities are slower at processing their kills, they may be at a further disadvantage in the wild by losing more of their kills in this way. It is also unknown what the implications of the physical defects, such as perforated palates as seen in extreme cases of FPE, may be for the overall health of affected wild individuals, although we know that they can lead to serious physical problems in captivity. For instance, one of the captive cheetahs reported with FPE died from severe kidney failure that was associated with oral-nasal osteomyelitis from FPE (Fitch and Fagan 1982), and kidney failure is one of the main causes of death for captive cheetahs (Marker-Kraus 1997, Munson 1993).

Overall, the development of dental abnormalities, including focal palatine erosion, is likely to be multifactorial, with genetics, diet, time spent in captivity, age and skull morphology all playing a role. The reporting of these conditions in wild cheetahs is important, as raising awareness amongst researchers will be vital in order to gain more information regarding the prevalence and severity of such abnormalities in different cheetah populations. This information will be crucial for a better understanding of how these conditions, particularly focal palatine erosion, may develop amongst wild cheetahs as well as those in captivity.

CHAPTER 9

DEMOGRAPHY OF THE NAMIBIAN CHEETAH

This thesis chapter has been submitted as the following paper:

Demography of the Namibian cheetah (*Acinonyx jubatus jubatus*). L.L. Marker, A.J. Dickman, R.M. Jeo, M.G.L. Mills & D.W. Macdonald. Submitted to *Biological Conservation.*

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CHAPTER 9: DEMOGRAPHY OF THE NAMIBIAN CHEETAH

ABSTRACT

Namibian cheetahs have suffered, and continue to suffer, high levels of removal due to conflict with local farmers, and it is important to understand the demography of this population in order to determine its likely persistence. Examination of cheetahs reported live-trapped or killed by local farmers, combined with subsequent information from radio-telemetry, allowed demographic parameters such as sex ratios, age and social structure, litter size, interbirth intervals and survivorship to be estimated for cheetahs on Namibian farmlands. Cub mortality was relatively low, but adult mortality was high, particularly for males, and peaked at 5-6 years of age. Neither marking nor relocating cheetahs seemed to affect survivorship, and there was no difference in survivorship between the sexes. Time spent in captivity did not appear to affect survival after release. These findings will be useful in formulating recommendations regarding the conservation and sustainable utilization of cheetah populations outside protected areas.

9.1 INTRODUCTION

Determining vital rates and demographic parameters is fundamentally important to the accurate understanding of any population (Eberhardt 1985, Lebreton et al. 1992, Lebreton et al. 1993). When a population is subject to high offtake, it is essential to establish whether the level of removal threatens its long-term viability. Large mammals are particularly sensitive in light of their long gestation and interbirth intervals, extended parental care and long maturation. Their life history parameters effectively lower the potential rate of population increase (Eisenberg 1981, Harvey et al. 1989), creating a higher extinction risk. Adult survival is a particularly important parameter, documented to exert a substantial impact on population viability for large, long-lived species (Crooks et al. 1998, Doak et al. 1994, Eberhardt 1985, Taylor et al. 1987).

The Namibian cheetah is an example of a threatened population which has been subject to a high level of removal, and whose vital rates require more accurate determination in order to assess and manage the impact of such removals. Vital rates of cheetahs have been reported in the Serengeti (Caro 1994, Kelly and Durant 2000, Kelly et al. 1998, Laurenson 1995, Laurenson et al. 1992), but the population in Namibia is subject to strikingly different pressures (Marker-Kraus et al. 1996). The intense conflict with humans results in a high number of adults being removed, which could have a more severe effect on long-term population viability (Crooks et al. 1998) than the lion-perpetrated high cub mortality reported in the Serengeti ecosystem (Laurenson 1995).

In order to ascertain the impact of such mortality, this paper reports and examines the vital rates and life history parameters of cheetahs on Namibian farmlands. Assessment of these reproduction and survivorship estimates provides insight into the vulnerability and likely persistence of the cheetah population in Namibia. In 1996, a Population and Habitat Viability Assessment was conducted, and called for, as a priority, more data on demographic parameters such as annual female mortality and reproductive information (Berry et al. 1996). Here, we provide these data.

9.2 METHODS

Demographic parameters were estimated using data from cheetahs captured opportunistically by farmers between 1991 and 2000. Some of these cheetahs were subsequently radio-collared and released, which provided information regarding reproduction and survivorship in the wild. Our interpretations take note of a potential bias in the sample population arising from the high proportion of cheetahs captured at 'playtrees', which are used more by adult males than by adult females (Marker-Kraus and Kraus 1995).

9.2.1 Trapping, immobilising and marking cheetahs

During the course of the study, we examined cheetahs that had been trapped on Namibian farms, using the capture and immobilisation protocols described in Chapter 3. Each live cheetah that we examined during the study was marked with a uniquely numbered implantable transponder (Trovan Electronic Identification Systems, Model-ID 100) placed at the base of its tail, and/or an aluminium ear-tag with a unique ID number in the individual's ear. On designated animals (those released in the core study area), a neoprene radio-telemetry collar with external antenna was also fitted (Advanced Telemetry Systems, Minnesota). The radio-collars were 3.8 cm wide with an adjustable strap from 30-45 cm long, with a 30 cm antenna extending about 18 cm from the collar. The collars were fitted with a "C" cell lithium battery with a life expectancy of over 36 months. Radio-collars weighed 280g and were equivalent to 0.56% of body mass for a 50kg male and 0.76% for a 37kg female, well below the limit suggested by Amlaner and Macdonald in 1980. In line with Caro (1994), we could detect no impact of these collars on cheetah survival.

9.2.2 Age classification

Age classification was based both on experience with captive cheetahs and on information from previous studies (Burney 1980, Caro 1994), and followed the protocol described in Chapter 3.

9.2.3 Determining social structure

Cheetahs are relatively social felids and often occur in groups: in many cases, farmers left adjoining traps open after catching a cheetah, to ensure that all members of any social group were captured at the same time. In other instances, capture was more random and it was likely that other cheetahs in the same social group remained free. Parameters such as coalition size, litter size and age-specific cub mortality were therefore determined using data from cases where determined attempts had been made to capture the entire group of cheetahs. Cheetahs were classified as to the social group of which they were a part when they were captured, using the following categories. Males over 18 months old were classed either as single males or as members of male coalitions, while females over 18 months old were classed as either being single females or as mothers trapped with cubs. The remaining classes were cubs (18 months old or younger) trapped without a dam, and mixed-sex groups of young independent cheetahs (19-30 months old), which were presumed to be littermate groups.

9.2.4 Estimating reproductive parameters

Age at parturition was estimated by examining females trapped with cubs, and by observing new litters of cubs produced by radio-collared females of known age. Long-term monitoring of six radio-collared females that had multiple litters provided information regarding interbirth intervals. Information regarding the distribution of births through the year was gathered from the examination and ageing of cubs trapped, and from observations made of females and cubs during radio-telemetry.

Litter size was determined from groups trapped where determined efforts had been made to capture the entire family unit, and from observations of radio-collared females with cubs during aerial tracking. Although we have no data regarding litter size at birth, observations of litters of different ages allowed some estimation of age-specific cub mortality.

9.2.5 Estimating mortality and survivorship

Most cheetahs were released at site of capture, but when this was not possible, the cheetahs were relocated. Relocation was classified as being 100km or more away, as this should be well beyond the diameter of a normal home range (Marker 2000).

The majority of cheetahs released within the core study area were radio-collared in order to gain information regarding post-release movements and home ranges. In addition, the tracking of cheetahs enabled information to be gathered regarding survivorship. Wild cheetah deaths reported to CCF included cheetahs that had been radio-collared, some that were tagged, and some that had not been marked at all. The deaths of marked cheetahs, whether radio-collared or simply ear-tagged, were often reported and enabled comparisons to be made about the approximate age of death of handled cheetahs versus those of cheetahs that had never been handled.

Mortality rates and life expectancy data were calculated following Downing (1980). The age of a cheetah at death was taken to be the midpoint of the age category in which it was recorded at the time of death. By using this midpoint, the formulae used should underestimate and overestimate the age at death for equal numbers of cheetahs and thereby give an approximation that is close to the actual distribution of ages at death.

Statistical analyses were performed using SPSS version 10.0 software (SPSS Inc. Chicago, USA). Means significance testing was carried out using the parametric independent samples t-test, using Levene's test to determine equality of variances, while departures from expected ratios were analysed using a chi-squared test. The non-parametric Spearman's rank correlation coefficient was used to determine the significance of relationships between variables measured on nominal scales, while Pearson's correlation coefficient was determined for interval data. Tests performed included one-way analysis of variance, and log rank for the equality of survival distributions following a Kaplan Meier analysis. All tests were two-tailed unless otherwise stated.

9.3 RESULTS

9.3.1 Social structure

The 412 cheetahs examined through the study were captured in 228 social groups, as summarized in Table 9.1.

Table 9.1 Annual demographic breakdown into social groups of the cheetahs captured and examined (SM = single males; C = coalition, CM = coalition males, CS = coalition size, SF = single females, LS = litter size, LM = littermate).

							Cubs with dam				Cubs without dam					No. LM						
Year	SM	C	CM	Mean CS	SF	Dams with cubs	M	F	∑	Mean LS with dam	M	F	∑	No. litters without dam	Mean LS without dam	M	F	∑	No. litters	Mean LM group size	No. animals	No. gps
Pre-91	5	2	4	2.0	0	0	0	0	0	-	1	1	2	1	2.0	1	1	2	1	2.0	13	9
1991	1	2	6	3.0	0	0	0	0	0	-	0	1	1	1	1.0	0	0	0	0	-	8	4
1992	2	3	8	2.7	6	3	5	2	7	2.3	3	3	6	4	1.5	1	1	2	1	2.0	34	19
1993	10	8	18	2.3	2	4	6	6	12	3.0	4	3	7	4	1.8	4	6	10	4	1.5	63	32
1994	8	6	16	2.7	4	2	2	2	4	2.0	4	2	6	4	1.5	2	1	3	1	3.0	43	25
1995	8	8	17	2.1	3	3	6	3	9	3.0	2	3	5	2	1.5	0	0	0	0	-	45	24
1996	1	2	4	2.0	3	2	4	5	9	4.5	4	3	7	4	1.8	0	0	0	0	-	26	12
1997	11	3	8	2.7	2	3	8	3	11	3.7	14	8	22	12	1.8	0	0	0	0	-	57	31
1998	9	4	8	2.0	3	7	11	9	20	2.9	6	7	13	7	1.9	0	0	0	0	-	60	30
1999	9	1	2	2.0	7	2	2	4	6	3.0	1	0	1	1	1.0	0	0	0	0	-	27	20
2000	9	3	6	2.0	3	1	2	1	3	3.0	4	5	9	4	2.3	2	3	5	2	1.5	36	22
Total	**73**	**42**	**97**	**2.3**	**33**	**27**	**46**	**35**	**81**	**3.0**	**43**	**36**	**79**	**44**	**1.7**	**10**	**12**	**22**	**9**	**2.4**	**412**	**228**

One hundred and seventy adult males were reported trapped, of which at least 97 (51.2%) were in coalitions. Coalition size (Figure 9.1) ranged from 2 to 4, with a mean of 2.3 throughout the study ($n = 42$), and showed no significant change through the course of the study ($F = 1.11$, $p = 0.389$).

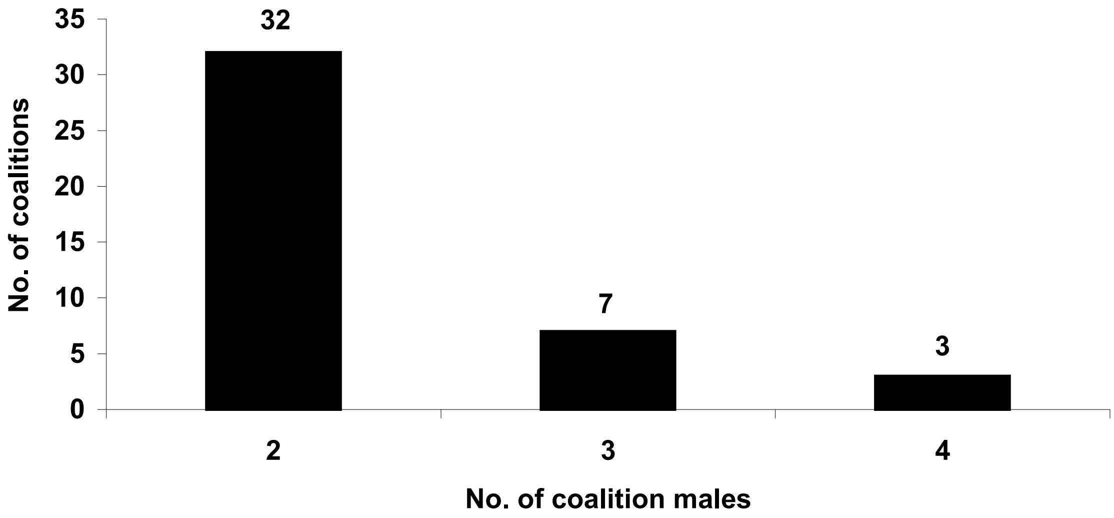


Figure 9.1 Coalition sizes for cheetahs captured throughout the study (n = 42 coalitions)

9.3.2 Age and sex structure of sample population

A summary of the age structure of captured cheetahs through the study is shown in Figure 9.2. There was a highly significant variation in overall capture frequency for each age cohort ($F = 2.02$, $p = 0.030$). Assuming that captures reflect trends in the wild population, the age structure of the population was not stable.

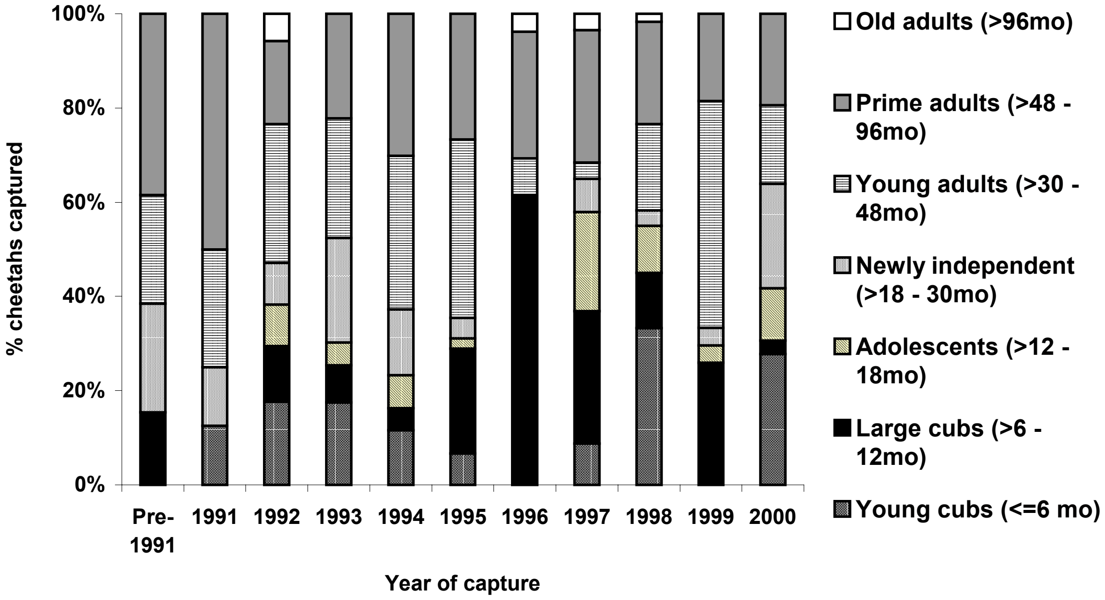


Figure 9.2 Breakdown into age groups of cheetahs captured throughout the study period.

Overall, the combined increase in the proportion of young animals and decline in the proportion of older animals meant that there was a significant relationship between age groups captured and year of the study ($F = 2.02$, $p = 0.030$), with more young animals being captured as time went on ($r_s = -0.12$, $p = 0.016$). This overall result arises from a combination of trends, although these were not in themselves statistically significant. Thus, the proportion of young cubs captured increased through time, although the trend was not statistically significant ($r_s = 0.15$, $p = 0.667$), and the same positive trends were seen for both large cubs ($r_s = 0.22$, $p = 0.519$) and adolescents ($r_s = 0.55$, $p = 0.079$). By contrast, the proportion of newly independent cheetahs captured showed some decline through time ($r_s = -0.47$, $p = 0.145$), as did the proportions of young adults ($r_s = -0.19$, $p = 0.574$) and prime adults ($r_s = -0.53$, $p = 0.096$). The proportion of old and very old adults (age groups 7 and 8 combined) captured stayed virtually constant through time ($r_s = 0.003$, $p = 0.989$).

There was a strong bias towards capturing adult males, with 2.9 adult males captured for every adult female. This proved to be a significant deviation from a 1:1 sex ratio with regard to the adult cheetahs trapped ($\chi^2 = 47.1$, $p = 0.000$). Amongst the adult cheetahs captured, the fraction of males trapped declined through the study, but the trend was not statistically significant ($r_s = -0.53$, $p = 0.097$).

9.3.3 Reproductive parameters

Age of breeding females ranged from 19 months to 12 years old ($n = 43$, mean = 5.3 years) (Figure 9.3). The percentage of adult females that were trapped with cubs each year ranged from 22.2% to 70.0%, with an overall mean of 44.5% ($n = 60$).

Figure 9.3 Estimation of age of dam at parturition, for the litters of cubs examined during the study.

Litters were produced throughout the year, but varied significantly between months ($\chi^2 = 18.3$, $p = 0.05$), indicating some degree of seasonality. Birth peaks were evident in March and July, with 40% of litters born in these two months, while only 5% of litters were born from October-December (Figure 9.4).

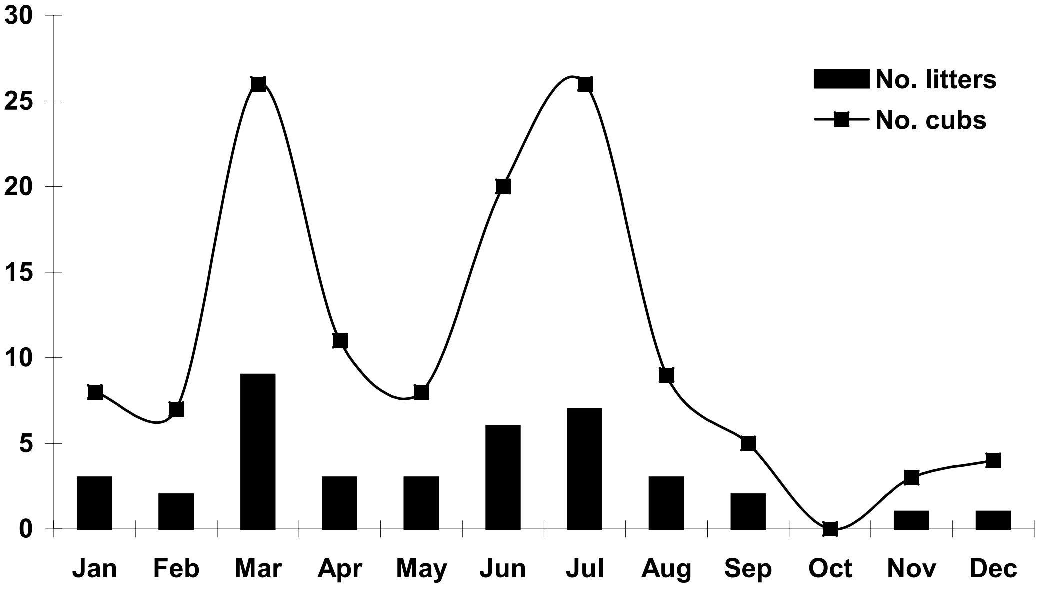


Figure 9.4 Distribution of cheetah cub births throughout the year, using estimated month of birth from examination of cubs captured.

Litter size obtained through trapping ranged from 1-6 with a mode of 3 (mean = 3.1, *n* = 27 litters), with no statistically significant variation between years (*F* = 0.56, *p* = 0.812). Litters observed during radio-telemetry alone ranged in size from 2 to 5 with equal modes of 3 and 4 cubs (mean = 3.4, *n* = 13 litters), and also did not vary significantly between years (*F* = 1.51, *p* = 0.131). There was no significant difference in mean litter size observed between the two techniques (*t* = -0.93, *p* = 0.357). Overall, therefore, the mean litter size observed, using data gathered from both methods, was 3.2 post-emergence (*n* = 40 litters, Figure 9.5).

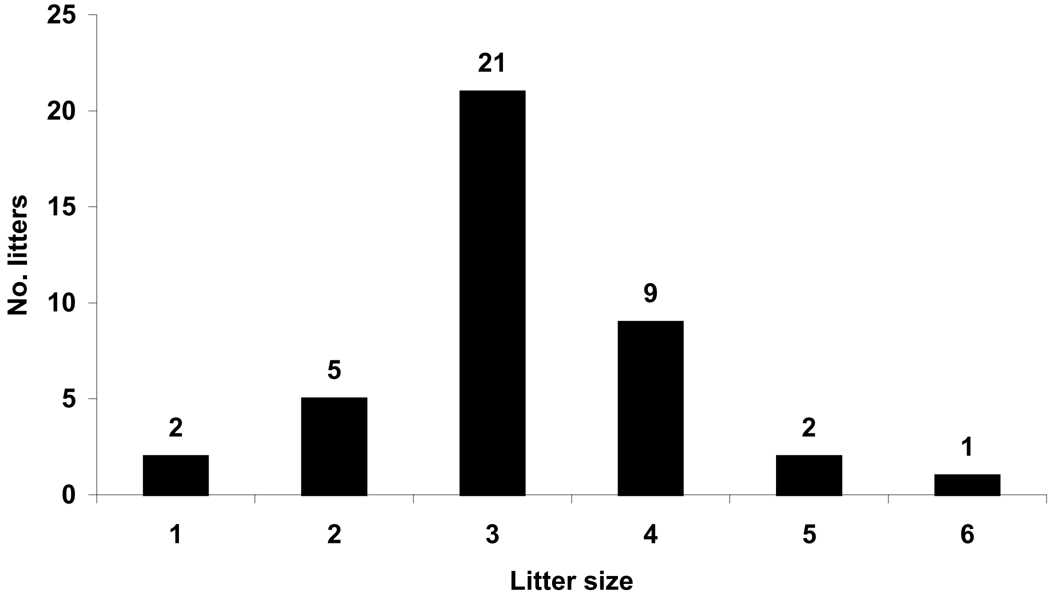


Figure 9.5 Litter sizes of cheetahs captured and examined throughout the study.

A regression on litter size and cub age for all the observed litters, including those seen multiple times at different ages (*n* = 65 observations) implies an estimated litter size at age 0 (birth) as 3.5 (Figure 9.6).

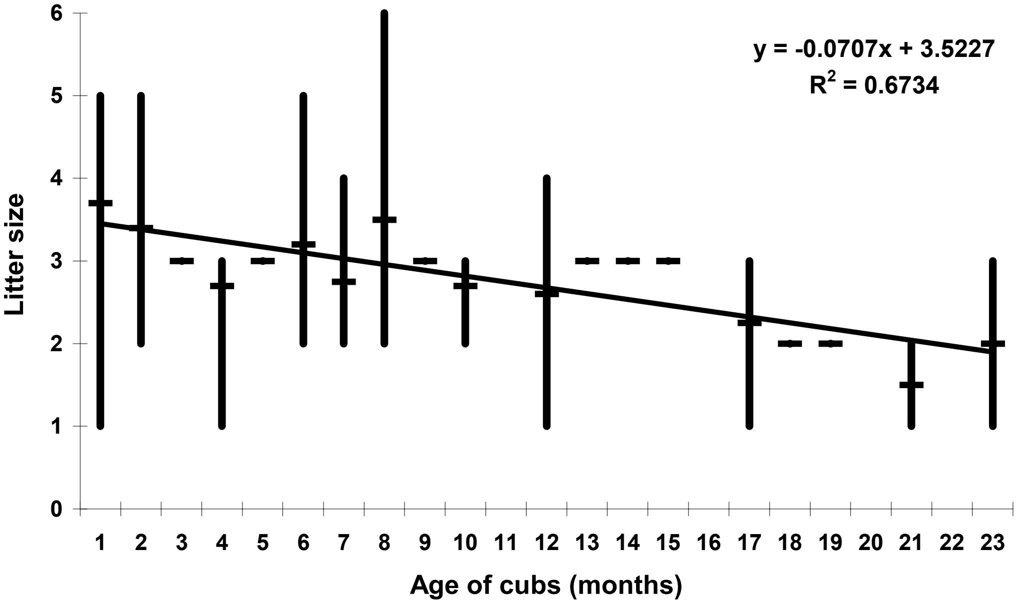


Figure 9.6 Regression of litter size with estimated cub age for cheetahs captured and examined during the study.

It is very likely, however, that field observation data underestimate mean litter size at birth, as there is likely to be pre-emergence mortality in the den (Laurenson et al., 1992). There was no significant deviation from an expected 1:1 sex ratio regarding cubs aged 12 months old or below ($\chi^2 = 0.62$, $p = 0.432$).

While females were captured with as many as six dependent cubs, average litter size for newly independent littermates ranged from one to three with a mode of 2 and a mean of 2.4 ($n = 9$ litters). This may be an underestimate, however, if newly independent animals are less likely to stay with a trapped littermate and are therefore less likely to be captured and recorded.

Reproductive information was gathered on 19 litters from 10 radio-collared dams (Table 9.2). Interbirth intervals following litters that were raised to independence ($n = 6$) ranged from 21 to 28 months, with a mean of 24 months.

Table 9.2 Information gathered from radio-collared dams (n = 10) regarding observed reproductive rates, interbirth intervals, litter sizes and cub mortality.

Dam	Litter date of birth	Age of dam at breeding	Age of cubs at first sighting	No. cubs at first sighting	Max. litter size seen	No. raised to 12 mo.	No. raised to independence
112	May-98	82	9	3	3	0	0
143	Aug-98	32	4	3	3	0	0
152	Dec-97	59	1	4	4	0	0
602	Jan-99	27	9	3	3	3	2
233-1	Feb-94	19	8	3	3	3	3
233-2	Jun-96	47	2	4	4	2	2
233-3	Mar-98	68	2	3	3	3	Unk
233-4	Jul-99	84	1	4	4	2	2
353-1	Mar-95	96	1	4	4	4	2
353-2	May-97	122	1	4	4	2	Unk
353-3	Mar-99	144	2	2	2	0	0
400-1	Jun-95	83	1	5	5	0	0
400-2	Jun-96	95	1	5	5	0	0
442-1	Feb-97	35	3	4	4	3	3
442-2	Jan-99	58	6	2	2	1	1
720-1	Mar-98	26	12	3	3	3	1
720-2	Mar-00	50	2	3	3	Unk	Unk
802-1	Jan-97	71	17	3	3	3	3
802-2	Nov-98	94	1	3	3	Unk	Unk

Although cheetahs have been known to survive for up to 21 years in captivity (Marker-Kraus, 1997) the maximum age recorded here for an animal that was still reproductively active was 12 years, so this can be regarded as the figure for effective longevity.

9.3.4 MORTALITY AND SURVIVORSHIP

Mortality rates were calculated from all recorded wild deaths (*n* = 67), including 45 marked cheetahs and 22 that had never been handled, and these are shown in Table 9.3. These data show that the age specific mortality ranged from 20% to 28% for the first three years of life and then dropped to virtually zero between three and five. There was then a large peak of mortality at age 5-6, but of the few cheetahs that reached six years of age (*n* = 4), all survived for a further four years.

Table 9.3 Life table showing mortality rates for wild cheetahs throughout the study period.

Age (years)	q_x			l_{x100}			d_{x100}			L_x			e_x		
	M	F	Overall	M	F	Overall	M	F	Overall	M	F	Overall	M	F	Overall
0-1	0.22	0.29	0.25	100	100	100	22.22	29.41	24.53	88.89	85.29	87.74	3.53	3.21	3.42
1-2	0.18	0.25	0.20	77.78	70.59	75.47	13.89	17.65	15.09	70.83	61.76	67.92	3.39	3.33	3.38
2-3	0.30	0.22	0.28	63.89	52.94	60.38	19.44	11.76	16.98	54.17	47.06	51.89	3.02	3.28	3.09
3-4	0.06	0.00	0.04	44.44	41.18	43.40	2.78	0.00	1.89	43.06	41.18	42.45	3.13	3.07	3.11
4-5	0.00	0.00	0.00	41.67	41.18	41.51	0.00	0.00	0.00	41.67	41.18	41.51	2.30	2.07	2.23
5-6	0.80	0.86	0.82	41.67	41.18	41.51	33.33	35.29	33.96	25.00	23.53	24.53	1.30	1.07	1.23
6-7	0.00	0.00	0.00	8.33	5.88	7.55	0.00	0.00	0.00	8.33	5.88	7.55	3.50	3.50	3.50
7-8	0.00	0.00	0.00	8.33	5.88	7.55	0.00	0.00	0.00	8.33	5.88	7.55	1.50	1.50	1.50
8-9	0.00	0.00	0.00	8.33	5.88	7.55	0.00	0.00	0.00	8.33	5.88	7.55	1.50	1.50	1.50
9-10	1.00	1.00	1.00	8.33	5.88	7.55	8.33	5.88	7.55	4.17	2.94	3.77	0.50	0.50	0.50

q_x = age specific mortality rate
l_{x100} = number attaining this age from a beginning cohort of 100
d_{x100} = number dying at each age from a beginning cohort of 100
L_x = mean number alive between age classes
E_x = mean expectation of life (average additional lifespan of those reaching this age)

Survivorship following release could be calculated for the 45 wild marked cheetahs, and ranged from 0.6 months to 48.5 months for males (*n* = 35) and 0.6 months to 65.4 months for females (*n* = 10). Survivorship of male and female marked cheetahs is shown in Figure 9.7.

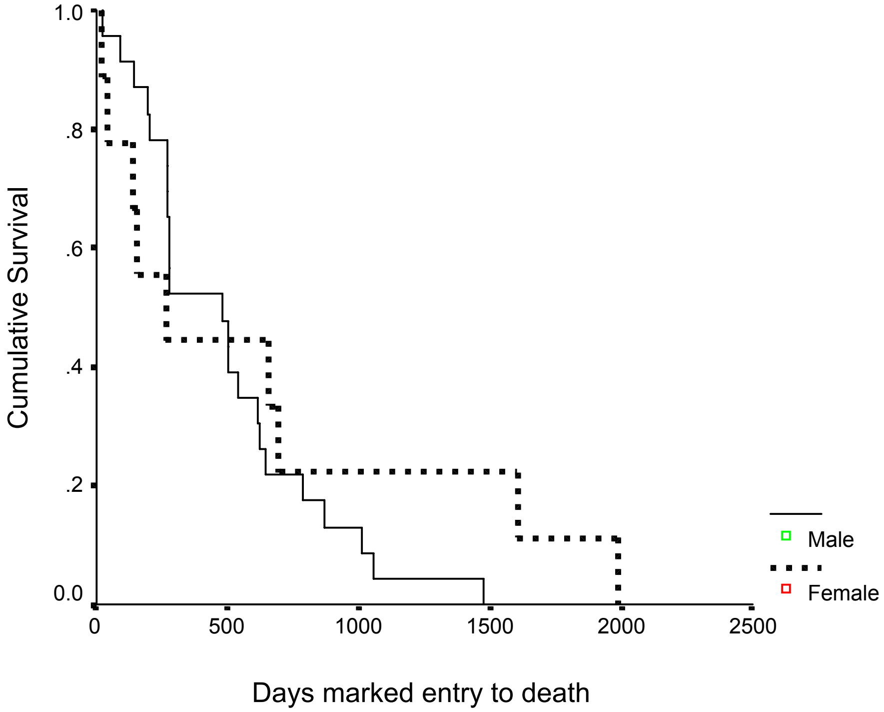
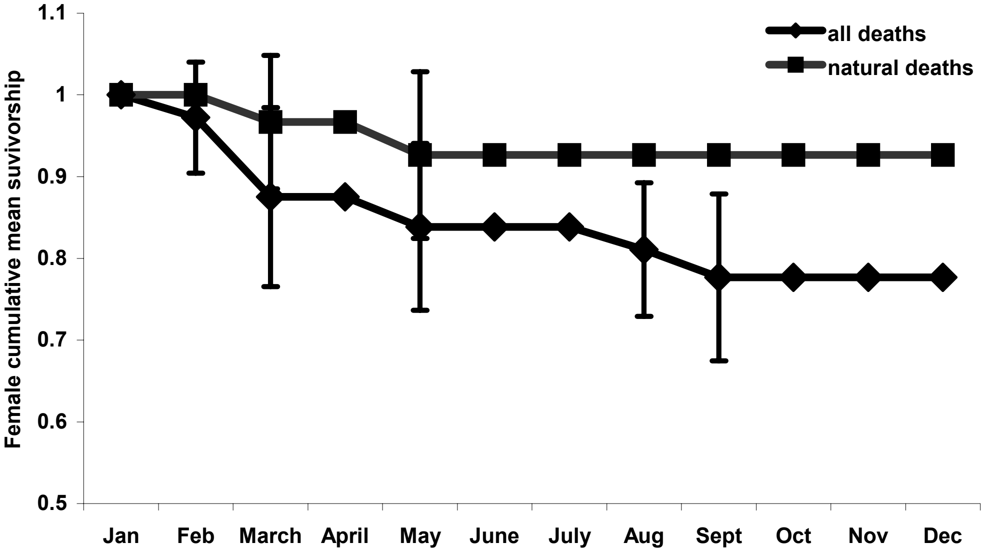
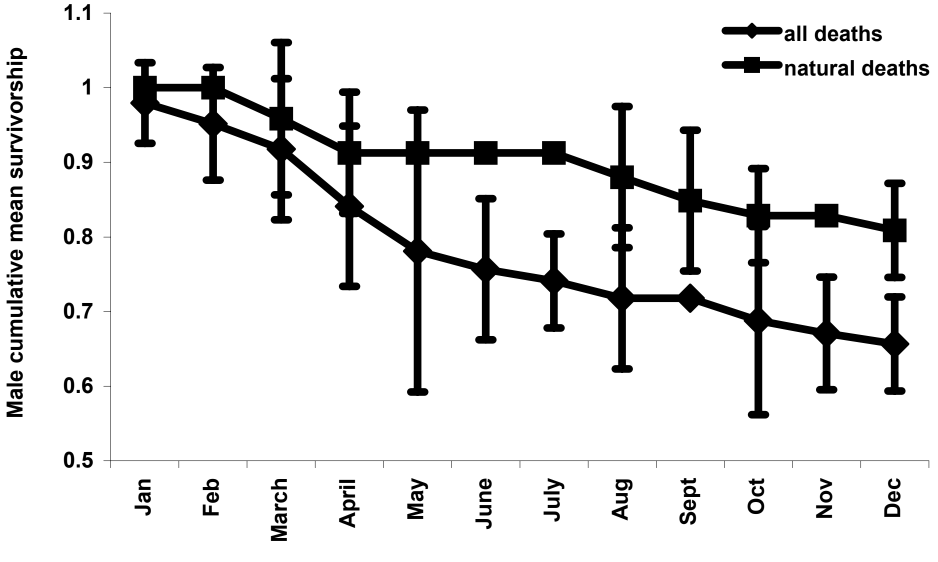


Figure 9.7 Survivorship of marked male and female cheetahs released during the study period.

Of the cheetahs shown in Figure 9.7, 71.1% (*n* = 32) were adults at the time of release, of which 46.9% (*n* = 15) were of prime breeding age. Mean survival time for tagged and released males was 14.4 months (*n* = 35), while for females it was 18.5 months (*n* = 10). Although females lived for slightly longer, the difference in survivorship was not statistically significant (*log rank* = 0.71, *p* = 0.401). When analysis was restricted to adult animals, to remove any effect of cub mortality following the death of a female, the mean survival time was 16.2 months for males (*n* = 23) and 20.3 months for females (*n* = 9), a difference that again was not significant (*log rank* = 0.58, *p* = 0.447). There was no significant difference in estimated age at release between the sexes (*t* = 0.24, *p* = 0.812).

Cumulative annual survival was calculated for radio-collared male and female cheetahs and is presented in Figures 9.8a and b.





Figures 9.8a and 9.8b Annual cumulative survivorship for (a) female and (b) male cheetahs. Error bars represent standard errors.

There was a significant difference between cumulative yearly survival rates between males (mean = 9.4 months) and females (mean = 10.2 months) ($t = 2.07$, $p = 0.009$). There was also a significant difference between the frequency of natural mortality and human caused mortality for both males ($t = -7.37$, $p = 0.000$) and females ($t = - 7.08$, $p = 0.000$), with the majority of deaths attributable to human causes.

Marked cheetahs were slightly older at death than unmarked cheetahs, but the difference was not statistically significant ($t = -1.94$, $p = 0.057$). Amongst marked cheetahs, survivorship of radio-collared animals was compared to those that were just ear-tagged and released. As only fully-grown (>18 months), healthy cheetahs were radio-collared, whereas the tagged population included subadults, the analysis was restricted to cheetahs that were released at age group 4 or above. Mean post-release survival time for radio-collared cheetahs was 20.2 months ($n = 24$), whereas cheetahs wearing only a tag survived on average for 9.8 months after release ($n = 8$): see Figure 9.9. Radio-collared cheetahs survived longer following release than tagged cats, and differed significantly in their survival distribution (*log rank* = 3.92, $p = 0.048$). This was not an effect of differing ages at release between the two groups ($t = -1.23$, $p = 0.230$).

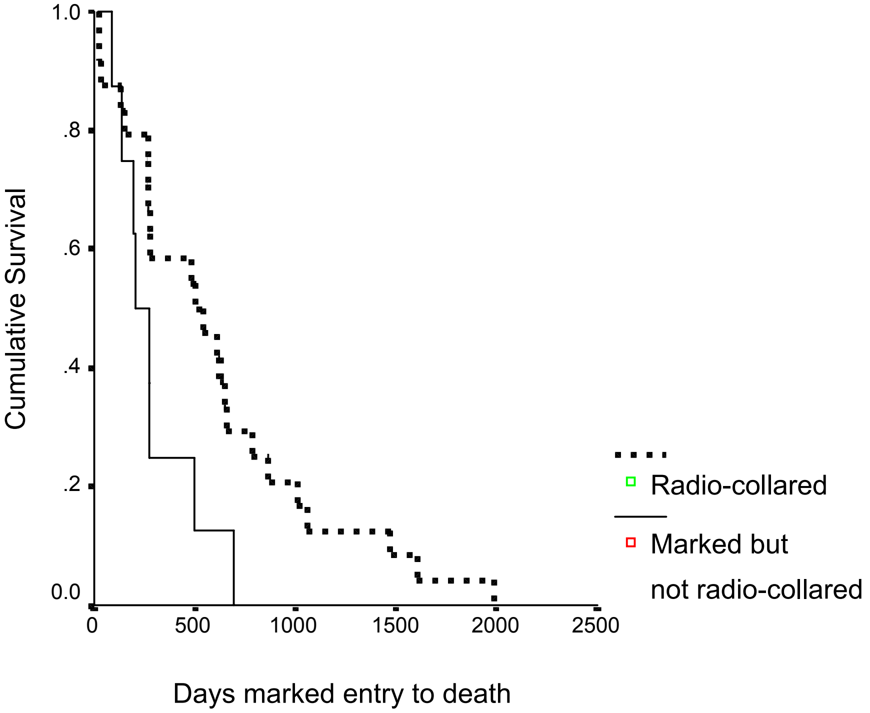


Figure 9.9 Kaplan-Meier survival curves for radio-collared versus marked cheetahs.

It is possible that since all cheetahs radio-collared were in our core research area, more people were aware of the presence of marked cheetahs which was a deterrent to killing cheetahs, whereas ear-tagging of cheetahs took place throughout the country, including places where many people were unaware of our research. There were 21 reported cases of human-caused mortality amongst the marked animals, and if the radio-collar acted as a deterrent then the expectation would be for there to be relatively few collared cheetahs within this sample. In fact, 14 of the 21 cheetahs reported killed by humans were radio-collared, which was not a significant deviation from an equal ratio of collared to tagged cats ($\chi^2 = 2.33$, $p = 0.127$). However, 36.8% of the released adult cheetahs were radio-collared, while 63.2% were only tagged. Using these proportions as the expected ratios, radio-collared cheetahs comprise a significantly greater percentage of human-caused mortality than would be expected ($\chi^2 = 8.05$, $p = 0.005$).

Often cheetahs with health problems spent longer time in captivity before release than healthy cheetahs. To investigate whether time spent in captivity was detrimental in terms of subsequent survival in the wild, survivorship following release for adult animals was correlated with total days spent captive prior to release. There was a slight negative correlation between the two variables, but it was not significant ($r = -0.52$, $p = 0.778$).

Cheetahs were either released at sight of capture or distances varying between 50km to 600 km away from the capture location. There was no significant difference in mean survivorship for adult cheetahs released at the site of capture (mean = 18.0 months, $n = 19$, $s = 13.6$), those released within 100km of the capture site (mean = 15.4 months, $n = 7$, $s = 9.1$) and those relocated over 100 km away (mean = 28.4 months, $n = 8$, $s = 27.3$) ($F = 1.34$, $p = 0.275$).

9.4 DISCUSSION

9.4.1 Social structure

The most common age groups trapped were young adults and prime adults; removal of these age classes is likely to have a particularly detrimental effect on the population (Crooks et al. 1998). If this sample is representative of the nationwide picture, then this finding is of particular concern. Males are often caught at the time of dispersal when they are trying to establish a territory, travelling long distances across many farms, presumably increasing their chances of being trapped. This bias towards young adult and prime adult males is likely to be a sampling bias rather than a true indication of population structure in the wild, due to the aforementioned 'play-tree' bias. The disproportionate removal of males has been seen in many mammalian species and, although probably less damaging to the viability of the population than a skew towards removing females, can nevertheless have serious impacts in terms of social structure and behaviour (Tuyttens and Macdonald 2000). In areas of fragmented populations and low density where removed males cannot easily be replaced by immigrants, continued removal of adult males could have a severe effect and lead to lower reproductive rates and an accelerated decline (Tuyttens and Macdonald 2000). This scenario is likely to become of greater importance if cheetah populations become more fragmented in the future. The removal of dominant, territorial males can also be counter-productive to farmers insofar as it may lead to the increased survival of subadult and transient animals that would not normally settle in the area (Young and Ruff, 1982, cited in Tuyttens and Macdonald, 2000) and which may be more likely to become 'problem' animals (Marker-Kraus et al. 1996).

9.4.2 Reproductive parameters

The live capture of females with cubs presented the opportunity to monitor the sex structure of cubs and to estimate reproductive parameters. Litters could not be studied before emergence from the den, and therefore provide no direct information regarding either sex structure or litter size at birth, as infant mortality can be substantial before emergence (Laurenson 1994). The litter size of 3.5 at birth extrapolated from the data in this study is slightly higher than the 3.1 found in previous studies in Namibia (Marker-Kraus et al. 1996), while information from captive studies give a mean litter size of 3.3 (Marker-Kraus 1997), and data compiled by Gittleman (1986) indicated an average of 3.8 cubs per litter. These data are difficult to compare directly as the litter size at various ages is not given, but the litter size at independence of 2.4 found in this study is similar to the 2.1 reported from the Serengeti (Kelly et al. 1998). Although females are capable of breeding at an earlier age (Marker-Kraus 1997, Wildt et al. 1993), reproduction on the Namibian farmlands usually does not occur before 1.5 to 3 years of age (Morsbach 1987). Similarly, whereas males are physiologically capable of breeding at less than 2 years of age (Marker-Kraus 1997, Wildt et al. 1993), social constraints may limit breeding of Namibian male cheetahs to older, territorial animals in the prime age category.

9.4.3 Mortality and survivorship

The mortality and life expectancy data reveal that for both male and female cheetahs in our sampled population, the highest peak of deaths is between five and six years of age. This is to be expected given that the trapping and removal methods tend to select prime breeding age adults, as discussed above. The mortality figure found here for the first year of life (25%) should be interpreted with caution as it cannot include mortality before emergence from the den, which has been found to be a period of high mortality in other studies (Laurenson 1994). However, it appears that in Namibia, the level of cub mortality is indeed far lower than in game reserves with a high density of intra-guild competitors. Despite this, even without intra-guild competition, fewer than 50% of the cubs reach independence. Data from the Serengeti show that female cheetahs surviving to independence had a good chance of reaching old age (Kelly et al. 1998). This was not the case here: in this study, female cheetahs that reached independence still had an 86% chance of dying before six years of age. This reflects the differing pressures on the two populations: in the Serengeti, the greatest threat to survival is predation by larger carnivores, particularly lions, on dependent cubs (Laurenson 1994). This threat recedes once a cheetah reaches adulthood, whereas the greatest threat to cheetahs in Namibia appears to be human-caused and focuses on cheetahs of prime breeding age. In this study the threshold seemed to be six years of age; the few cheetahs monitored that lived that long managed to survive until old age.

The removal of adult cheetahs has been shown to have a far more significant impact on the overall population than the removal of cubs (Crooks et al. 1998). The selection by trapping adult cheetahs is therefore of major concern regarding the ability of the Namibian cheetah population to persist long-term. The majority of these removals are in reaction to a perceived threat to livestock and/or game by commercial farmers (Marker-Kraus et al. 1996). As a result, conservation efforts should be concentrated on educating farmers in alternative game and livestock management techniques to reduce losses and lessen conflict.

Much of the information gathered through this study was only possible by directly handling cheetahs, including fitting radio-collars prior to release. However, the invasive handling and monitoring of wildlife, particularly when it involves an endangered species, has been the focus of much debate (Bateson 1991, Burrows et al. 1994, Creel et al. 1997, Cuthill 1991, Driscoll and Bateson 1986, Smith and Boyd 1991). The handling of wild animals is likely to involve some degree of stress (Laurenson and Caro 1994), and it has been argued that this stress may hamper the eventual survival of the animals (Cuthill 1991, Martin and Bateson 1986). This may be particularly important with cheetahs, a species potentially more vulnerable due to its inherent genetic uniformity (Laurenson and Caro 1994, Smith and Boyd 1991). However, this study showed that the survivorship of the wild cheetahs we handled and marked was no lower than that of wild cheetahs that had never been handled. In addition, there was no evidence that putting a radio-collar on a wild cheetah had a negative impact on survival following release, and the radio-collared cheetahs studied here lived longer post-release than their tagged counterparts. Collaring of cheetahs was conducted in a relatively concentrated area, where farmers were well aware of the research being conducted. Therefore, public awareness may have contributed to the longevity of radio-collared cheetahs that are not causing problems with farmers. Marking of cheetahs in other parts of the country, where public awareness was not as extensive, may have caused the differences between the post-release longevity. It could not be ascertained whether the collars acted as a deterrent to farmers who would otherwise kill the cats, instead prompting them to contact CCF or another authority to deal with problem or trapped cheetahs. The higher than expected incidence of radio-collared cheetahs amongst those killed by humans may indicate that people are more likely to report a death if they see a radio-collar on the cheetah concerned.

Cheetahs that were relocated far from their capture site provided important survival information. The relocated cheetahs did not have significantly different survival rates from those released in close proximity to their capture site, which suggests that relocating cheetahs into suitable habitat can be an effective conservation strategy without negatively impacting the survivorship of the individual cheetah.

Of importance in our monitoring was the possible effect of keeping cheetahs in captivity prior to release. There is a chance that holding an animal in captivity could have a detrimental effect on survivorship after release, either through a reduction in physical fitness and hunting ability, or by animals losing their territories and being forced into marginal areas. Analysis of cheetahs we handled, however, showed that there was no relationship between the length of time spent in captivity and subsequent survivorship following release, despite the fact that some of the cheetahs were held in captivity due to being in poorer physical condition.

From this 10-year study we have identified certain areas of concern, e.g. the continued removal of prime adults from the population, the skewed sex ratio resulting from capture methodology and the apparently unstable age distribution. In addition, we have been able to establish parameters that can be used in future modelling efforts. Such modelling exercises will provide a basis for long-term conservation strategies for cheetahs on Namibian farmlands.

CHAPTER 10

NOTES ON THE DIET AND FEEDING ECOLOGY OF THE CHEETAH ON NAMIBIAN FARMLANDS

This thesis chapter has been submitted as the following paper:

The feeding ecology of the cheetah (*Acinonyx jubatus)* on Namibian farmlands. L.L. Marker, J.R. Muntifering, A.J. Dickman, M.G.L. Mills & D.W. Macdonald. Submitted to the *South African Journal of Wildlife Research.*

Chapter 10: Table of Contents

CHAPTER 10: THE FEEDING ECOLOGY OF THE CHEETAH ON NAMIBIAN FARMLANDS

ABSTRACT

The cheetah has long been regarded as a significant threat to the interests of farmers of both game and livestock in Namibia, and for this reason has been removed in large numbers. However, the actual diet of these cheetahs has not been documented, and such documentation is an important component of any effective conservation plan. We performed feeding trials to relate more accurately the remains found in scats to the numbers of prey animals consumed. Prey size ranged from birds and hares to large antelope, and cheetahs seldom preyed upon domestic stock, with apparent selection towards common, indigenous game species. Information gathered from aerial sightings of kills was significantly biased towards larger species, while data on the proportion of times cheetahs were seen near either livestock or game were also misleading when compared to corrected scat analysis. Due to the diurnal nature and wide-ranging habits of cheetahs, they are sighted near stock relatively frequently, which may contribute to an exaggerated perception of their predation on stock. Livestock depredation by cheetahs was calculated to account for at least 0.01 calves and 0.004 sheep per km^2, and may be substantially more depending on cheetah density. Any losses to cheetahs and other predators can have economic impacts for farmers, and management techniques for mitigating such losses are suggested.

10.1 INTRODUCTION

Extensive information regarding the feeding ecology of cheetahs has been collected from the Serengeti (Caro 1994, Frame 1986, Kruuk and Turner 1967, Schaller 1968), where 21 prey species were recorded, ranging in size from mole rats (*Cryptomys spp.*) to wildebeest, with a strong bias towards Thomson's gazelles. Other studies in East Africa (Burney 1980, Eaton 1974, Graham 1966, McLaughlin 1970) have also revealed preferences for gazelles (*Gazella spp.*) and impala, amongst a diverse prey base.

In northern Kenya, cheetahs were observed taking kudu, gerenuk and dik-dik (Hamilton 1986) while kob and oribi have been noted as prey in west Africa (Nowell and Jackson 1996). Data from Kafue National Park, Zambia showed puku to be the favoured prey species (Mitchell et al. 1965), while cheetahs in the Lowveld Region of South Africa (Hirst 1969, Pienaar 1969) took a preponderance of impala amongst 15 species taken. In the Southern Kalahari, (Mills 1984) found that cheetahs killed prey ranging from bat-eared foxes (*Otocyon megalotis)* to wildebeest, with springbok as the favoured species.

The summary to date, then, is that cheetahs predominantly kill medium-sized (10 – 35 kg) antelope, but will opportunistically take other prey if available. Against this background, the diet of cheetahs on Namibian farmlands is interesting for two reasons. First, the cheetahs in this habitat exist in a highly managed ecosystem, where kleptoparasites such as spotted hyaenas and lions have been eliminated, whereas previous studies of cheetah diet have been conducted in areas where they are sympatric with other larger carnivores, by which they are potentially disadvantaged by intra-guild competition. It is interesting to investigate how their dietary preferences change in the absence of such competition. Secondly, this population is threatened by farmers who kill them because of the perception that cheetahs kill substantial numbers of domestic stock and ranched game, particularly expensive and exotic game. Cheetahs are known to kill smallstock and calves up to six months old (Marker-Kraus et al. 1996), but it is important to investigate whether the level of predation corroborates the perception of them being a serious problem.

Throat bites are indicative of a cheetah

Picture 10.1 Calf injured by suspected cheetah attack – such incidents can cause significant economic losses to farmers.

Through surveys conducted with Namibian farmers, the cheetah was reported to prey upon a wide range of species on the farmlands, including livestock as well as both indigenous and exotic game species (Marker-Kraus et al. 1996). This paper aims to identify the relative importance of the different species in the diet of cheetahs on Namibian farmlands, so that problems and potential solutions can be identified in order to develop suitable cheetah conservation strategies.

Diet estimation of carnivorous mammals can be tackled by various methods, each subject to different biases (Mills 1984, Reynolds and Aebischer 1991). Opportunistic and direct observation of kills, while the predominant method for large carnivores in East and South Africa, is impractical in the dense bushveld of Namibian farmland. The traditional solution involves quantification of undigested prey remains in scats (e.g. Emmons 1987, Geffen et al. 1992, Lanszki et al. 1999, Previtali et al. 1998). However, it has long been obvious that extrapolation from volumetric analysis of undigested prey remains in faeces is an unsafe basis for quantifying carnivore diet unless corrected for differential digestibility of different prey sizes and species (Ackerman et al. 1984, Floyd et al. 1978, Lockie 1959, Scott 1941). Such uncorrected extrapolation risks, for small prey, the over-estimation of biomass and under-estimation of numbers consumed. Therefore, as one step in our diet analysis we calculated digestibility indices for captive cheetahs following the protocol established by (Floyd et al. 1978) for grey wolves (*Canis lupus*), and used these indices to estimate rates of livestock depredation caused by cheetahs on the farmlands. We also compared estimates of cheetah diet derived by contrasting methodologies (e.g. faecal analysis versus aerial surveys of kills) to evaluate the biases inherent in each.

10.2 METHODS

10.2.1 Feeding trials

Following (Floyd et al. 1978), nine trials were conducted in two 256m^2 captive holding pens at the Cheetah Conservation Fund's research farm near Otjiwarongo, Namibia. Before each trial, the cheetahs were fasted until no fresh scats were being produced, a process which took 40-96 hours. This was similar to fasting periods experienced in the wild: Caro (1994) reported fasting times of 30-36 hours, McLaughlin (1970) reported fasts of 48-72 hours, and Broomhall (2001) described fasting periods ranging from 84 to 168 hours.

Carcasses were weighed and then fed intact to the cheetahs. Five carcasses were fed to two wild-born, two-year old females. Four carcasses were fed to three wild-born, three-year-old males. Four species were used with prey weights <30kg (hare, lamb, goat and steenbok); while two species were heavier, namely kudu and oryx. Since a high percentage of cheetah kills are either abandoned after gorging or are stolen by a competing predator (Caro 1994), the carcasses were removed when all feeding cheetahs remained lying down for more than 10 minutes without returning to feed (33-125 minutes). After feeding, the carcass was removed and weighed to the nearest 0.5 kg.

Scats were collected twice daily, in order to minimise both trampling and desiccation. Scat consistency varied from liquid or semi-liquid scats that would be unlikely to be found and collected during a field study, which were categorised as non-collectable scats (NC), to firmer scats that were likely to be found and collected in the field (field-collectable, FC). Field-collectable scats were counted and weighed immediately after collection.

Statistical analyses were conducted using SPSS version 10.05 (SPSS, Chicago, Illinois). Kolmogorov-Smirnov and Shapiro-Wilk tests were used to investigate normality, and non-parametric procedures were used where there was significant deviation from normality. Analysis followed (Floyd et al. 1978) and (Weaver 1993), using a least squares regression plot, which yielded a regression equation, where y is the kg of prey consumed per collectable scat and x is the average weight of an individual of a given prey species. By multiplying *y* by the frequency of occurrence (*n*) of each prey species in the sample, it was possible to obtain a total weight consumed of each species and calculate the ratios of biomass consumed between prey species. The total weight of each species consumed was then divided by the average estimated weight in order to compute the number of individuals consumed, and ratios were computed relative to a kudu calf weighing 16kg. Masses of subadult animals were used for eland, oryx, kudu and red hartebeest, as cheetahs most commonly prey upon the calves of these large species rather than hunting adult animals (Marker-Kraus et al. 1996).

10.2.2 Scat analysis

Scats were collected from wild cheetahs that were live-trapped by farmers (as described in Chapter 3), both from the traps themselves and during examination, and were also collected in the field, particularly from 'playtrees', which are certain trees used by cheetahs for scent-marking with urine and faeces (Marker-Kraus and Kraus 1995). Once collected, scats were individually placed in nylon stockings and washed through two complete regular cycles in a conventional washing machine. No bleach or detergents were used. The washing process left in the stocking only hair, bones, teeth and hooves, and the stockings and their contents were then hung out to dry. The dried remains were spread evenly into a dissecting pan with a grid base of six 67.5cm^2 squares, and one hair was randomly sampled from each square, carefully examined, and cuticle scale imprints were made.

Hairs were sandwiched between two glass slides on a plastic cover slip, held together by four small (no. 20) binder clips, and heated for five minutes in a toaster oven at 108°C, removed, and left to air cool. The hair was then gently removed from the cover slip using forceps or fingernail, and the hair's scale characteristics were used to determine which species it was from. Macroscopic distinctions narrowed the options and cuticle imprints finalized the identification. Kudu and eland hairs were often difficult to distinguish, so were categorized together in some instances. In compiling our reference collection, we were mindful of Koegh's (1983) result that hair from fresh carcasses and preserved skins is identical (Buys and Koegh 1984, Koegh 1983). Our collection involved hairs and imprints from neck, back, belly, and hindquarter regions of each possible prey species in the study area.

10.2.3 Information on kills from radio-tracking flights and from farmers

Between 1993 and 1999, radio-collared cheetahs were tracked on a weekly basis from a fixed-wing Cessna 172, as described in Chapter 11. During these flights, cheetahs were occasionally sighted on identifiable kills. Although they may do so exceptionally (Caro 1982, Pienaar 1969, Stander 1990), cheetahs do not generally scavenge from other predators (Caro 1994, Wrogemann 1975) and we therefore assumed that the cheetah had killed the animal being eaten. We also recorded whether the cheetah was sighted within 500m of livestock or game. Interpretation of the scat analysis data was also made in the context of farmers' answers during a questionnaire survey conducted between 1991 and 1999 regarding their observations and perceptions of cheetah predation (Marker-Kraus et al. 1996), as detailed in Chapter 12. The results of the feeding trials and corrected scat analysis were used to estimate rates of livestock depredation by cheetahs in the study area.

10.3 RESULTS

10.3.1. Feeding trials

Scats containing the presented prey item were produced from 48 to 111 hours after feeding, and the feeding trial results are shown in Table 10.1.

Table 10.1 Results of feeding trials performed on captive Namibian cheetahs. Scats were classified as either field-collectable (FC) or non-collectable (NC).

	Prey mass (kg)				No. scats produced			Weight of FC scats				
Prey Item	Presented	Consumed	% consumed	Mean prey consumed per cheetah (kg)	FC	NC	Total	Total (kg)	% of prey weight presented	% of prey weight consumed	Kg of Prey consumed / FC scat	No. FC scats / kg of prey consumed
Hares (2)*	3.8	3.0	80.0	1.5	9	1	10	0.4	10.9	13.7	0.3	3.0
Lamb	3.8	3.3	86.7	1.6	10	0	10	0.5	14.0	16.2	0.3	3.1
Kudu	109.5	10.0	9.1	5.0	7	6	13	0.9	0.8	8.7	1.4	0.7
Goat	22.5	8.9	39.4	4.4	11	1	12	0.9	4.0	10.2	0.8	1.2
Goat	29.5	10.0	33.9	5.0	10	1	11	1.0	3.3	9.6	1.0	1.0
Goat	28.8	15.1	52.5	5.0	32	8	40	2.2	7.8	14.8	0.5	2.1
Oryx	83.5	20.5	24.6	6.8	18	4	22	1.4	1.7	6.9	1.1	0.9
Steenbok	9.3	6.5	70.3	2.2	13	2	15	0.8	8.6	12.2	0.5	2.0
Mean	36.3	9.7	49.6	3.9	13.8	2.9	16.6	1.0	6.4	11.5	0.8	1.8

* Average weight per carcass = 1.88kg

Of the four smaller prey species, the mean percentage consumed was 69.7%, but for the two species of large antelope this dropped to 16.8%. There was a strong correlation both between prey mass presented and prey mass consumed ($r_s = 0.86$, $p = 0.007$, $n = 8$), and between prey mass presented and fresh collectable scat weight ($r_s = 0.74$, $p = 0.038$, $n = 8$). However, the smaller prey items consumed gave a proportionally greater fresh weight of field-collectable scats in relation to the prey mass presented, with the mass of field-collectable scats averaging 8.1% of the prey mass presented for the four smaller species, but only 1.2% for the kudu and oryx. The number of field-collectable scats per kg of food consumed diminished with increased prey weight – on average, the four small species gave 2.4 field-collectable scats per kg of prey eaten, while kudu and oryx gave a mean of 0.8 scats/kg.

Data summarised in Table 10.2 revealed a strong correlation (r = 0.89, p = 0.017, n = 6) between the weight of prey consumed per collectable scat and average weight of the prey species presented.

Table 10.2 Summary of results from the feeding trials for each prey species presented.

	Mass of prey (kg)			No. scats produced			No. scats per kg prey consumed			Kg prey eaten per FC scat
Prey type	Presented	Consumed	% consumed	FC	NC	Total	FC	NC	Total	
Hare (2)*	3.8	3.0	80.0	9	1	10	3.0	0.3	3.3	0.3
Lamb	3.8	3.3	86.7	10	0	10	3.1	0.0	3.1	0.3
Steenbok	9.3	6.5	70.3	13	2	15	2.0	0.3	2.3	0.5
Goat (3)**	80.8	34.0	42.1	53	10	63	1.6	0.3	1.9	0.6
Kudu	109.5	10.0	9.1	7	6	13	0.7	0.6	1.3	1.4
Oryx	83.5	20.5	24.6	18	4	22	0.9	0.2	1.1	1.1

* Average weight per carcass = 1.88kg
** Average weight per carcass = 26.92kg

A regression on these variables generated the following equation: $y = 0.0098x + 0.3425$, which can be used to provide valuable information on the relative contribution of different prey species reported as part of the cheetah's diet (Marker-Kraus et al. 1996). This information is shown in Table 10.3.

Table 10.3 Ratios of prey animals consumed, using the corrected scat analysis, for 100 scats containing prey species.

Species	Age/sex	Assumed weight of prey (kg)[1,2,3]	Prey consumed per scat (kg)	No. of scats	Mass of prey consumed (kg)	Ratio of weight consumed*	No. of individuals consumed	Ratio of no. individuals consumed
Kudu	Adult female	200	2.30	100	230.3	4.61	1.15	0.37
	Juvenile	100	1.32	100	132.3	2.65	1.32	0.42
	Calf	16.0	0.50	100	49.9	1.00	3.12	1.00
Red Hartebeest	Adult	135	1.67	100	166.6	3.34	1.23	0.40
	Juvenile	67.5	1.00	100	100.4	2.01	1.49	0.48
	Calf	15.0	0.49	100	49.0	0.98	3.26	1.05
Oryx	Adult	225	2.55	100	254.8	5.10	1.13	0.36
	Juvenile	113	1.45	100	145.0	2.90	1.28	0.41
	Calf	15.0	0.49	100	49.0	0.98	3.26	1.05
Eland	Juvenile	270	2.99	100	298.9	5.99	1.11	0.35
	Calf	36.0	0.70	100	69.5	1.39	1.93	0.62
Impala	Adult	55	0.88	100	88.2	1.77	1.60	0.51
	Calf	5.5	0.40	100	39.6	0.79	7.21	2.31
Springbok	Adult	39	0.72	100	72.5	1.45	1.86	0.60
	Calf	5.0	0.39	100	39.2	0.78	7.83	2.51
Blesbok	Adult	65	0.98	100	98.0	1.96	1.51	0.48
	Calf	7.0	0.41	100	41.1	0.82	5.87	1.88
Duiker	Adult	18	0.52	100	51.9	1.04	2.88	0.92
	Calf	1.9	0.36	100	36.1	0.72	19.01	6.09
Steenbok	Adult	11	0.45	100	45.0	0.90	4.09	1.31
	Calf	0.9	0.35	100	35.1	0.70	39.04	12.51
Dik-dik	Adult	5	0.39	100	39.2	0.78	7.83	2.51
	Infant	0.8	0.35	100	35.0	0.70	43.79	14.03
Warthog	Piglet	1.2	0.35	100	35.4	0.71	29.52	9.46
Domestic stock	Calf	40	0.73	100	73.5	1.47	1.84	0.59
	Goat	43	0.76	100	76.4	1.53	1.78	0.57
	Sheep	37	0.71	100	70.5	1.41	1.91	0.61
Birds	Ostrich	69	1.02	100	101.9	2.04	1.48	0.47
	Guinea Fowl	1.0	0.35	100	35.2	0.71	34.76	11.14
	Kori Bustard	14	0.48	100	48.0	0.96	3.43	1.10

[1] References for wild mammal weights were taken from (Bothma 1989)

[2] Domestic mammal weights were obtained through pers. comm. (Deshaies, Diekmann 2001)

[3] References for bird weights were taken from Maclean (1993)

* Calculated relative to the mass of a kudu calf (16kg), which was reported as the most common prey item for cheetahs on Namibian farmlands (Marker-Kraus et al. 1996)

10.3.2 Scat analysis

Ninety-eight cheetah scats were analysed, of which 79.6% (n = 78) were from cheetahs held for 4 days or less, and 20.4% (n = 20) were from cheetahs held captive for over 4 days. From the feeding trial results, only cheetahs that had been captive for 4 days or less were considered to be indicative of diet in the wild, as any scats produced after this time would not reflect diet before capture. Of the 78 scats from wild cheetahs, 33.3% (n = 26) were from game farms (either from captured cheetahs or collected from playtrees), 48.7% (n = 38) were from livestock farms, and 17.9% (n = 14) from unknown locations. Table 10.4 presents the total number of scats collected from wild cheetahs, location of collection and the prey species identified in them. In the majority of cases, the cheetahs appeared to be predating upon indigenous game species, while in 6.4% of cases the prey species identified were domestic stock.

Table 10.4 Contents of wild cheetah scats collected from various locations on the Namibian farmlands.

	Game farm		Livestock farm		Unknown location in wild		Overall			
	Total	%	Total	%	Total	%	Total	% of all scats collected	% of scats containing identifiable remains	% of scats containing identifiable prey remains
Total scats collected	26	33.3	38.0	48.7	14	17.9	78	-	-	-
No. with identifiable remains	20	33.3	32.0	53.3	8	13.3	60	76.9	-	-
Cheetah hair only	6	46.2	7.0	53.8	0	0.0	13	16.7	21.7	-
Kudu	2	20.0	8.0	80.0	0	0.0	10	12.8	16.7	21.3
Eland	1	14.3	6.0	85.7	0	0.0	7	9.0	11.7	14.9
Kudu/eland	5	41.7	5.0	41.7	2	16.7	12	15.4	20.0	25.5
Steenbok	3	75.0	1.0	25.0	0	0.0	4	5.1	6.7	8.5
Oryx	0	0.0	2.0	100.0	0	0.0	2	2.6	3.3	4.3
Red hartebeest	2	66.7	1.0	33.3	0	0.0	3	3.8	5.0	6.4
Hare	1	33.3	0.0	0.0	2	66.7	3	3.8	5.0	6.4
Bird	0	0.0	0.0	0.0	2	100.0	2	2.6	3.3	4.3
Domestic calf	0	0.0	1.0	50.0	1	50.0	2	2.6	3.3	4.3
Sheep	0	0.0	1.0	100.0	0	0.0	1	1.3	1.7	2.1

Warthog	0	0.0	0.0	0.0	1	100.0	1	1.3	1.7	2.1

Applying corrections for differential digestibility (Table 10.5), the prey selection can be more accurately determined. Only the scats where kudu and eland hairs could be distinguished were used for these two species.

Table 10.5 Ratios of prey animals consumed, calculated using the corrected scat analysis.

Prey type in scats	Assumed weight of prey (kg)*	Prey per scat	No. of scats	Kg eaten	Ratio of weight eaten	No. of individuals eaten	Ratio of no. individuals eaten
Kudu calf	16	0.50	10	4.99	1	0.31	1
Eland calf	36	0.70	7	4.87	0.97	0.14	0.43
Red hartebeest calf	15.0	0.49	3	1.47	0.29	0.10	0.31
Oryx calf	15.0	0.49	2	0.98	0.20	0.07	0.21
Steenbok	11.2	0.45	4	1.81	0.36	0.16	0.52
Domestic calf	40.0	0.73	2	1.47	0.29	0.04	0.12
Domestic sheep	59.0	0.92	1	0.92	0.18	0.02	0.05
Warthog	45.0	0.78	1	0.78	0.16	0.02	0.06
Hare	1.9	0.36	3	1.08	0.22	0.58	1.85

* Assumed adult weight for hare and steenbok but calf for others

This table highlights the importance of applying correction factors to scat analysis to avoid under-representing the consumption of smaller prey animals. For instance, although hare remains were found in only 3 scats and accounted for only one fifth of the biomass that kudu did, we deduced that nearly twice as many hares as kudu were preyed upon. Conversely, a similar biomass of eland and kudu appeared to have been consumed, but use of the correction factor indicated that fewer than half the number of eland would have been killed compared to kudu.

Forty-six scats were analysed from wild cheetahs of known sex (37 from males and 9 from females), and identifiable prey remains were found in 27 cases, from 23 male and 4 female cheetahs. A higher percentage of scats from male cheetahs contained the remains of large antelope species (kudu, eland, red hartebeest and oryx), while those from females more frequently contained evidence of smaller antelope such as steenbok (Figure 10.1). The remains of domestic stock were found only in scats collected from male cheetahs, but the sample size of scats from female cheetahs was too low to draw any substantial conclusions from this.

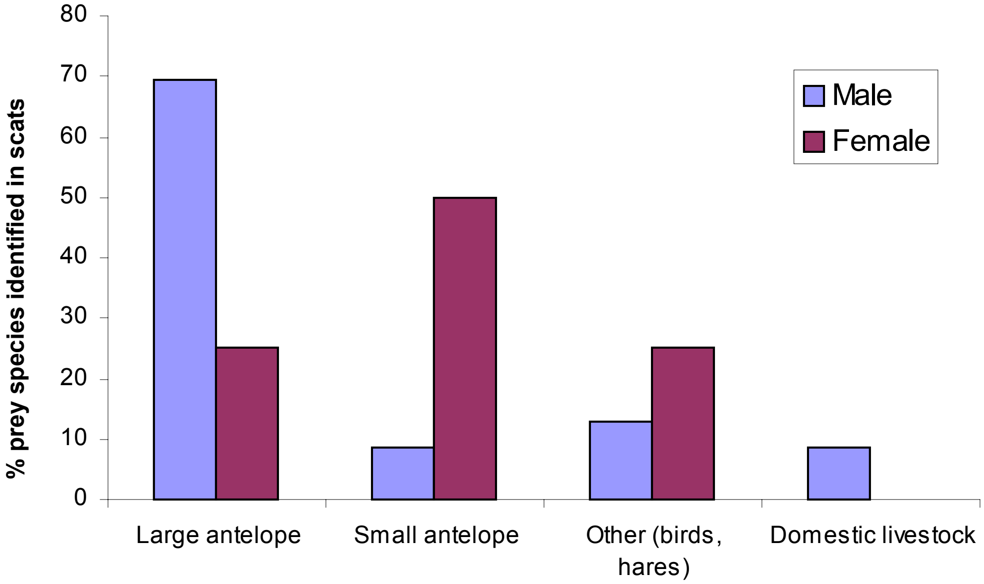


Figure 10.1 The percentage of scats from male and female cheetahs that contained remains of large and small species of antelope, other species such as hares and birds, and domestic stock.

10.3.3 Additional information regarding kills

Between 1993 and 1999, 325 visual observations of radio-collared cheetahs were made. From these observations, 21 cases were recorded of cheetahs on identifiable kills, and the prey consumption determined using this method was compared to that from the corrected scat analysis (Figure 10.2).

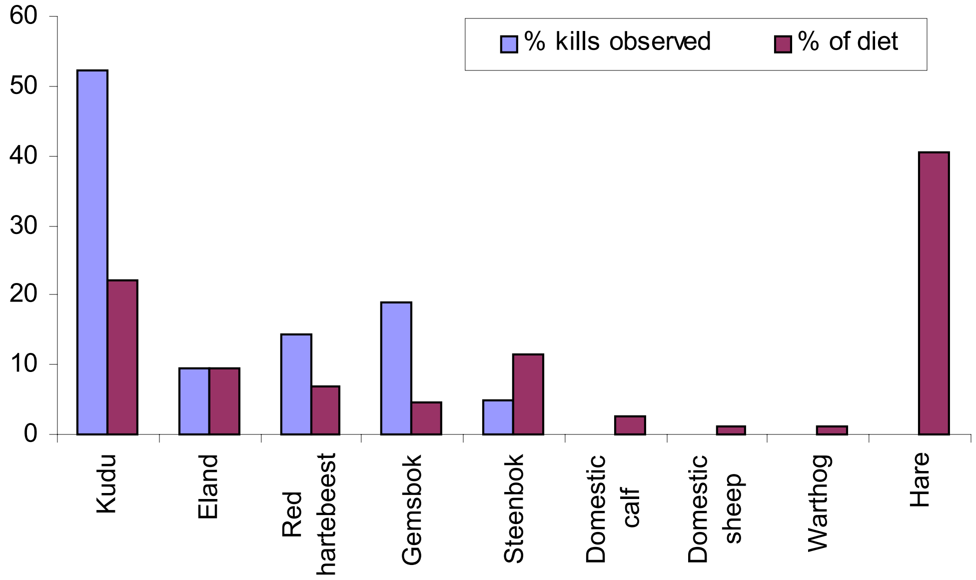


Figure 10.2 Estimates of the relative contributions of different prey species to the diet of Namibian cheetahs, using data from observed kills during radio-tracking flights, and from corrected scat analysis.

Even when limited to the prey species identified through both techniques, the composition of the diet indicated by visual observations and corrected scat analysis differed significantly ($\chi^2 = 33.1$, df = 4, p = 0.000). Aerial sightings led to higher representation of kudu, red hartebeest and oryx than estimated through the scat analysis, with the other species less represented. In the instances where cheetahs were located near potential prey (n = 1088 locations), they were within 500m of game species 77.6% of the time and to livestock 22.4% of the time.

From the farm survey conducted, 58.6% (n = 81) of the farmers believed that kudu calves were the primary prey of the cheetah. Springbok, where regionally available, was also reported as a main component of the diet, as were warthog and steenbok. Oryx and hartebeest calves were considered to be common prey, followed by a variety of other animals including duiker, eland, ostrich, small game birds, guinea fowl (*Numida meleagris*), kori bustards (*Ardeotis kori*), and hares.

10.3.4 Estimating rate of livestock depredation caused by cheetahs

The maximum rate of food consumption for wild cheetahs has been estimated as 5.5kg/cheetah/day (Eaton 1974), which equates to 1958 kg of prey consumed/cheetah/year. Our feeding trials revealed that 1.87 field collectable scats were likely to be produced per kilogram of prey consumed, leading to an estimated production of 3661 field-collectable scats/cheetah/year. The scat analysis showed that on the Namibian farmlands, 4.3% of scats collected contained evidence of domestic calf consumption, while 2.1% contained sheep remains. Using the correction factor, we calculated a consumption of 0.018 calves for each scat containing calf remains, while the figure was 0.016 individuals for sheep. Therefore, out of 3661 scats, 157 would be likely to contain calf remains and 77 would contain sheep remains, indicating the consumption of 2.8 calves and 1.2 sheep per cheetah per year. However, Schaller (1972) calculated that cheetahs killed 35% more prey than they consumed, leading to estimated kill rates of 3.8 calves and 1.6 sheep per cheetah per year.

Assuming a minimum density of 2.5 cheetahs per 1000km^2 on the farmlands and an average farm size of 8000ha (80km^2) (see Chapter 11), the minimum rate of livestock depredation due to cheetahs can be calculated as 0.01 calves and 0.004 sheep per km^2, or 0.76 calves and 0.32 sheep annually on an averagely-sized farm. The accuracy of these calculations obviously depends on the density of cheetahs living in the study area, estimates of which vary widely (Stander 2001). Using the highest reported estimates of cheetah density on the Namibian farmlands (34 cheetahs/1000km^2: Stander 2001), the approximate rates of livestock depredation due to cheetahs would be 10.3 calves and 4.4 sheep per farm per year.

10.4 DISCUSSION

The feeding trials supported the conclusions of Lockie (1959) and Floyd et al. (1978), that, if analysis is based on uncorrected volumetric measures of undigested remains in scats, then smaller prey items are over-represented in biomass consumed but under-represented in numbers if uncorrected scat analysis is performed. The cheetah is an opportunistic predator whose prey varies in size from rodents to adult ungulates (Burney 1980, Caro 1994, Frame 1986, Marker-Kraus et al. 1996, Schaller 1968), and this great variation in prey size makes accurate interpretation of scat analysis more complicated.

Consumption of smaller prey gave a higher number of field-collectable scats relative to the mass consumed, because they are composed of relatively more indigestible matter. Feeding on meat alone, rather than bone and hide, tends to result in the production of more liquid scats, and these would probably not be collected during field studies (Ackerman et al. 1984, Floyd et al. 1978). This is likely to be of particular importance regarding cheetah dietary habits due to their method of prey consumption. Although cheetahs are known to consume some bone (Phillips 1993), they consume more pure muscle (rather than skin or bone) than do other large carnivores (van Valkenburgh 1996, Wrogemann 1975), and this is likely to be even more pronounced when eating from a large carcass. Use of correction factors is therefore very important for accurately estimating cheetah diets.

Accurate analysis of wild cheetah diet relies upon the collection of enough scats from which prey remains can be identified. Using the equations in Reynolds and Aebischer (1991), 9600 scats containing identifiable prey remains would be required to establish that these estimated prey proportions are accurate. Given that only 76.9% of the wild cheetah scats analysed contained identifiable prey remains, it would necessitate 12 500 scats to achieve the aforementioned statistical power, which is unrealistic. Our experience has shown that collecting cheetah scats is very difficult due to several factors, including the large home ranges cheetahs occupy (Marker 2000) and the rapid desiccation of scats in arid environments. Additionally, scats are hard to collect from cheetahs trapped by farmers, as the cats have often gone without food for several days and any scats in the traps are frequently trampled. The available data, therefore, based on a much smaller sample size, can only give a basic insight into the dietary habits of cheetahs on Namibian farmlands. Collecting scats from playtrees and trapped cheetahs biases the data towards males, as the majority of cheetahs visiting playtrees and being trapped are male (Marker-Kraus et al. 1996). Male cheetahs are likely to take larger prey than do females (Mills 1992), so the prey selection determined during this study may not be entirely representative of female cheetahs. Additionally, the interpretation of the scat analysis in terms of numbers of prey animals consumed assumes that the prey animals taken weighed approximately the average masses shown. However, despite these limitations, and especially given the lack of other information available, these data can contribute usefully to understanding the diet of wild Namibian cheetahs on farmlands.

The radio-tracking data reveal that cheetahs are sighted near livestock relatively frequently, and this is exacerbated by the species' diurnal nature and consequently greater visibility than other predators. Such sightings by farmers who are experiencing stock loss potentially leads to the assumption that cheetahs are the cause, and creates the perception of them as being frequent stock-killers. The corrected scat analysis indicates, however, that cheetahs preferentially take wild game species over domestic ones. Although 38 scats were collected on livestock farms (over half from cheetahs that had been trapped as a supposed threat to livestock), only 2 of those contained any evidence of domestic stock consumption. The fact that domestic stock was evident in 6.4% of the scats does verify that cheetahs prey upon livestock, but as two-thirds of the available prey base is livestock (Marker-Kraus et al., 1996), cheetahs appear to show selection towards game species.

It is difficult to estimate rates of livestock depredation due to cheetahs from this information, as estimated figures for cheetah density in the study area vary greatly (Stander 2001). In a recent survey (see Chapter 12) farmers in the region reported losing an average of 0.9 calves and 1.3 smallstock annually to cheetahs, which was slightly higher than estimated using the minimum density figures, but far less than would be expected if cheetahs exist at maximum density. Conducting further research into gaining a more accurate estimate of cheetah density will be vital for independently examining the level of stock loss that cheetahs are likely to be responsible for. Relying therefore on reports by farmers (see Chapter 12), the level of livestock depredation attributed to cheetahs was substantially less than that caused by other predators, and indicate that livestock depredation due to cheetahs is unlikely to be a major financial burden for Namibia’s commercial farmers.

However, the predominance of game species in the diet does mean that the cheetah is likely to be perceived as a threat on game farms. Many game farmers stock exotic game species on their land for trophy hunters, which are more valuable economically than indigenous game but can be more liable to predation than the better-adapted indigenous species (Marker and Schumann 1998, Marker-Kraus et al. 1996). Although these results suggest that cheetahs are preying mainly upon indigenous game species rather than the more expensive exotic game, losses to large carnivores remain a potential problem for game farmers.

Picture 10.2 Introducing game species into areas where they would not naturally occur can have serious consequences in terms of losses. Species such as springbok, which are adapted for short-grass plains, are highly susceptible to predation in the thickly bushed farmland habitat, and often suffer high levels of depredation, reducing game farmers' tolerance for predators.

In line with comparable studies of other carnivores, (e.g. Karanth and Sunquist 1995, Mills 1992) the diet estimated from sighted kills contained a greater proportion of large prey than did that estimated from faeces. The only exception in this study was for eland, where fewer kills were seen than would be expected from the scat analysis. This may be due to the fact that eland are nomadic (Smithers 1983) and for much of the time would not be on the relatively small area of farmland where radio-tracked cheetahs were being followed.

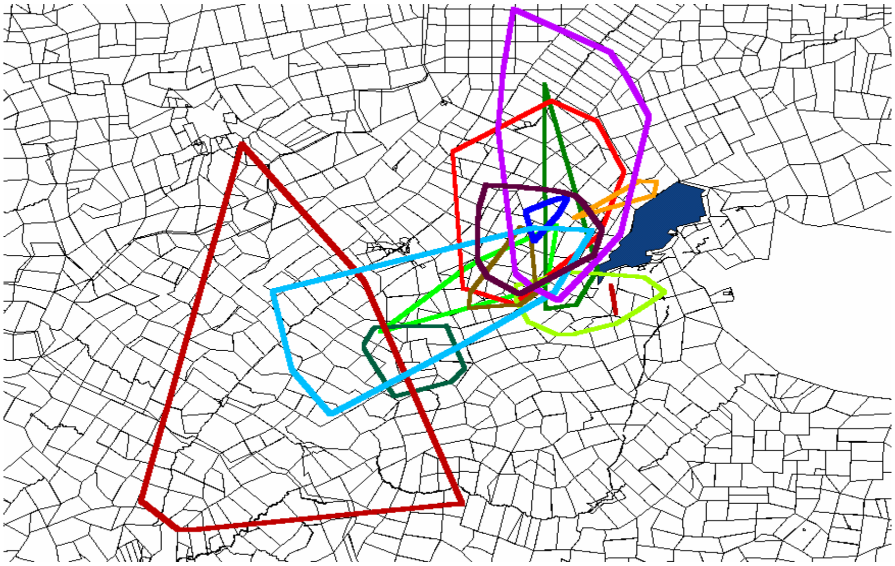
The wild prey base available to the cheetah is critical in the issue of predator conflict. According to many Namibian farmers, maintaining a higher ratio of wildlife to cattle is the most important feature in reducing livestock predation in the survey area (Marker-Kraus et al. 1996), as a plentiful wildlife population provides an abundance of prey, which in turn reduces the farmers' conflict with predators. Overall, these data indicate that cheetahs show selection for indigenous game species rather than for domestic stock. However, even a relatively low level of predation upon expensive, introduced game, or upon livestock, can have a serious economic impact on farmers (Oli et al. 1994). In order to conserve cheetahs successfully on farmlands and reduce the level of removal, strategies must be found that mitigate the economic loss caused by them. Fenced sections of farms containing expensive game animals can be protected through effective maintenance of perimeter fences, or, more sustainably, by the removal of game fencing and the development instead of cooperative game management areas in the form of conservancies.

Picture 10.3 Forming conservancies, where game is managed collectively rather than being split into small, game-fenced areas, provides several advantages such as allowing the natural movement of game populations across the farmlands, and reducing the impact of losses due to predators for individual farmers.

There are also several livestock management practices, such as the use of guarding animals, calving corrals and synchronized breeding seasons, that have been shown to be effective in reducing stock losses both to cheetahs and other predators (Marker-Kraus et al. 1996). Additionally, the development of ecotourism and sustainable trophy hunting both have the potential to turn predators into an economic asset rather than a detriment to the farmers on whose lands they survive.

CHAPTER 11

MOVEMENTS AND SPATIAL ORGANISATION OF CHEETAHS ON NORTH-CENTRAL NAMIBIAN FARMLANDS: THE INFLUENCE OF PREY-BASE, COMPETITION AND PERTURBATION



This thesis chapter is in preparation as the following paper:

Movements and spatial organisation of cheetahs on north-central Namibian farmlands: the influence of prey-base, competition and perturbation. Marker, L.L, Mills, M.G.L., Jeo, R.J., Dickman, A.J., Johnson, W. and Macdonald, D.W.

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CHAPTER 11: MOVEMENTS AND SPATIAL ORGANISATION OF CHEETAHS ON NORTH-CENTRAL NAMIBIAN FARMLANDS: THE INFLUENCE OF PREY BASE, COMPETITION AND PERTURBATION

ABSTRACT

In Namibia, as in much of Africa, the majority of biodiversity exists on unprotected rangelands, including the world's largest extant population of free-ranging cheetahs. We sought to better understand factors that influenced the home ranges and spatial distribution of cheetahs outside of protected areas, on commercial livestock farmland, in north-central Namibia. Factors distinguishing this population from those previously studied are: a) the non-migratory prey-base, b) the absence of intra-guild competitors, and c) perturbation caused by intensive control, although the latter declined significantly during the study period. Over a period of eight years, 41 farmland cheetahs were radio-collared, released and located weekly. Annual, lifetime, seasonal and core home range areas were calculated using both the minimum convex polygon (MCP) and probability kernel methods.

Relative to those studied elsewhere, Namibian cheetahs had very large home ranges, averaging 1056km^2 (± 791km^2) annually and 1642 km^2 (± 1565km^2) over a lifetime (95% kernel). Ranges were significantly smaller during the wet season, and were inversely related to rainfall. Cheetahs showed intensive utilisation of core areas, which comprised a mean of 13.9% of their total home range area.

There was some evidence of habitat preference, with female cheetahs preferentially occupying areas of sparse bush and single males appearing to select for thicker bush. Habitat patches of sparse bush supported the highest prey biomass, suggesting that female distribution was determined by prey abundance, while single males could be suffering competitive exclusion from such areas by coalitions of males. Despite an apparent abundance of prey, and a lack of significant intraguild competition, cheetahs were found at lower density on the farmlands than

has been reported in other studies, with a minimum density of 2.5 cheetahs / 1000 km^2 in the study area. Cheetah density and home range size appear to be governed by factors other than prey alone, and may still be influenced by recent perturbation of the Namibian population.

Irrespective of the cause, the large ranges and low density mean that large tracts of contiguous habitat are necessary for cheetah conservation outside of protected areas. Conflict with humans is an important contributor to the species' decline. Translocated cheetahs did not return to their original sites of capture and their home range sizes were no different than that of resident cheetahs. Habitat degradation, and the resulting bush encroachment, may also represent significant threats to cheetah populations in Namibia. Therefore, conservation efforts should focus on maintaining and restoring suitable habitat and should promote land-management practices that are compatible with the continued existence of large carnivores.

11.1 INTRODUCTION

Although the creation and maintenance of a connected, representative protected area network is important for both large carnivore persistence and biodiversity conservation (Margules and Pressey 2000, Soule and Terborgh 1999), the inadequate size and sub-optimal location of most protected areas means that management of the surrounding matrix lands may be equally important for successful conservation (Newmark 1996, Soule and Sanjayan 1998). In Namibia, as in much of Africa, the majority of biodiversity exists outside of strictly protected areas (Barnard 1998, Pimentel et al. 1992), including the world's largest extant population of free-ranging cheetahs (Marker-Kraus et al. 1996, Morsbach 1987, Myers 1975).

Approximately 90% of Namibia's cheetahs are found on a contiguous 275 000 km^2 parcel of privately-owned commercial farmland, located in north-central Namibia. Commercial farms in Namibia are large, averaging about 8,000 ha (Marker-Kraus et al. 1996), and are mostly individually owned. The majority of Namibia's large ungulate populations resides on these lands (Richardson 1998). However, this often leads to direct conflict between humans and wildlife, and cheetahs, often perceived as threats to livestock and game, are at particular risk. As a consequence, the cheetah population has undergone severe persecution and a high rate of removal in the past, with an estimated halving of the population size due to such persecution during the 1980s (Morsbach 1987). As a result of long-term conservation education, attitudes towards cheetahs appear to have changed over the past decade (see Chapter 12), and the level of removals has dropped significantly.

Researching cheetah ecology in this situation is important, for several reasons. Our first goal concerned intra-specific variation. While the species' behavioural and spatial ecology has been documented previously (Broomhall 2001, Caro 1994, Durant et al. 1988, Laurenson 1991, Mills 1991), the only detailed, long-term study to date has been conducted in the Serengeti, in an ecosystem that is predominantly composed of short grass plains with an abundant, migratory prey base (Bertram 1979, Caro 1994, Frame and Frame 1980, Kruuk and Turner 1967, Schaller 1972). Many carnivores show a remarkable degree of behavioural plasticity under varying environment conditions (Macdonald 1983), and our first aim was to test the hypothesis that the ecology of cheetahs on the bush-encroached farmland of Namibia, with a non-migratory prey base, would differ from that exhibited in the Serengeti.

In the Serengeti, cheetahs suffer high levels of intra-guild competition within protected areas (Durant 1998, Durant 2000a). Their principal competitors are absent from Namibian farmland as farmers have almost entirely eliminated lions and spotted hyaenas from the commercial farms (Joubert and Mostert 1975, Marker-Kraus et al. 1996, Shortridge 1934). Thus our second goal was to investigate how their ecology and behaviour alter once freed from such competitors.

Thirdly, the Serengeti cheetah population has been officially protected since 1937 (Caro 1994), while the Namibian population has suffered serious perturbation due to the high levels of removals sustained on the farmlands. Such perturbation can have noteworthy consequences in terms of a species' ecology and behaviour (Tuyttens and Macdonald 2000), and it is interesting to compare whether any inter-population differences can be attributed to this persecution. In our study area, while we have no reason to believe or evidence that the prey-base and level of intra-guild competition changed significantly throughout the study, farmers killed far more cheetahs before 1993, and so we predicted that changes attributable to the resulting perturbation would diminish thereafter.

Lastly, the demands of some farmers that we move cheetahs off their properties mean that cheetahs were released at varying distances from their capture site. In some cases they were doubtless within their home range, or at least within familiar country, but in others the release sites must have been unfamiliar. As translocation is an increasingly common management tool for resolving conflicts between humans and large carnivores (Breitenmoser et al. 2001, Hunter

1998, Purchase 1998, Zank 1995), we used distances between capture and release sites to explore the consequences for cheetah behaviour of translocation.

A fundamental spatial parameter is ‘home range’, a concept that has been variously defined (e.g. Baker 1978, Burt 1943, Jewell 1966, Mohr 1947, Seton 1909); here we follow (Burt 1943), defining a home range as ‘that area traversed by the individual in its normal activities of food gathering, mating and caring for young’. Intersexual differences in home range have proved important in ecological studies of several species (Crook et al. 1976, Eisenberg 1981, Wilson 1975), and we examined spatial differences in relation to social group composition, genetic relatedness, season, rainfall, prey biomass and habitat density. Specifically, we asked what factors influenced home range size, spatial distribution and habitat utilisation, and we tackled this with respect to core home range areas, overlaps between cheetah home ranges, cheetah density estimation and comparisons to other sympatric carnivores. We discuss the relevance of our results to cheetah conservation in Namibia and elsewhere.

11.2 STUDY AREA

Radio-tracking was conducted within a 17,928 km^2 area in north-central Namibia. The study area encompassed the Waterberg Plateau (a 100 km-long protected area that rises 1800m above sea level), commercial and communal livestock farmland, and several fenced game-farms (Figure 11.1a). The study area was semi-arid and lay between the 400mm and 500mm annual rainfall isopleths (Barnard 1998). There was marked seasonality, with most rainfall occurring between November and April, and an average of 472mm ($\pm$ 156.28) rainfall annually. There were three major seasons; a wet-hot season (January - April), a dry-cold season (May - August) and an intermediate season (September - December) (Berry 1980). We refer to these as seasons 1,2 and 3 respectively. The wet (1) and intermediate (3) seasons were characterised by extensive thundershowers and flooding, with considerable variation in the amount of precipitation between years (Barnard 1998). The topography of the farmland was generally flat; consequently, rainfall run-off was slow and there were no permanent river systems on the farms, although most farms had a number of man-made semi-permanent water reservoirs.

The land-use in the area was primarily commercial cattle and wildlife farming, and the human population density was low, averaging 15 people per km^2 (United States Bureau of Census 1982). The majority of commercial farms ranged in size from 5,000 to 20,000 ha, with a mean of 8,000 ha (Marker-Kraus et al. 1996). The study area was situated in the Thornbush Savannah vegetation zone as defined by Geiss (1971). Vegetation was typical of xeromorphic thornbush savannah, with dominant woody plant genera consisting of *Acacia*, *Dichrostachys*, *Grewia*, *Terminalia*, and *Boscia*. Understory vegetation was relatively sparse, although ephemeral forbs are present following rain. This region has been extensively modified over the last century through human-mediated causes compounded by natural climatic fluctuations (Hoffmann 1997, Louw and Seely 1982, Pallet 1997, Prins and van der Jaeugd 1993). Consequently, a few native woody species (primarily *Acacia mellifera*, *Acacia tortillis*, and *Dichrostachys cinerea)* have proliferated, and perennial grasses have been reduced in a process known as bush encroachment. Bush encroachment has resulted in the conversion of former grasslands and thornveld savannahs with sparse shrub density, to dense, *Acacia*-dominated thickets with little grass cover (Bester 1996, Rhode 1997).

Figure 11.1a Radio-tracking study area showing all radio-tracking fixes between 1993 – 2000.

Figure 11.1b Cumulative dates of 41 cheetahs radio-tracked between 1993-2000.

* Indicates inclusion in lifetime home range analysis only

** Indicates inclusion in lifetime and annual home range analyses

11.3 METHODS

11.3.1 Cheetah capture and immobilisation

Between 1991 and 2000, we examined and released 120 cheetahs within the study area, using the capture and immobilisation procedures described in Chapter 3. All released cheetahs were marked with a metal ear-tag, and 41 (Figure 11.1b) were also fitted with a neoprene radio-telemetry collar with an external antenna (Advanced Telemetry Systems, Minnesota). The radio-collars were 3.8 cm wide with an adjustable strap of 30-45cm long, with a 30 cm antenna that extended about 18 cm from the collar. The collars were fitted with a "C" cell lithium battery with a life expectancy of over 36 months. Radio-collars weighed 280 g; equivalent to 0.56% of body mass for a 50 kg male and 0.76% for a 37 kg female, well below the limit recommended at 3% by Kenward (2001). We believe these collars did not have a substantial impact that would be likely to affect the survival of collared cheetahs (see Chapter 9), as they have been used in previous studies without evidence of significant adverse effects (Caro 1994).

From 1993-2000, 54.8% (n = 23) of the radio-collared cheetahs were caught on one of three neighbouring farms (Figure 11.1a), of which 73.9% (n = 17) of these were caught on a single farm. Between 1983 and 1992, at least 140 cheetahs had been removed (trapped and either killed, translocated or placed in captivity) from these farms, with a mean removal rate of 14 (± 10.3) cheetahs per year. From 1993 onwards, cheetahs captured on these farms were made available for research, and removals declined sharply. Initially, all cheetahs released within the study area were radio-collared, and the majority of these were males. After 1995, the rate of reported captures increased, and then females were preferentially radio-collared over males.

Cheetahs were released in the same groupings as they were captured in (either single males, male coalitions, or females), on the assumption that animals trapped together represented social units. Only one cheetah per social group was radio-collared, and the selected animal was randomly chosen from the adults amongst the group. One male (identification number AJU 320) was collared initially as part of a coalition, and later as a single male. For this reason, 42 cheetahs are represented in the analyses. In 63% of cases, radio-collars were retrieved after tracking had ceased.

11.3.2 Radio-telemetry methodology

Following release, radio-collared cheetahs were tracked from a fixed-wing Cessna 172 aeroplane, utilising a dual antenna procedure common to aerial tracking. Searching was initiated at an altitude of approximately 243 m (800 ft), and once a signal was detected the pilot would drop to an altitude of approximately 50 m (152 ft). The location of the cheetah was determined after making a series of banking turns, and visual observations were made on 12.4% of occasions (n = 350), providing information on demographic parameters.

Cheetah locations were determined using a portable Global Positioning System (GPS), and attempts were made to find all collared cheetahs during each flight, and the location success rate was high over 87% (see Table 11.1). Between May 1993 and May 1996, aerial tracking was conducted twice a week, while from June 1996 to December 2000 it was conducted once a week due to financial constraints.

11.3.3 Home range area calculations

Data were plotted and analysed using ArcView GIS (version 3.2, ESRI, Redlands, CA.) and the Animal Movement extension (Hooge et al. 1999). Latitude and longitude recordings were used to calculate 95% MCP (Minimum Convex Polygon) home ranges (Mohr 1947, White and Garrott 1990), as well as 95% and 50% kernel home range estimates (Seaman et al. 1999, Silverman 1986, Worton 1989).

The number of fixes necessary for home range sizes to reach an asymptote was determined using Ranges V (Kenward and Hodder 1992), and all cheetahs used for the analysis of lifetime home range calculations had reached asymptotic levels (Table 11.1). We estimated lifetime home range sizes for cheetahs with 30 fixes or more using both the 95% MCP and 95% kernel methods (Seaman et al. 1999), and statistical comparisons were made between the estimates provided by the two methods. Annual home range sizes were calculated for cheetahs that had been tracked for at least 12 months, using the 95% kernel method.

11.3.4 Influence of age, sex and social group on home range size

Home range size was compared between different age groups of independent cheetahs (i.e. aged > 18 months of age). Age classification was based both on experience with captive cheetahs and upon information from previous studies (Burney 1980, Caro 1994). Age estimations were derived from weight and body measurements of the animal, and scored for tooth wear and discolouration, gum recession, pelage condition, reproductive condition and the social groupings of animals caught together, as described in Chapter 3. These factors enabled us to categorise examined cheetahs as being in one of the following age groups: newly independent (> 18 months - 30 months), young adults (> 30 months - 48 months), prime adults (> 48 months - 96 months), old adults (>96 - 144 months), or very old adults (> 144 months). To give confidence to the process above, cementum ageing was used and revealed a good agreement between estimated and actual ages (Matson's Laboratory, LLC, Milltown, MT, USA).

Home range size was compared between single males and those in coalition groups, between the sexes, and between all three social groups (single males, coalition males, and females).

11.3.5 Effect of translocation

Stable home ranges revealed by radio-tracking indicate that an animal released up to 100 km from its capture site might still be within its normal home range. In order to distinguish animals that, following release, were able immediately to resume their natural movements from those who were translocated outside their familiar area, we studied movement parameters with respect to release distance, seeking particularly for signs in the early weeks of tracking that an animal's movements were stabilising.

As will be reported below, we could detect erratic movements indicative of a translocation effect in the movements of one animal (a female), during the first three months of tracking. To investigate if these movements were significant, we compared the movement data for the first three months after release between the translocated cheetahs and resident cheetahs (i.e. those released within their presumed home range). Following this, more extensive comparisons of home-range size were made between translocated cheetahs and resident animals.

11.3.6 Seasonal home ranges

Seasonal home ranges were calculated using the 95% kernel method. Analyses were conducted across the three seasons defined above, while comparisons were also made between the dry and the wet seasons. Using rainfall figures throughout the study period, we defined the wet season as being from 15th September to 14th April, when 93% of the rain fell, and the dry season from 15th April to 14th September, when 7% fell. Because we were only able to track once per week, analyses were restricted to cheetahs with $\geq$15 fix locations each for the dry and wet seasons and $\geq$10 fix locations each for Seasons 1, 2 and 3.

11.3.7 Distances moved

We analysed the minimum distance moved per day and the distance moved between fixes, and compared these factors between sexes, social groups, and between females with cubs of different ages.

11.3.8 Core home range size and utilisation

Core home ranges (defined as the 50% probability kernel) were determined for all cheetahs whose lifetime home range had been calculated. To investigate core range utilisation, core home range was compared to the 95% kernel home ranges for all social groups, age classes and seasons.

11.3.9 Overlap and density estimations

The percentage of overlap between the yearly ranges of 41 cheetahs was calculated using Ranges V (Todd 1993). Minimum cheetah density in the study area was estimated by dividing the annual radio-tracking area by the number of collared cheetahs known to be in the area that year, and the relationship between home range size and density was examined.

11.3.10 Genetic relatedness and degree of home range overlap

In order to investigate the relationships between overlapping groups of radio-collared cheetahs, likelihood ratio tests were performed to compare the probability of obtaining the pair of multi-locus genotypes of two individuals. In order to calculate these probabilities, baseline gene frequencies of unrelated individuals were required. Genetic analysis was done on 313 cheetahs trapped in the study area (see Chapter 5) and these results were used to calculate relatedness in this study. The average pairwise relatedness among categories of cheetahs was estimated using the program RELATEDNESS 5.0.5 (Queller and Goodnight 1989). Cheetahs were categorised as either related (having relatedness values of > 0.2) or unrelated (< 0.2), and the overlaps of social groups were investigated with regard to their relatedness. The relatedness of 37 (24 males and 13 females) radio-collared cheetahs was compared to each other, as well as to 89 (65 males and 24 females) of the 120 other cheetahs that were marked during this study.

11.3.11 Cheetah habitat selection

Habitat data were collected from March 1996 onwards; for each cheetah location, we visually estimated bush density into the following classes: sparse bush (< 30% canopy), medium bush (30 – 75% bush canopy) and thick bush (> 75% bush canopy). In order to determine the relative proportion of each habitat type, we flew stratified random transects 20 km apart over the entire study area at 170 km per hour at an altitude of 230m. Bush density was visually estimated and classified into 3 classes, every 5km, using the criteria described above. To independently verify the visual estimates of bush density, habitat data were compared with a satellite image of the study area, which was classified by relative bush density.

Habitat preference was tested using a χ^2 goodness of fit test (Neu et al. 1974, White and Garrott 1990), using the null hypothesis described by Alldredge and Ratti (1986) that usage occurs in proportion to the expected distribution. A Friedman (1937) test (White and Garrott 1990), was used to test for differences in percentage availability and percentage utilisation of each habitat. The differences were ranked for each animal to calculate the test statistic. The sum of the preferences by each animal in different habitats is described by Equation 1, where a = number of animals, and h = number of habitats, and R= the mean ratio of time in each habitat (White and Garrott 1990).

Equation 1: $\chi^2 = R_{ah}$

11.3.12 Prey biomass and bush density

Prey density in different habitat types was calculated using data collected from driving strip counts conducted on one commercial farm in our study area. A minimum of three replicate counts, over a standardized 50 km route, was conducted each month. To compute density, sighting distances were used to calculate estimated strip width using the program DISTANCE (Thomas et al. 1998) and game densities for seven ungulate species were calculated by averaging density estimates from all counts that occurred between 1995 and 2000. The strip was classified by bush density, and game density in sparse, medium and thick bush cover areas was calculated to correspond with habitat types scored while radio-tracking. We assumed that these density values were representative of the relative prey density, in different habitat types, throughout the study area. Biomass of prey species was then calculated following Coe et al. (1976). In order to compare relative prey biomass in each habitat type, the assumed weight of the prey species was simply multiplied by game density. Mean biomass was calculated to facilitate habitat comparisons to other areas where cheetahs have been studied.

11.3.13 Comparisons of home range estimations with sympatric carnivore species

Eleven (6 male and 5 female) leopards and four male caracals (*Felis caracal*) were opportunistically radio-collared within the same area during the study, and their home ranges analysed for comparative purposes. Methods of home range estimates were compared, as well as intersexual differences for leopards, and seasonal variation in home range size for both species. Percentage overlap between leopards, caracal and cheetah were calculated using Ranges V.

11.3.14 Statistical methods

Statistical analyses were performed using SPSS version 10.0 software (SPSS Inc. Chicago, USA). Means are presented with the standard deviation ($\underline{+}$) after the mean. Normality of variables was tested using the Kolmogorov-Smirnov and Shapiro-Wilk tests, and in cases where there was significant deviation from normality, non-parametric tests were used. These included Kruskal-Wallis tests, presented using the χ^2 approximation, and Mann-Whitney U tests, using the z approximation. Departures from expected ratios were analysed using chi-squared tests and correlations were investigated using Spearman's correlation coefficient. Other statistical analyses conducted included linear regression, and all tests were two-tailed unless otherwise stated.

11.4 RESULTS

Forty-two cheetahs (27 males and 15 females) were radio-tracked between May 1993 and December 2001 (Figure 11.1b). Details of the 42 tracked cheetahs are shown in Table 11.1. Lifetime, annual and seasonal home ranges and habitat use were determined from 2,763 fix locations. Eighty-two percent of the cheetahs were tracked for more than a year, while 12% were tracked for more than three consecutive years (Figure 11.1b). Table 11.1 presents the lifetime and annual home ranges sizes for the cheetahs used in each analysis.

Table 11.1 Mean age, time tracked, and number of fixes of all radio-collared cheetahs (n=42) and minimum distance moved between fixes for all cheetahs radio-tracked from 1993 to 2000; mean number of fixes for cheetahs to reach first asymptotic home range; mean age at collaring, mean number of months tracked and mean number of fixes for cheetahs used in overall home range analysis (n=28); and mean age and mean number of fixes for cheetahs used in annual home range analysis (n=39). Statistical differences between social groups and different home range analysis, including overall 95% kernel home range size to 95% MCP home range size, and 95% kernel overall home range size to 95% kernel annual home range size.

	Single males (n=18)		Coalition males (n=9)		Total males (n=27)		Comparison between male groups ^{1}		Females (n=15)		Comparison between sexes ^{1}		Total cheetahs (n=42)		Comparison between social groups ^{2}		
All cheetahs	**Mean**	**S**	**Mean**	**s**	**Mean**	**s**	**z**	**P**	**Mean**	**s**	**z**	**p**	**Mean**	**s**	**X^2**	**df**	**p**
Mean age (months) at collaring	53.6	17.7	36.7	12.5	48.0	17.9	-2.22	0.026*	52.7	30.4	-0.04	0.968	49.6	22.9	3.63	2	0.163
Mean no. fixes	57.5	39.8	82.3	73.3	65.8	53.2	-0.72	0.471	65.8	81.8	-0.93	0.351	65.8	63.9	1.06	2	0.588
Mean no. of months tracked	13.2	7.9	18.2	17.1	14.9	11.7	-0.77	0.938	19.1	23.9	-0.37	0.712	16.4	16.9	0.14	2	0.934
% flights located	84.5	11.7	87.4	17.3	85.5	13.6	-1.03	0.304	90.9	10.2	-1.58	0.115	87.4	12.6	3.41	2	0.181
Mean days between fixes	7.0	2.4	6.4	2.4	6.8	2.4	-0.72	0.470	8.4	3.4	-1.25	0.213	7.4	2.8	2.05	2	0.360
Min. mean distance (km) per day	2.5	1.9	2.3	0.7	2.4	1.6	-0.56	0.956	1.4	0.5	-3.22	0.001*	2.0	1.4	10.44	2	0.005*
	Single males (n=9)		**Coalition males (n=5)**		**Total males (n=14)**		**Comparison between male groups ^{1}**		**Females (n=6)**		**Comparison between sexes ^{1}**		**Total cheetahs (n=20)**		**Comparison between social groups ^{2}**		
All cheetahs	**Mean**	**S**	**Mean**	**s**	**Mean**	**s**	**z**	**P**	**Mean**	**s**	**z**	**p**	**Mean**	**s**	**X^2**	**df**	**p**
No. fixes to reach 1st Asymptote	15.4	7.9	10.1	5.6	13.5	7.4	-1.07	0.286	17.4	12.3	-0.25	0.804	14.7	9.0	1.79	2	0.409
	Single males (n=13)		**Coalition males (n=7)**		**Total males (n=20)**		**Comparison between male groups ^{1}**		**Females (n=8)**		**Comparison between sexes ^{1}**		**Total cheetahs (n=28)**		**Comparison between social groups ^{2}**		
Lifetime home ranges	**Mean**	**S**	**Mean**	**s**	**Mean**	**s**	**z**	**P**	**Mean**	**s**	**z**	**p**	**Mean**	**s**	**X^2**	**df**	**p**
Mean age (months) at collaring	52.3	18.0	41.1	14.0	48.0	17.1	-1.429	0.153	54.8	32.3	-0.10	0.918	49.1	6.9	1.53	2	0.466
Mean no. fixes	73.6	31.3	104.6	68	84.5	48.1	-0.915	0.341	118.3	95.1	-0.127	0.899	94.1	64.9	0.40	2	0.819
Lifetime 95% kernel	1483.8	1151.9	1344.3	1358.2	1435.0	1193.8	-0.476	0.634	2160.7	2269.4	-0.458	0.647	1642.3	1565.1	0.464	2	0.793
Lifetime 95% MCP	1829.0	1659.0	1608.4	1091.0	1751.8	1484.0	-0.079	0.937	1836.3	2010.3	0.000	1.000	1775.9	1612.1	0.029	2	0.985
95% MCP vs 95% kernel ^{1}	z = -0.28	p = 0.78	z = -0.83	p = 0.41	z = -0.57	p = 0.57			z = -0.32	p = 0.75			z = -0.20	p = 0.84			
	Single males (n=13)		**Coalition males (n=8)**		**Total males (n=21)**		**Comparison between male groups^1**		**Females (n=18)**		**Comparison between sexes^1**		**Total cheetahs (n=39)**		**Comparison between social groups ^{2}**		
Annual home ranges	**Mean**	**S**	**Mean**	**s**	**Mean**	**s**	**z**	**P**	**Mean**	**s**	**z**	**p**	**Mean**	**s**	**X^2**	**df**	**p**
Mean age (months) annually	56.7	15.9	51.8	15.8	54.81	15.67	-0.218	0.827	65.6	33.2	-0.648	0.517	59.8	25.5	0.539	2	0.764
Mean no. fixes	51.1	16.9	57.5	15.3	53.5	16.2	-0.87	0.384	41.6	8	-2.45	.014*	48.0	14.3	7.36	2	0.025*
Annual 95% kernel	1083.0	1091.7	630.1	379.1	910.4	903.4	-1.159	0.247	1226.5	618.6	-2.479	.013*	1056.3	791.4	7.685	2	.021*
Annual 95% kernel vs Lifetime 95% kernel^1	z = -1.13	p = 0.26	z = 1.85	p = 0.06	z = -1.76	p = 0.078			z = -0.56	p = 0.58			z = -1.583	p = 0.113			

* denotes significance at the p< 0.05 level, 1 Mann-Whitney U Test, 2 Kruskal Wallis Test

Table 11.2 Radio-collared cheetahs (n = 28) used in lifetime (95% kernel) home range analysis 1993 - 2000

Radio Collar ID #	CCF Aju Id#	Sex	Sex Code*	Distance Relocated	Age category at first collaring	Est. age in months	Dates tracked	No. months tracked	% flights where found	Total No. Fixes	Lifetime home range (95% MCP)	Lifetime home range (95% kernel)	Lifetime home range (50% kernel)
190(1)	867	M	1	75	Young adult	36	Jul 93 - Jan 94	7	84.7%	50	596.1	1763.7	171.4
572(1)	1163	M	1	200	Young adult	36	Apr 99 - Oct 2000	19	98.3%	59	989.5	3333.1	450.9
671(1)	1158	M	1		Young adult	36	Feb 99 - Oct 2000	21	67.0%	61	1343.0	1227.7	135.5
293(1)	868	M	1	75	Young adult	36	Jul 94 - Dec 96	30	77.2%	132	4221.5	1723.8	268.0
442(1)	842	M	1	50	Prime adult	48	May 93 - Nov 94	19	93.9%	124	917.2	1146.5	254.1
559/893(1)	1061	M	1	200	Prime adult	48	Jul 99 - Dec 2000	18	98.3%	58	2292.3	1297.9	57.1
711(1)	952	M	1		Prime adult	48	Jun 95 - Apr 96	11	96.6%	56	382.0	119.6	16.8
742(1)	1105	M	1	50	Prime adult	48	Jun 98 - May 99	12	71.4%	30	266.3	2205.4	345.6
320((1)	831	M	1	50	Prime adult	48	May 93 - Apr 94	12	94.9%	75	147.4	193.3	30.8
640(1)	881	M	1		Prime adult	60	Aug 93 - Apr 95	21	89.6%	120	419.1	281.6	16.9
052(1)	821	M	1		Prime adult	72	Jun 93 - Jun 94	13	73.4%	69	147.4	272.0	38.8
160(1)	1025	M	1		Prime adult	72	Oct 96 - Mar 98	18	90.1%	64	774.2	574.1	47.6
987(1)	985	M	1		Old adult	96	Oct 95 - Mar 97	18	84.5%	71	2514.9	3938.1	833.3
Single male mean						**52.6 (±18.0) mo**		**16.9 (± 5.9) mo**		**74.5 (± 31.1) fixes**			
174(2)	865	M	2		Independent	24	Jul 93 - Aug 95	26	94.0%	172	385.3	710.7	78.8
559(2)	1167	M	2		Independent	24	Sep 97 - May 98	9	83.3%	30	824.6	4347.6	872.3
082(2)	869	M	2	75	Young adult	36	Oct 93 - Apr 94	7	93.6%	44	1371.6	644.1	98.0
540(2)	974	M	2		Young adult	42	Jun 95 - Jun 99	49	96.4%	216	1392.4	1076.2	138.5
730(2)	979	M	2		Prime adult	48	Aug 95 - Dec 96	17	97.6%	80	2124.2	680.4	74.6
771(2)	990	M	2		Prime adult	54	Dec 95 - Apr 98	41	95.8%	115	712.8	544.5	49.1
320(2)	831	M	2	50	Prime adult	60	Apr 94 - Apr 95	12	89.2%	65	1392.4	2242.8	308.6
Coalition male mean						**41.1 (±14.0) mo**		**23.0 (±16.4) mo**		**103.1 (±68.9) fixes**			
442(3)	984	F	3	275	Independent	18	Oct 95 - Dec 2000	63	94.4%	220	1445.8	1282.5	221.5
233(3)	948	F	3	260	Independent	24	Oct 94 - Dec2000	79	86.9%	257	6353.7	4024.7	473.4
602(3)	1184	F	3		Independent	24	Oct 99 - Dec 2000	14	97.9%	47	1190.8	626.3	122.7
720(3)	1154	F	3		Young adult	36	Mar 99 - Sept 2000	19	98.2%	56	1041.7	1705.6	126.7
841(3)	1026	F	3	50	Prime adult	72	Nov 96 - Jul 97	9	82.5%	33	3012.1	553.9	67.2
400(3)	978	F	3	300	Prime adult	84	Oct 95 - Mar 97	18	98.5%	67	306.6	999.9	217.6
802(3)	1100	F	3	600	Prime adult	84	Jun 98 - Dec 99	19	94.1%	48	1016.0	7063.3	1795.3
353(3)	967	F	3		Old adult	96	Feb 95 - Aug 99	43	92.0%	218	324.0	1029.3	157.7
Female mean		**F**	**3**			**54.8 (± 32.3) mo**		**33.0 (±25.8) mo**		**118.23 (±95.1) fixes**			
Overall mean						**49.1 (± 6.9) mo**		**24.3 (±8.2) mo**		**94.1 (± 64.9) fixes**			

*sex code - 1 = single male, 2 = coalition male, 3 = female

Table 11.3 Radio collared cheetahs (n = 23) used in annual (95% kernel) home range analysis 1993 – 2000.

Radio-collar ID#	CCF Aju#	Sex	Distance relocated	Age group	Est. Age (mo.)	Year radio tracked	No. Fixes	Annual Home Range (95% kernel)
293 (4)(1)	868	M	0	young adult	41	95	64	805.37
293 (4)(1)	868	M	0	prime adult	53	96	44	639.635
572(1)	1163	M	200	young adult	42	99/2000	38	1524.90
671(1)	1158	M	0	young adult	44	99/2000	36	736.57
559/893(1)	1061	M	200	prime adult	48	2000	40	1202.97
711(1)	952	M	0	prime adult	48	95/96	56	119.57
742(1)	1105	M	0	prime adult	48	98/99	30	2205.37
442(1)	842	M	0	prime adult	54	93/94	76	907.54
320(4)(1)	831	M	0	prime adult	55	94	70	519.91
640(1)	881	M	0	prime adult	60	94	64	246.28
52(1)	821	M	0	prime adult	72	93/94	69	272.02
160(1)	1025	M	0	prime adult	76	97	24	706.74
987(1)	985	M	0	old adult	96	96	53	4191.49
Single male mean					**56.7(±15.9) mo**		**51.1(±16.9) fixes**	
174(2)	865	M	0	newly independent	24	93/94	87	520.69
174(2)	865	M	0	young adult	36	94/95	72	710.11
540(2)	974	M	0	prime adult	48	96	58	701.75
540(2)	974	M	0	prime adult	60	97	44	459.26
540(2)	974	M	0	prime adult	72	98	47	382.38
730(2)	979	M	0	prime adult	52	96	53	541.67
771(2)	990	M	0	prime adult	55	96	57	239.50
771(2)	990	M	0	prime adult	67	97	42	1485.47
Coalition male mean					**51.8(±15.8) mo**		**57.5(±15.3) fixes**	
233(3)	948	F	260	newly independent	28	95	55	2116.19
233(3)	948	F	0	young adult	40	96	49	2726.84
233(3)	948	F	0	prime adult	52	97	42	1017.61
233(3)	948	F	0	prime adult	64	98	32	1269.12
233(3)	948	F	0	prime adult	76	99	29	1652.11
233(3)	948	F	0	old adult	98	2000	38	1290.38
353(3)	967	F	0	old adult	106	96	53	759.44
353(4)	967	F	0	old adult	118	97	43	1018.44
353(3)	967	F	0	old adult	130	98	45	1175.03
400(3)	978	F	300	prime adult	87	96	50	561.32
442(3)	984	F	275	newly independent	21	96	48	823.31
442(3)	984	F	0	young adult	33	97	44	409.29
442(3)	984	F	0	young adult	45	98	39	1081.80
442(3)	984	F	0	prime adult	57	99	38	957.85
442(3)	984	F	0	prime adult	69	2000	39	1256.20
602(3)	1181	F	0	newly independent	27	2000	40	637.94
802(3)	1100	F	600	prime adult	90	99	24	2323.89
720(3)	1154	F	0	young adult	40	99/2000	40	1000.68
Female mean					**65.6(±33.2) mo**		**41.6(±8.1) fixes**	
Overall mean					**59.8(±25.5) mo**		**48(±14.2) fixes**	

11.4.1 Lifetime home ranges

Lifetime home range estimations for 28 cheetahs (Table 11.2) are shown in Table 11.1. These varied from 119.6 km^2 to 4347.6 km^2 for males and 553.9 km^2 to 7063.3 km^2 for females, and both the 95% kernel and 95% MCP methods provided similar estimates of home range size (Table 11.1). As there was no significant difference between estimations produced by the two methods, the 95% kernel home range method was used for all further analyses except overlap.

11.4.2 Annual home ranges

Annual home ranges were calculated for 23 cheetahs (seven had more than one annual home range) (Table 11.3), and were compared to lifetime home range size (Table 11.1). Annual home range size varied significantly by sex, with males utilizing smaller annual home ranges than females. Annual home ranges tended to be smaller than lifetime home ranges, particularly for coalition males, but the differences were not statistically significant.

11.4.3 Yearly and seasonal home range and rainfall

Mean home range size for each year was calculated for single males, coalition males and females (Table 11.4a). Mean home range for each year did not differ significantly from the mean lifetime home range size.

There was a significant negative relationship between annual home range size and rainfall ($r_s = -0.821$, $n = 7$, $p = 0.023$) (Figure 11.2). Similarly, home range size differed significantly between seasons (KW $\chi^2 = 6.752$, df = 2, $p = 0.034$), with smallest home ranges being evident in the hot wet season, although no significant differences were detected when examined by social groups (Table 11.4b). There was no significant difference in home range size between Season 1, Season 3 and the wet season (KW $\chi^2 = 4.44$, df = 2, $p = 0.109$), or between Season 2 and the dry season ($z = -0.50$, $p = 0.617$). Further analyses were therefore conducted using just the dry and wet seasons.

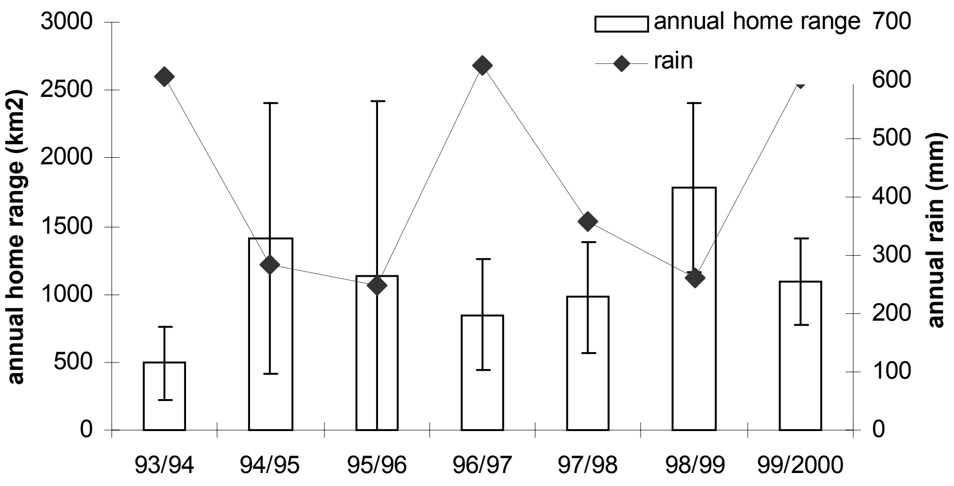


Figure 11.2 Relationship between annual home range (km^2) and annual rainfall (mm).

11.4.4 Influence of age and sex on home range

Because our study group of radio-collared cheetahs was opportunistically caught, we examined the differences of the ages of collared animals in order to reveal potential biases in sampling, before making comparisons between social groups and sexes. Single males were significantly older than coalition males at age at collaring, but overall there was no difference in age at collaring between the sexes (Table 11.1). There were no significant differences between the age groups regarding lifetime home range size (KW $\chi^2 = 3.94$, df = 3, p = 0.268). When age groups were examined within social groups, lifetime home range size decreased slightly between young single males and single males in their prime, although the difference was not quite statistically significant (KW $\chi^2 = 5.56$, df = 2, p = 0.062).

Table 11.4a 95% kernel lifetime yearly home range for different social groups 1993 – 2000

	Lifetime yearly home ranges 95% kernel			Comparison between yearly and lifetime home range [1]		Single Male			Coalition Male			Female			Comparison between social groups			
Year	**N**	**Mean Home Range**	**s**	**Z**	**p**	**n**	**Mean Home Range**	**s**	**n**	**Mean Home Range**	**s**	**n**	**Mean Home Range**	**s**	***Test**	**Stat**	**df**	**p**
1993	6	1021.82	633.02	-0.86	0.391	4	829.04	610.89	2	1407.40	661.86	0			1	-1.39		0.165
1994	4	634.96	318.77	-1.82	0.068	3	578.56	365.16	1	804.16		0			1	-0.447		0.655
1995	6	930.45	618.13	-0.95	0.343	2	538.39	377.57	2	800.43	24.64	2	1452.54	938.54	2	1.14	2	0.565
1996	9	1242.77	1319.37	-1.13	0.257	3	1619.63	2248.21	3	494.31	234.73	4	1217.73	1012.24	2	2.09	2	0.352
1997	6	849.47	406.87	-1.27	0.206	1	706.74		2	972.36	725.64	3	815.11	351.45	2	0.24	2	0.888
1998	4	977.08	403.78	0.63	0.531	0			1	382.38		3	1175.32	93.66	1	-1.34		0.180
1999	4	1411.66	574.44	-0.29	0.776	1	925.28		0			3	1573.79	580.75	1	-1.34		0.180
2000	6	1360.86	768.87	-0.05	0.964	3	1660.22	1036.45	0			3	1061.51	367.22	1	-0.22		0.827
Overall	28	1642.33	1565.12															

Test* 1 = Mann-Whitney U Test, 2 = Kruskal Wallis Test

Table 11.4b Mean home range (lifetime 95% kernel) and statistical analysis for social groups and sex by seasons - Seasons 1, 2 and 3 are compared to the dry and wet seasons.

	Seasons												Seasons							
	Hot - Wet (season 1)			Cold - Dry (season 2)			Intermediate (season 3)			Comparisions [2]			Dry Season			Wet Season			Comparisions [1]	
	n	**mean**	**s**	**n**	**Mean**	**s**	**n**	**mean**	**s**	**X^2**	**df**	**p**	**n**	**mean**	**s**	**n**	**mean**	**s**	**z**	**p**
Single male	12	902.8	782.0	13	1544.6	1045.9	14	1437.6	1047.7	1.880	2	0.391	13	1901.4	1701.0	13	1136.5	917.0	-1.155	0.248
Coaliation male	7	794.7	550.7	5	1216.9	863.0	7	1478.4	1280.7	3.169	2	0.205	5	1154.2	472.5	7	1013.2	852.7	-1.543	0.123
All male	19	863.0	691.2	18	1453.6	985.0	21	1451.2	1098.2	4.391	2	0.111	18	1693.8	1487.8	20	1093.3	874.3	-1.632	0.103
Female	10	1281.1	1154.5	7	2098.0	2493.2	8	2251.6	1407.1	1.821	2	0.402	7	2158.5	2364.0	10	1405.1	1032.4	-0.098	0.922
All cheetahs	29	1007.2	881.2	25	1634.0	1526.0	29	1672.0	1220.2	0.135	2	0.135	25	1824.0	1735.0	30	1197.3	924.1	-1.269	0.205
	X^2	**df**	**p**	**X^2**	**df**	**p**	**X^2**	**df**	**p**				**X^2**	**df**	**p**	**X^2**	**df**	**p**		
Comparisons between social groups [2]	**2.320**	**2**	**0.313**	**0.016**	**2**	**0.992**	**3.660**	**2**	**0.160**				**0.065**	**2**	**0.968**	**1.85**	**2**	**0.397**		

[1] Mann-Whitney U Test, [2] Kruskal Wallis Test

11.4.5 Effect of translocation

Fourteen cheetahs were translocated during the study of which six (21.4%) were moved outside of the areas (greater than100 km^2) for which lifetime home range size could be estimated (Table 11.2). None of the translocated animals returned to their original sites of capture, and translocation appeared to have little effect on their movements. As it was noted that one cheetah made fairly extensive movements after translocations, we looked at the initial effects of translocation on cheetahs. Home range size for the first three months after release was compared for translocated cheetahs and resident cheetahs, showing no significant difference ($z = -1.405$, $p = 0.160$). In addition, there was no correlation between the distance moved and home range size during the first three months for translocated versus resident cheetahs ($r_s = 0.305$, $n = 28$, $p = 0.115$). Cheetahs released within 100 km of the capture site had no larger home ranges than those released at the site of capture ($z = -1.502$, $p = 0.133$), which supported our definition of release within 100km as not constituting translocation.

Overall there was no statistically significant difference in the lifetime home range size between translocated cheetahs and non-translocated cheetahs ($z = -1.960$, $p = 0.050$), and no significant relationship between translocation distances from the capture site and home range size (KW $\chi^2 = 8.082$, df = 4, $p = 0.089$). Distance translocated was not significantly related to the number of fixes required to establish an asymptote ($r_s = 0.271$, $n = 19$, $p = 0.262$). Additionally, there was no evident relationship between distance translocated and home range size ($r_s = 0.278$, $n = 14$, $p = 0.335$), and translocated cheetahs took no longer to establish an asymptotic home range than did resident cheetahs ($z = -1.9$, $p = .057$).

Annual home range size also did not significantly differ between translocated cheetahs (mean = 1425 km^2, $\pm$ 700 km^2), and non-translocated cheetahs (mean = 989 km^2, $\pm$ 798 km^2) ($z = -1.713$, $P = 0.087$). There were no significant differences between translocated and non-translocated cheetahs regarding the average distance moved per day ($z = -0.809$, $p = 0.419$).

11.4.6 Distance moved

The average minimum distance moved per day varied between the sexes, with single males travelling further on a daily basis than females or coalition males (Table 11.1). Eight females, three of which had multiple litters, were tracked with cubs that, during the period of tracking, varied in age from birth through independence. Females with cubs were tracked on average every 8.5 (± 1.9) days. The mean minimum distance moved between fixes was 10.3 (± 3.9) km, while the mean minimum distance moved per day was 1.40 (± 0.41) km. The minimum distance moved per day differed significantly between females with cubs of different ages (KW $\chi^2 = 29.4$, df = 4, $p < 0.001$), with females with cubs under two months old moving shorter distances than those with older cubs (Figure 11.3). There was a significant relationship between the distance moved by the females and the age of the cubs ($r_s = 0.636$, $n = 45$, $p < 0.001$).

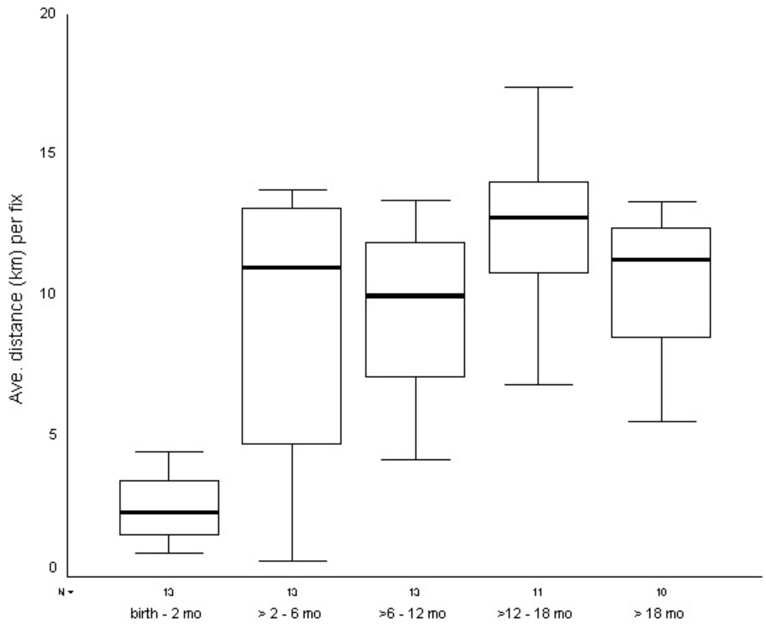


Figure 11.3 Average distance moved between fixes for females with cubs of varying ages.

11.4.7 Core home range size and utilisation

Illustrative examples of core home range areas in relation to the 95% kernel home range area are shown for a female cheetah (Figure 11.4a) and a group of coalition males (Figure 11.4b). Overall, there were no significant differences in core home range area between social groups (KW $\chi^2 = 3.50$, df = 2, p = 0.174) (Figure 11.4c). Core home range area did not vary significantly between single males and coalition males (z = 10.37, p = 0.712) or between single males and females (z = -1.18, p = 0.237), but coalition males' core home range areas were significantly smaller than those of females (z = -2.19, p = 0.028). However, when considered as a percentage of overall home range size, there was no significant difference between the social groups, and core areas comprised on average 13.9% ($\pm$ 5.3) of the 95% kernel home range size (Figure 11.4d).

Core home range area did not differ between social groups either in the dry season (KW $\chi^2 = 1.03$, df = 2, p = 0.599) or the wet season (KW $\chi^2 = 3.58$, df = 2, p = 0.167). Overall, therefore, there was no significant variation in core home range area between the dry and wet seasons (z = -1.237, p = 0.216) (Figure 11.4c). However, for single males, core areas comprised a significantly smaller percentage of their overall home range in the wet season (11.3%, $\pm$ 5.0) than in the dry season (14.5%, $\pm$ 2.9) (z = -2.13, p = 0.034).

Figure 11.4a and 11.4b 95% and 50% kernel home range analysis for female cheetah 353 (a) and male cheetah 540 (b), showing core area utilisation.
Figure 11.4c 50% kernel, core home range size (km^2) for social groups, showing overall (lifetime) core area home range, and dry and wet seasons.
Figure 11.4d Size (km^2) of 50% kernel home range compared to 95% kernel home range size for social groups by overall (lifetime) and seasons.

11.4.8 Overlap and density estimations

The degree of home range overlap differed significantly between years (KW $\chi^2 = 17.8$, df = 7, $p = 0.013$) (Figure 11.5 a-h). Overlap was greatest in 1993 ($z = -3.17$, $p = 0.002$), and then declined significantly through time ($r_s = 0.87$, $p < 0.001$). Mean overlap for all radio-collared cheetahs was 15.8% ($\pm$ 17.0) and male radio-collared cheetah home ranges overlapped more than female home ranges ($z = -2.23$, $p = 0.026$) (Figure 11.5 a-h). Of the radio-collared cheetahs we found that single males overlapped with one another more than either male coalitions or females did, although only the difference between single males and females was statistically significant ($z = -2.10$, $p = 0.036$).

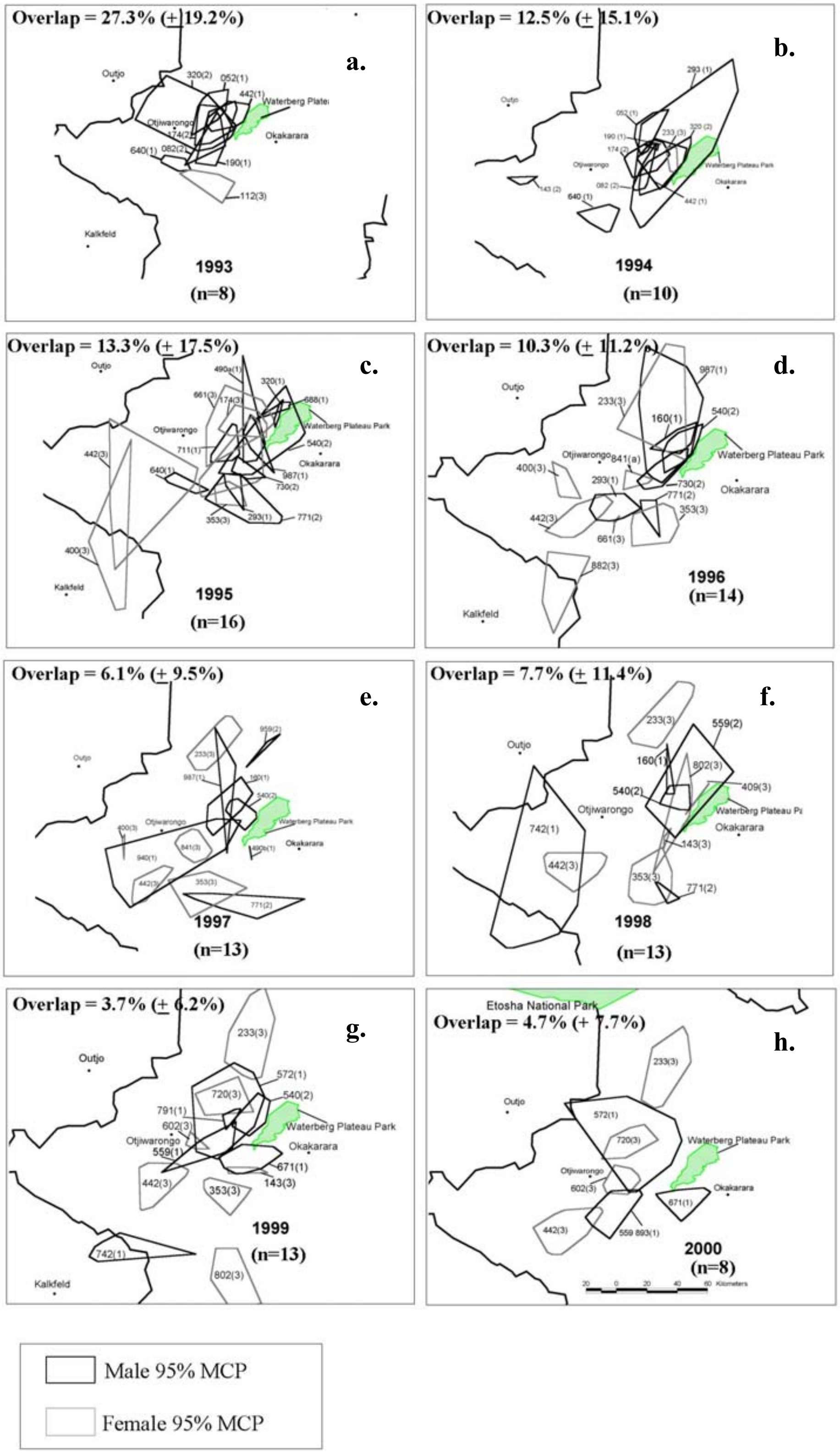


Figure 11.5 a-h 95% MCP home ranges for male and female cheetahs 1993 – 2000, respectively, showing annual percentage overlap of radio-tracked cheetahs through time.

On average, 15 (± 4.4) cheetahs were tracked per year during the study, and the area covered was 6026 (± 1199) km^2/yr. Using these figures, the overall minimum density of cheetahs in the study area was 2.53 (± 0.73) per 1000 km^2, and the annual minimum density of cheetahs in the study area is presented in Table 11.5. Using cumulative numbers of tagged cheetahs from the study area, maximum density of tagged cheetahs within the radio-tracking area would be 8.3 per 1000km^2 (Table 11.5). There was some decrease in annual home range size as cheetah density increased, but the relationship was not statistically significant ($r_s = -0.57$, n = 10, p = 0.087).

Table 11.5 Minimum density of cheetahs annually – includes all males in coalition group, and cumulative minimum density of cheetahs per 1000km^2 using all cheetahs tagged and released in study area.

	No. cheetahs radio tracked	**No. cheetahs in radio tracked groups**	**Radio tracking area km^2**	**Minimum density of radio-collared cheetahs per 1000km^2**	**Cumulative no. cheetahs tagged in study area (17928.4 km^2)**	**Cumulative minimum density per 1000km^2 using 17928.4km^2**	**Maximum density per 1000km^2 using tagged cheetahs in radio-tracking area only**
1993	9	11	5363.7	2.05	18	1.00	3.4
1994	10	13	4059.9	3.20	16	0.89	3.9
1995	15	21	7416.1	2.83	25	1.39	3.4
1996	14	18	5263.6	3.42	22	1.23	4.2
1997	13	17	5663.2	3.00	29	1.62	5.1
1998	13	17	7390.0	2.30	41	2.29	5.5
1999	14	16	7138.1	2.24	35	1.95	4.9
2000	7	7	5911.2	1.18	49	2.73	8.3
Overall			17928.4	2.53		1.64	

11.4.9 Genetic relatedness and degree of home range overlap

The percentage of cheetahs, both radio-collared and tagged and released within the study area, that individual male and female radio-collared cheetahs were related to at > 0.2 (*R*) are shown in Figure 11.6a and 11.6b. The mean overall relatedness of all cheetahs in the study area was 13.4% (± 7.6%), while between the radio-collared cheetahs it was 11.3% (± 7.2%). Although female cheetahs had a higher mean relatedness to both the study area population

(14.9%, ±12.9%) and to the other radio-collared cheetahs (12.9%, ± 11.2%), neither difference was statistically significant.

There was no significant relationship between the degree of home range overlap and relatedness when the study area population was considered (r_s = -0.002, n = 1016, p = 0.953). However, when the social groups were analysed separately (Figure 11.6c and 11.6d), related females overlapped to a greater extent with one another than non-related females did (z = -2.315, p = 0.021) (Figure 11.6c).

Figure 11.6a and 11.6b Percentage relatedness of radio-collared females (6a) to tagged females (n = 24) in the study area and to other radio-collared females (n = 13) for which genetic analysis was conducted; 6b shows the relatedness of radio-collared males to tagged males in the region (n = 65) and to other radio-collared (n = 24) male cheetahs.

Figure 11.6c and 11.6d Percentage relatedness (*R*) of radio-collared females (c) and males (d) to the percent of overlap to genetically analysed female (n=24) and male (n = 65) cheetahs in the Otjiwarongo region.

11.4.10 Cheetah habitat selection

Habitat preference scores calculated for 25 cheetahs revealed that, overall, cheetahs appeared to show some degree of habitat preference, although it only touched statistical significance (KW $\chi^2 = 2.24$, df = 2, p = 0.053). However, significant differences in habitat preference were evident between social group types, with females preferring sparse and medium bush, single males appearing to select medium and thick bush, and coalitions of males showing no discernible preference (Table 11.6). During the dry season, cheetahs showed significant habitat preference for sparse bush (KW $\chi^2 = 6.59$, df = 2, p = 0.037), while in the wet season there appeared to be some selection towards thick bush, although it was not statistically significant.

Table 11.6 Mean habitat preference by social group and sex

		Sparse Bush (25%)		Medium Bush (54%)		Dense Bush (21%)		Overall habitat preference		
	N	**Mean**	**s**	**Mean**	**s**	**Mean**	**s**	X^2	**df**	**p**
Females	10	0.26	0.23	0.63	0.22	0.10	0.20	16.59	2	0.000*
Single Males	10	0.17	0.28	0.60	0.37	0.23	0.33	6.32	2	0.042*
Coalition Males	5	0.25	0.25	0.35	0.29	0.40	0.42	0.38	2	0.826
Male groups combined	15	0.20	0.26	0.51	0.36	0.29	0.36	5.70	2	0.058
All cheetahs	25	0.22	0.25	0.56	0.31	0.21	0.31	17.04	2	0.000*

* = statistically significant at $p < 0.05$

There was no significant relationship between home range size and habitat cover ($r_s = -0.18$, n = 21, p = 0 .434). However, habitat density had a significant bearing on home range size, which decreased with the proportion of sparse ($r_s = -0.46$, n = 25, p = 0.020) and medium ($r_s = -0.45$, n = 25, p = 0.026) habitat utilised

11.4.11 Prey biomass and bush density and comparison to other studies

Sparse bush areas had the greatest ungulate biomass (Table 11.7), while the overall prey biomass in the study area was comparable to that of protected areas where cheetahs have been studied (Table 11.8). Both home range size and cheetah density varied significantly between the different studies (KW $\chi^2 = 800.00$, df = 13, $p < 0.001$, KW $\chi^2 = 995.24$, df = 13, $p < 0.001$, respectively) and cheetah density was inversely related to home range size ($r_s = -0.648$, n = 14, p = 0.012) when data from all the studies were combined. Despite the apparent equality of prey biomass, home range sizes reported in this study were much larger, and the minimum cheetah density much lower, than results from other studies. These data suggest that prey density is not the primary determinant for home range size and density of Namibian cheetahs.

Table 11.7 Game densities (animals/km^2) and estimated biomass (kg/km^2) by habitat type (sparse, medium, thick) using bush canopy.

	Game Density by Habitat (animals / km^2)				Estimated Biomass (kg/km^2)		
	Sparse Bush < 30% canopy	**Medium Bush 30 to 75% canopy**	**Thick Bush > 75% canopy**	**average weight**	**Sparse Bush < 30% canopy**	**Medium Bush 30 to 75% canopy**	**Thick Bush > 75% canopy**
Oryx	2.34	0.77	0.99	150	351.4	115.9	148.6
Kudu	0.56	0.74	0.77	136	76.0	101.0	104.8
Red Hartebeest	0.49	0.06	0.18	125	61.5	7.2	22.9
Eland	0.34	0.06	0.10	340	114.5	20.6	35.2
Duiker	0.08	0.12	0.02	18	1.5	2.1	0.4
Steenbok	0.27	0.30	0.12	11	3.0	3.3	1.3
Warthog	0.26	0.22	0.21	45	11.5	9.7	9.6
	TOTAL BIOMASS BY HABITAT				619.4	260.0	322.8
	MEAN BIOMASS				**400.7**		

Table 11.8 Density of cheetahs in this study compared to other studies.

		Home range size (km^2)							
Area *	Size (km^2)	Female	Coalition male	Single male	Overall male	Mean overall	Medium-sized prey biomass (kg/km^2)	Density per 100 km^2	Reference ***
NNCF****	6025	1836.3	1608.4	1829.0	1751.8	1775.9	400.7	0.25	this study
NSCF	1000	1400	650	1210	800	1015.0		2.00	1
SP	2200 **	833	37.4	777	37.4	549.1		9.00	2,3,4,5
KTP	1915**	320	125			222.5	24	4.40	5, 6, 7
MMR (outside)		-	-	-		-		3.40	5, 8
MMR (inside)		-	-	-		-		1.50	5, 8
KNP		246	159	504	331.5	303.0		2.30	5
KNP		-	-	-		-		0.52	5, 9
KNP	350**	185.9			173	179.5	246	2.30	6, 10
MNP	388**	23.6			32.5	28.1	1517	4.40	11
SNR	134**	76.6			48.8	62.7	400.4	21.60	12, 13
NNP	115**	79			102	90.5	461	15.20	6, 14, 15
PNP	550**	200			100	150.0	232.6	3.10	16, 17, 18
PRR	170**	94.4			109.1	101.8	724.2	9.40	19, 20

* NNCF- Namibia north central Farmland; NSCF - Namibia south central farmland; SP - Serengeti Plains; KTP - Kgalagadi Transfrontier Park; MMR - Masai Mara Reserve; KNP - Kruger National Park; MNP - Matusssadona National Park; SNR - Suikerbosrand Nature Reserve; NNR - Nairobi National Park; PNP - Pilanesberg National Park; PRR - Phinda Reseource Reserve.

** From Broomhall 2001

*** 1, Morsbach 1985; 2, Caro, 1994; 3, Laurenson 1994; 4, Kelly & Durant 2000; 5, Mills 1998; 6, Gross et al. 1996; 7, Knight 1999; 8, Burney, 1980; 9, Boland, 1990; 10, Broomhall 2001; 11, Purchase 1998; 12, Pettifer et al. 1979; 13, Pettifer 1981; 14, McLaughlin 1970 cited by Schaller 1972; 15, Eaton 1974; 16, van Dyke 1995; 17, Adcock 1996; 18, Hofmeyer & van Dyke 1998; 19, Hunter, 1998; 20, Butchart 1999.

**** home range calculated in 95% MCP

11.4.12 Comparisons of home range estimations with sympatric carnivore species

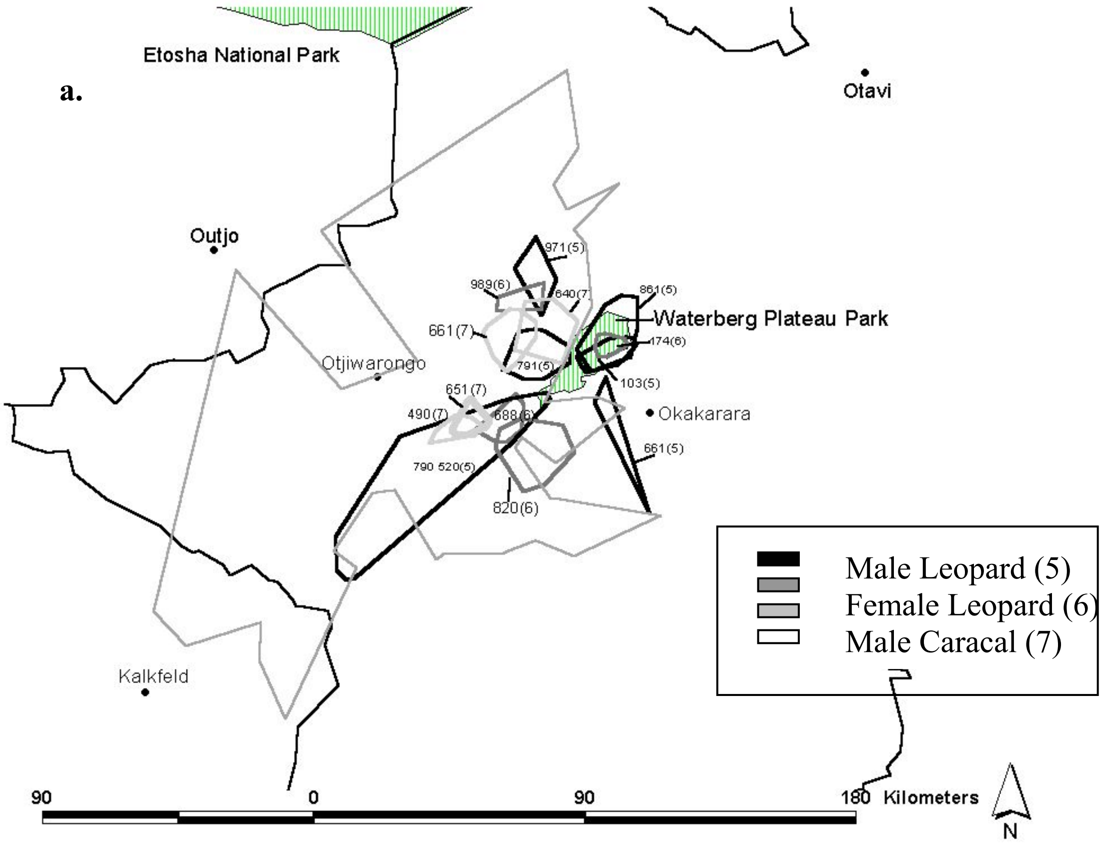
Table 11.9 presents the individual 95% kernel home range estimations for 11 leopards and 4 caracals radio-tracked during this study. Figure 11.7a presents the lifetime 95% MCP home ranges for leopards and caracals within the radio-tracking area of the cheetahs. There were no significant differences in the 95% MCP or 95% kernel estimations of home range size for either leopards or caracals (Table 11.10), nor were there any significant differences in the 95% kernel home ranges between the dry and wet seasons for either species (Table 11.10). Lifetime home range size varied significantly between the three carnivore species (KW $\chi^2 = 9.20$, df = 2, p = 0.010), with cheetahs having the largest ranges. Mean interspecific overlap between the three species was 35.1% (± 12.3) (Figure 11.7b). The degree of home range overlap did not differ significantly either between or within species, although cheetahs displayed slightly more overlap with leopards and caracals than with other cheetahs.

Table 11.9 Data on individual leopards and caracals radio-tracked during this study

Radio Collar #	ID #	Sex	Age at 1st collaring (mo)	Dates tracked	# months tracked	Total # Fixes	95% kernel home range
Leopard							
971	31	M	38	May 99 - Nov 99	20	20	459.0
661	15	M	36	Jan 98 - Apr 98	6	6	963.8
790(520)	7	M	36	Jun 96 - Oct 98	29	100	2408.8
791	27	M	40	Apr 98 - Feb 99	11	36	449.1
861	3	M	60	Feb 96 - Mar 98	26	77	581.6
103	2	M	60	Jan 96 - May 96	5	43	293.5
Male (mean)			**45 (± 11.7) mo**		**16.2 (± 10.3) mo**	**47 (± 35.4) fixes**	
174	1	F	60	Jan 96 - Feb 97	14	80	206.5
688	6	F	24	Jun 96 - Sep 98	28	79	382.3
820	4	F	24	Apr 96 - Jun 98	27	100	3148.1
918(561)	5	F	48	Jun 96 - Dec 98	31	109	226.6
986	29	F	144	Jan 99 - Jun 99	6	17	309.6
Female (mean)			**60 (± 49.5) mo**		**21.2 (± 10.7) mo**	**77 (± 35.9) fixes**	
Caracal							
661	1	M	24	Nov 96 - Nov 98	25	83	456.6
640	2	M	84	Sep 98 - Dec 99	16	46	308.2
490	3	M	42	Oct 98 - Dec 99	15	32	388.2
651	4	M		Jun 00- Dec 00	6	24	274.7
Male caracal (mean)			**50 (± 30.8) mo**		**15.5 (± 7.8) mo**	**46.3 (± 26.1) fixes**	

Table 11.10 Mean lifetime home range estimations (95% MCP and 95% kernel for male and female leopards and male caracals. Statistical differences in lifetime home range estimations are shown between 95% MCP and 95% kernel home ranges as well as between sexes and between the wet and dry seasons.

	Male			**Female**			**Comparison between sexes**		**Total All Leopards**			**Total all Caracals**		
	N	**Mean**	**s**	**n**	**mean**	**s**			**n**	**mean**	**s**	**n**	**mean**	**s**
Mean months tracked	4	16.2	10.3	5	21.2	10.7						4	15.5	7.8
Mean age at collaring	4	45	11.7	5	60	49.5						4	50	30.8
Home range estimations	**N**	**Mean**	**s**	**n**	**mean**	**s**	**z**	**p**	**n**	**mean**	**s**	**n**	**mean**	**s**
Mean no. fixes (lifetime)	4	60.8	28.7	5	77.0	35.9	-1.597	0.11	9	69.8	32.1	4	54.0	25.6
Overall 95% kernel	4	933.3	990.7	5	854.6	1284.0	-0.980	0.327	9	889.6	1092.7	4	356.9	81.7
Overall 95% MCP	4	541.2	629.1	4	179.0	148.2	-0.866	0.386	8	360.1	465.3	3	312.6	116.3
Comparisons	**Z**	**P**		**z**	**p**				**z**	**p**		**z**	**p**	
95% kernel vs 95% MCP	-1.155	0.248		-1.443	0.149				-1.785	0.074		-1.091	0.275	
	Male			**Female**			**Comparison between seasons**		**Total All Leopards**			**Total all Caracals**		
Home range estimations	**N**	**Mean**	**s**	**n**	**mean**	**s**	**z**	**p**	**n**	**mean**	**s**	**n**	**mean**	**s**
Dry Season	4	927.7	932.3	4	408.35	325.8	**-0.756**	**0.45**	8	688.0	703.6	3	393.1	106
Wet Season	4	1098.3	1337.3	4	329.71	99.4	**-0.567**	**0.571**	8	714.0	969.3	3	344.8	89.4
Comparisons	**Z**	**P**		**Z**	**p**				**Z**	**p**		**z**	**p**	
Dry and Wet seaons	-0.289	0.77		0.00	0.100				-0.420	0.674		-0.218	0.827	



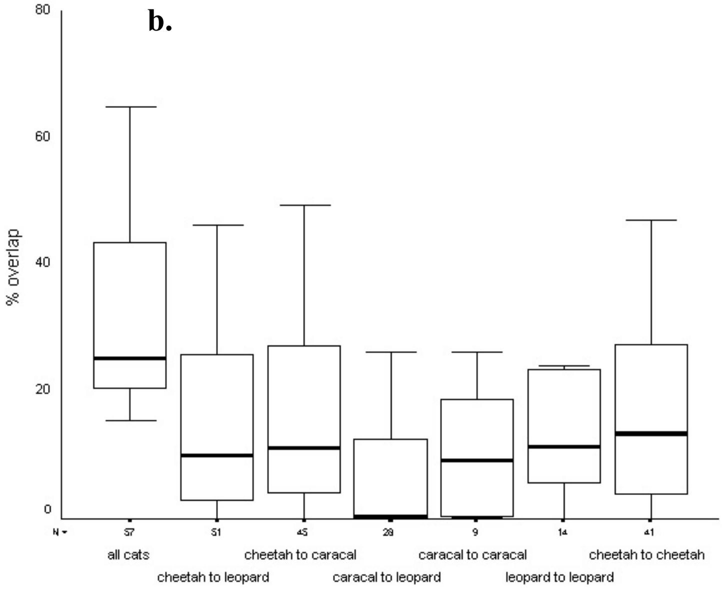


Figure 11.7a 95% MCP lifetime home ranges for male and female leopards and male caracal in proximity to the Waterberg Plateau park, the same area where cheetahs were radio-tracked during this study.

Figure 11.7b Overall intra- and inter-specific home range overlap for cheetah, leopard and caracal.

11.5 DISCUSSION

Cheetahs tracked on the Namibian farmlands showed marked differences in their ecology compared to those studied elsewhere, revealing an apparent flexibility in the spatial organisation of the species. The most evident difference was the very large home ranges found in this study, which were on average over three times larger than those found on the short-grass plains of the Serengeti (Caro 1994). This was unexpected, as other authors have hypothesised (Broomhall 2001, Caro 1994) that cheetahs utilising a migratory prey-base, such as in the Serengeti, should have larger ranges than those utilising a sedentary prey-base. The uniformity of this large home range size across all age groups suggests that it is the result of environmental characteristics, such as habitat type or effects of perturbation. Prey abundance alone does not provide an obvious explanation, as the biomass of ungulates on the Namibian farmlands was no lower than that that reported in other studies, so other explanations must be proposed for these vary large home ranges.

One important factor that is likely to play a role in influencing the ecology of cheetahs in Namibia is the alteration of habitat, particularly the heavy bush encroachment that has proliferated across the country (Quan et al. 1994). Although the prey biomass in the study area was as abundant as in other areas, the thick bush, which is likely to decrease hunting efficiency, probably had an effect on the availability of that prey base. Hunting in habitat that is densely bushed with *Acacia* also increases the risk of injury to cheetahs, with eye damage from thorns being a particular problem (Bauer 1998, Marker-Kraus et al. 1996). Females, in particular, showed habitat selection for areas of sparse bush, which were resource-rich in terms of ungulate biomass. Home range size decreased in proportion to the amount of sparse and medium bush utilised, indicating that the size of cheetah home ranges was dictated by the need to incorporate a certain amount of productive habitat, as predicted by the Resource Dispersion Hypothesis (Macdonald 1983). Availability of water, although considered a vital resource for lactating females in the Serengeti (Caro 1994), was unlikely to be a key determinant of home range size in Namibia, as there is a year-round abundance of water-points on the farmlands.

Expansion of female home ranges to incorporate rewarding patches has been described previously (Caro 1994), although, interestingly, female cheetahs on the Serengeti plains appeared to configure their home ranges in order to encompass areas of denser vegetation, rather than seeking sparse areas as in Namibia. Patches of thickly bushed habitat have been documented as being advantageous in terms of providing cover and ambushing prey (Broomhall 2001, Caro 1994), and it seems evident that female cheetahs select ‘patchy’ home ranges that contain a matrix of different habitat types, in order to maximise both the chances of encountering suitable prey, and improving hunting success.

In contrast to this selection, the apparent preference towards thick bush shown by single males in Namibia may not in fact be an active preference, but rather a result of competitive exclusion from patches rich in resources (both prey and females) by more powerful coalitions of males. Intraspecific aggression amongst male cheetahs has been documented numerous times, with coalition males having a clear advantage over singletons in disputes (Caro 1989, Caro 1994, Frame and Frame 1981, Kuenkel 1978). This supported the theory of female distribution being determined by that of resources, while male distribution was determined in turn by females (Macdonald 1983).

11.5.1 Degree of home range overlap and evidence of territoriality

In most solitary large carnivores, ranges of territorial males overlap with two or more female ranges, presumably to provide an area where they can mate with as many females as possible without interference from surrounding males (Kitchener 1991, Mizutani and Jewell 1998, Sunquist 1981). Both in this study and the Serengeti, however, female cheetah home ranges were far larger than those of males (Broomhall 2001, Caro 1994), and a similar social system was also observed in the Kgalagadi Transfrontier Park, which has a low-density nomadic prey base (Broomhall 2001, Mills 1998). Female cheetahs have been observed to show a high level of mate choice

(Wielebnowski 1996) and this may be an important determinant of social structure, leading to females crossing the home ranges of several males in order to choose a mate, rather than the male encompassing the ranges of several females.

In the Serengeti, female cheetahs have been reported as overlapping extensively, both with each other and with males, while the degree of overlap exhibited by males depended on their status: 'non-resident' males showed a high degree of home range overlap, but 'resident' males were distinctly territorial and responded aggressively to intruders (Caro 1994). In this study, neither sex demonstrated exclusivity in terms of home range (defined by Sandell in 1989) as showing an overlap of adjacent ranges of under 10%) and there was considerable home range overlap, although females overlapped with one another less than males did. Resources concentrated in discrete patches of sparse habitat are too scattered to be defensible, so the maintenance of an exclusive territory on the farmlands may not be worth the energetic cost (Brown and Orians 1970). Under such conditions, the home ranges of females are likely to be large and unpredictable, making it futile for males to inhabit small, defensible territories.

However, despite the degree of home range overlap recorded, behavioural indicators (e.g. scent-marking and defaecation upon prominent land-marks) were used to define territoriality in Serengeti cheetahs (Caro 1994), and these behaviours have been well documented on the Namibian farmlands (Marker-Kraus and Kraus 1995, Marker-Kraus et al. 1996, Morsbach 1986), providing some evidence of male territoriality (Macdonald 1985). It is likely that the large home range sizes necessary to survive on the farmlands preclude the active defence of territorial boundaries, but that territories are demarcated using indirect signals, which provoke intraspecific avoidance (Eaton 1970, Hornocker 1969, King 1975). Coalition males are likely to become territory-holders than singletons (Caro 1994), explaining their lower tolerance for overlap with conspecifics than was recorded for single males.

While cheetahs on the Namibian farmlands do not defend contiguous, exclusive territories, they did show intensive utilisation of core areas, which held important resources such as den sites for females (L.M., pers. obs.). While overall home ranges showed seasonal variation, contracting at times of higher prey density, there was no seasonal variation in core area, indicating that such areas contain enough resources to maintain cheetahs in times of both high and low resource availability. Males, particularly coalitions, held smaller core areas than did females, perhaps because male core areas would be determined by prey availability alone, while females require the inclusion of additional resources such as suitable denning sites. Although these core areas could not strictly be defined as 'territories' (Brown and Orians 1970, Mizutani and Jewell 1998), because they were not spatially stable and moved over time, there was evidence of territorial defence by males, especially in times of low prey availability, although we found no evidence for such defence by females.

Rainfall was an important determinant of home range size on the Namibian farmlands, as would be expected in a habitat where precipitation is very important for determining prey abundance and distribution (Marker-Kraus et al. 1996). The onset of the rainy season leads rapidly to increases in vegetation density, aggregation of prey at vegetation-rich sites, coincides with the birth of young antelope, and leads to the contraction of cheetah home ranges in response to the increased prey availability. The level of rainfall also has important consequences for cheetah conservation on the Namibian farmlands, as drought is common, and leads to reductions in prey through increased vulnerability of prey to predation, starvation, disease, and farmers culling wild game to protect their grazing for livestock (Marker-Kraus et al. 1996).

Females home ranges may be influenced by other factors, such as avoiding males when not in oestrous, and by avoiding places where other cheetahs have recently hunted. Females may also move extensively around their home ranges in order to familiarise cubs with the territory (Bekoff et al. 1984), which would provide advantages to offspring, particularly as the genetic analyses revealed that related female cheetahs overlap more extensively than average, which may be a result of female cubs utilising some of their mother's home range following dispersal. The exception to this was when females had young cubs, whereupon they stayed in a restricted range, particularly during the two months following parturition. Intense utilisation and hunting in these small areas by a female with dependent cubs is likely to increase the level of conflict with local farmers. When the cubs were old enough to travel, the female covered greater distances, thus crossing multiple farms, allowing access to more available game.

11.5.2 Competitive release

Within protected areas, cheetahs frequently suffer from asymmetric competition with larger carnivores, leading to high levels of juvenile mortality and kleptoparasitism (Caro 1994, Durant 1998, Durant 2000a, Durant 2000b, Laurenson and Caro 1994). Such competition can have serious impacts on the ecology and distribution of the subordinate competitor, leading to direct energetic costs from losing prey (Gorman et al. 1998) and indirect costs such as having to resort to avoidance behaviour (Creel et al. 2001, Johnson et al. 1996, Mills and Gorman 1997). Avoidance behaviour has been reported for Serengeti cheetahs, where their density was inversely related to that of lions (Laurenson 1995), and this appeared to have implications in terms of cheetahs being restricted to areas of lower prey density when competitors were present (Durant 1998).

Lions and spotted hyaenas have been removed from the Namibian farmlands, and although leopards and caracals remain, the level of intraguild competition should be considerably reduced. Cheetahs show a high degree of home range overlap with both leopards and caracals, but the three species differ substantially in hunting strategies and demonstrate temporal avoidance. Cheetahs are diurnal or crepuscular hunters (Caro 1994), leopards are predominantly nocturnal (Bailey 1993), and caracals tend to utilize different prey species (Avenant and Nel 1998, Palmer and Fairall 1988). Such strategies for sympatric carnivore species have been documented before, where species competing for the same prey can co-exist due to variations in hunting techniques, prey selection, activity patterns, and mutual avoidance (Bertram 1979, Radinsky 1981, Rosenzweig 1966). Due to these behavioural differences, competition for resources may be reduced, reducing the level of intraguild competition.

Significant changes in carnivore densities have been reported after the removal of intraguild interference (Henke and Bryant 1999); following this, cheetahs on the Namibian farmlands should, all else being equal, live at higher densities than reported in other studies. This did not appear to be the case, however, as the estimated minimum 0.23/100 km^2 and maximum density of 0.83/ 100 km^2 presented in this study was much lower than that reported elsewhere in Africa.

Although we cannot be certain about other limiting factors, the lack of evidence for any competitive release under such circumstances may demonstrate that other factors are restricting density, e.g. habitat quality or intraspecific mechanisms (Barbour and Litvaitis 1993, Scott and Dueser 1992). For Namibian cheetahs, such factors are likely to be complex and interrelated, including prey abundance and distribution, habitat structure, and not least, human pressures. Removals by local farmers, particularly as it targets mainly adult animals (see Chapter 9) are likely to keep the cheetah population density at a figure determined by the tolerance of the landowners rather than by ecological mechanisms.

Another important consideration regarding the dynamics of this population is that it has suffered high levels of removal, and the effects of mass removals can persist in populations for considerable periods of time (Lessios 1995). Studies of badgers (*Meles meles*) have revealed that removals from populations have important consequences, both in terms of both spatial organisation (Tuyttens and Macdonald 2000) and behaviour (Tuyttens et al. 2001). Tuyttens et al. reported in 2000 that population disruption resulted in increased home range overlap, and a similar mechanism may exist with cheetahs, as greatest home range overlap was observed shortly after removals ended, but gradually diminished over time, presumably as the population became more settled. Cheetah density is unlikely, however, to reach pre-removal levels, due to the habitat alterations and bush encroachment discussed above.

11.5.3 Effect of translocation

The ecological effects of translocations have been documented for various species, and have also been investigated for cheetahs elsewhere in Africa (Hunter 1998, Pettifer 1981, Pettifer et al. 1979, Purchase 1998, Zank 1995). The efficacy of using translocation as a strategy to reduce conflict with large carnivores has been the subject of considerable debate (Blanchard and Knight 1995, Fischer and Lindenmayer 2000, Lenain and Warrington 2001, Linnell et al. 1997). In many cases, translocated individuals moved remarkably long distances back to their original home ranges, which obviously limits the value of undertaking such efforts in order to resolve conflict situations (Linnell et al. 1997), and translocated animals also suffered from lower survival rates (Blanchard and Knight 1995, Ruth et al. 1998). We found, however, that no cheetahs returned to their original ranges after translocation, and that survival rates of translocated cheetahs were no lower than those released within their presumed home ranges (see Chapter 9). Although one cheetah moved a long distance following translocation, which would be expected as movement after translocation has been reported as being proportional to home range size (Bowman et al. 2002), overall translocation seemed to have little effect on movement parameters, and there was no difference between the movements per day between those translocated and those moved by resident cheetahs, or between home range size. It did not take translocated cheetahs any longer to reach asymptotic home ranges than for resident cheetahs, and although there was evidence of a positive relationship between home range size and the distance translocated, this was not significant.

Despite the apparent ease with which cheetahs appeared to settle after translocation, there are problems with using it as a method of conflict resolution. Removing animals from conflict situations is usually only a temporary solution, as conflicts tend to re-occur in the same sites, even if the original offending animal has been removed or killed (Stahl et al. 2001, Stahl et al. 2002). The only long-term methods of alleviating such conflicts are likely to involve developing techniques to prevent conflict occurring in the first place, such as improving livestock husbandry practices in areas where livestock depredation is a recurring problem.

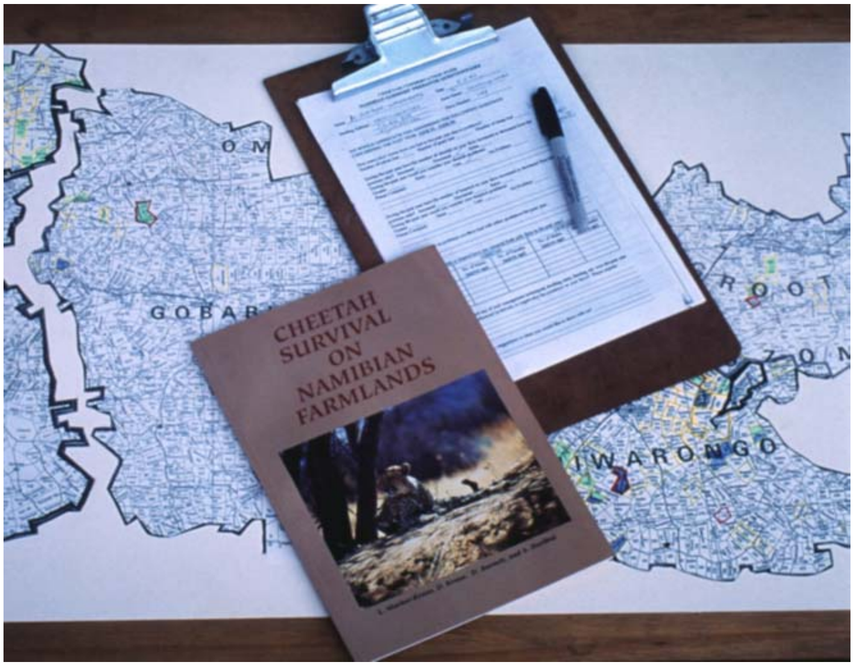
11.6 CONSERVATION IMPLICATIONS

We found that Namibian cheetahs live at low densities and have extremely large home ranges, despite a relatively diverse and abundant prey base. Successful conservation of this population will rely upon maintaining very large, intact landscapes with suitable habitat and sufficient prey density. Habitat restoration programmes may be important in maintaining sufficient suitable areas for both cheetah and prey and are currently being investigated in Namibia.

The requirement for large areas is likely to be necessary in arid environments, as prey biomass tends to be lower and the habitat less productive. Fluctuations in rainfall are well documented in such areas, and have important impacts on habitat, prey and the economics of local people. As important as habitat requirements are, however, physically suitable habitat is not as fundamentally important as reducing the level of human-cheetah conflict on the farmlands, through the provision of economic incentives. The development of conservancies may be critical to cheetah survival in Namibia, where game is still maintained in free-ranging systems in sustainable numbers that prevents conflict with mixed livestock farming initiatives.

CHAPTER 12

FACTORS INFLUENCING PERCEPTION AND TOLERANCE TOWARDS CHEETAHS ON NAMIBIAN FARMLANDS



This thesis chapter has been submitted as the following paper:

Factors Influencing Perceptions and Tolerance Toward Cheetahs (*Acinonyx jubatus*) on Namibian Farmlands. L.L. Marker, M.G.L. Mills & D.W. Macdonald. Submitted to *Conservation Biology.*

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CHAPTER 12: FACTORS INFLUENCING PERCEPTIONS AND TOLERANCE TOWARD CHEETAHS ON NAMIBIAN FARMLANDS

ABSTRACT

We conducted a baseline survey of Namibian farmers between 1991 and 1993, with a yearly follow-up thereafter until 1999 to quantify the attitudes of farmers toward cheetahs. Specifically, we sought to identify factors causing cheetahs to be perceived as pests and any management practices that mitigated this perception. The baseline survey revealed that farmers that regarded cheetahs as problems removed an average of 29 cheetahs annually, while even those that did consider them to be problematic removed a mean of 14 cheetahs annually. The number of removals dropped significantly during the follow-ups, with a mean of 3.5 cheetahs removed annually on 'problem' farms in the 1993-1999 study, and 2.0 cheetahs removed per year on farms where they were not considered problematic.

The perception of cheetahs as pests was significantly associated with game farms. The incidence of reported problems and removals correlated with stock losses, particularly in the later survey, and the presence of 'playtrees' on farms was an important factor for both cheetah problems and removals. Playtrees emerge as significant corollaries of both negative perceptions and removals of cheetahs. Between 1991 and 1999, the annual tallies of cheetah killed by farmers significantly decreased, with an overall mean of 19.0 cheetahs killed annually in the initial survey falling to 2.1 in the follow-up. Latterly, cheetah killing was more closely correlated with locations of perceived problems than in the early years of the study. Furthermore, the proportion of farmers reporting cheetahs to be a problem, but not removing them, has risen from 16% to 22%. These findings suggest that although

cheetahs are still perceived as a problem, farmers' tolerance toward the cheetah has increased. Management strategies that reduce livestock losses and economic incentives that promote cheetah conservation are discussed and deemed essential for the conservation of cheetahs outside protected areas.

12.1 INTRODUCTION

The concentration of cheetahs on Namibian farmland is noteworthy for its significance in terms of ecological theory, as a consequence of intra-guild competition and practical conservation. Irrespective of its explanation, the presence of such a large proportion of the world's cheetah population on farmland where they have traditionally been perceived as a pest makes evaluating the farmers' perception and treatment of the cheetah an obvious conservation priority. Worldwide, farmers hold, and act upon, strong perceptions about predators; a first step in resolving the conflict is to disentangle which aspects of these perceptions are real (e.g. Baker and Macdonald 2000). An important tool in this 'human dimension' of conservation biology is to use questionnaires and interviews to assess the farmers' opinions and the evidence on which they are founded.

Approximately 70% of Namibians are directly or indirectly dependent upon agriculture (Schneider 1994). Nearly 6 000 commercial livestock farms utilise 44% of Namibia's available agricultural land (Schneider 1994) and beef products generate 87% of the country's gross agricultural income (van Schalkwyk 1995).

Namibian commercial farms fall into two broad categories of 'livestock farms' and 'game farms'. However, livestock farms still have relatively high numbers of free-ranging game, while many game farms also have certain sectors where livestock is raised. Therefore, although there is some overlap between the two farming strategies, farms are categorized depending on whether their primary income is generated through livestock production or through the utilization of game. Each category is characterized by a particular type of fencing and an associated management system that may, in turn, affect the farmer's perception of cheetahs – for instance, the stocking of rare and valuable game species may diminish the tolerance of predation upon that stock. In the 1980s, game farms began to proliferate and today contribute a significant amount of foreign currency to Namibia, the majority from trophy hunting. From 1972 to 1992 the percentage of land-use revenue attributed to wildlife increased from 5% to 11%, and by 1999, trophy hunting alone contributed US$ 4.7 million to the Namibian economy (Ministry of Environment and Tourism (M.E.T.) 2000)

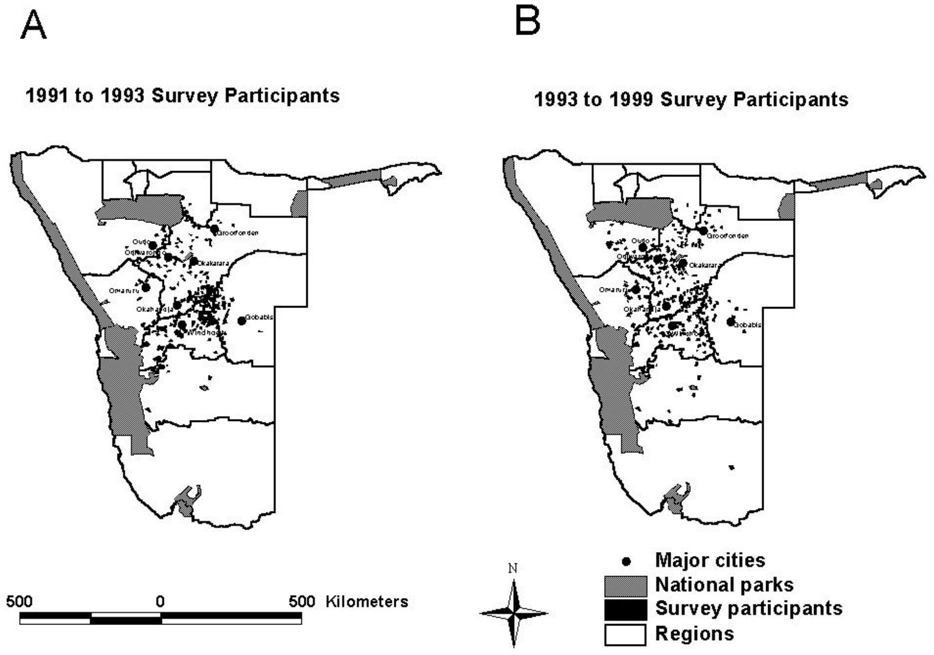
As seen worldwide, there is a widespread perception amongst farmers that predators are responsible for significant stock losses and should be removed from property in order to protect their livelihoods. In the case of the cheetah in Namibia, little evidence corroborates this perception in terms of proven losses (M.E.T. 1999). However, indiscriminate removal of predators due to their perceived, but unproven, contribution to stock loss is a common characteristic of carnivore management and is well illustrated by the case of the red fox on farmlands in the United Kingdom (Baker and Macdonald 2000) as well as other predators throughout the world such as grey wolves, coyotes and jaguars (Johnson et al. 2001, Sillero-Zubiri and Laurenson 2001).

Certain questions have therefore become crucial in the context of the cheetah's presence on Namibian farms. First, how do reported cheetah problems, cheetah removals and livestock loss relate to farmland characteristics and farm management practices? Secondly, have farmers' perceptions of and tolerance towards cheetahs changed over time? In order to answer these questions, and with the goal of analysing the farmers' perceptions as a basis for evaluating and mitigating their conflict with cheetahs, we report on the results of two surveys: an initial survey conducted between 1991 and 1993 and a follow-up survey between 1993 and 1999.

12.2 METHODS

Having recruited a large sample of farmers (see subjects below), each was given an initial questionnaire to obtain information on physical features of farmlands, farm management practices, confirmed and perceived predator problems and livestock loss, and the number of cheetahs removed between 1991 and 1993. A follow-up questionnaire, along with an informational newsletter on farm management and cheetah behaviour, was sent to survey participants annually from 1993 to 1999.

Subjects were recruited at farmers' association meetings in the study area. These farmers then were either interviewed personally or requested to complete the questionnaire at the meeting. The locations of the survey participants for both surveys are shown in Figures 12.1a and 12.1b.



Figures 12.1a and 12.1 b. Location of the survey participants in the (a) initial, 1991-1993, survey, and (b) follow-up, 1993-1999, survey.

Namibian farmers have been shown to be a homogenous group (Harvey and Isaksen 1990); thus, subjects used in the analyses were considered to be a representative sample of the general population of farmers in the study area.

The 1991-1993 data were analysed first, in order to gain baseline information that subsequent data could be compared to. The questionnaire responses were separated into the following four sections for analysis:

12.2.1 Attitudes and removals

(a) Whether farmers perceived cheetahs, leopards, caracals and jackals to be problems or not

(b) If a farmer considered cheetahs to be a problem, whether or not they thought that the problem was seasonal

(c) Whether farmers removed cheetahs or not

(d) If a farmer did remove cheetahs, the number removed per year

(e) Whether the farmer considered the problem with cheetahs to be greater, less or the same as that experienced in the 1980s.

12.2.2 Characteristics of the farm

(a) Whether the farm was managed primarily for the production of livestock (referred to as ‘livestock farms’, or for the utilization of game (‘game farms’).

(b) Farm size in hectares

(c) The density of water points per 1000ha

(d) The density of farm camps per 1000ha

(e) The presence of playtrees

(f) The frequency of sighting cheetah tracks (mean number of sightings per year)

12.2.3 Stocking rates and livestock management techniques

This section was only applicable to livestock farms

(a) The number of cattle owned, and the timing and use of calving seasons

(b) The number of smallstock owned, and the use of dogs and herders with the smallstock,

(c) The total number of livestock animals owned, and density (head per hectare)

(d) The total number of game animals owned, and density (head per hectare)

(e) The proportion of game animals owned

12.2.4 Livestock losses

This section was only applicable to livestock farms.

(a) Number and percentage of cattle owned lost to cheetahs, other predators, and in total

(b) Number and percentage of smallstock owned lost to cheetahs, other predators, and in total

(c) Overall livestock losses (number and percentage of those owned) to cheetahs, other predators and in total

The 1993 – 1999 follow-up questionnaires were shorter and repeated a subset of these questions. Data were analysed using SPSS PC version 10.0.5 for Windows 95/98 & NT (SPSS Inc., Chicago, USA). A specific code was assigned in cases where the respondent failed to answer a question, and another when the question was not relevant (e.g. for number of smallstock lost where none were owned). In both cases, data were excluded from analyses. Details of the questionnaires are shown in Appendix IX.

Each variable was first compared between farms where a cheetah problem was reported and those which had no problem, and then between farms where cheetahs were removed and those where they were not. For variables measured on an interval scale, these comparisons were made using independent samples t-tests, with Levene's test for equality of variances. For binary variables such as farm type, a contingency table was constructed and a Pearson's chi-squared test was used instead. These analyses were then repeated with the 1993-1999 data to investigate changes in significant variables and, most importantly, any changes in attitudes and the level of perceived problems and cheetah removals.

To detect changes in farmers' attitudes over time, perception and tolerance indices relating to livestock losses and cheetah removals were constructed for the seven-year period from 1993 to 1999. The tolerance and perception indices were constructed by scoring farmers on a scale of 1 to 4 according to their level of perceived cheetah problems and cheetah removals. Farmers were scored annually for their perception of (1 being the lowest) and tolerance toward (4 being the highest) cheetahs (Table 12.1).

Table 12.1. Method of calculating the Perception and Tolerance indices

Tolerance Index			Perception Index		
Score	Cattle loss	Cheetah removal	Score	Cattle loss	Cheetah problem
4	Yes	No	1	Yes	No
3	No	No	2	No	No
2	Yes	Yes	3	Yes	Yes
1	No	Yes	4	No	Yes

The tolerance and perception indices were calculated to determine if exposure to conservation education had any perceptible effect on farmers' attitudes over time, and was tested using chi-squared analyses. For all statistical analyses, the significance level was defined as $p < 0.05$, and all tests are two-tailed unless otherwise stated.

12.3 RESULTS

12.3.1 Attitudes and removals

Details of subject response for this section are shown in Table 12.2a for the 1993-1999 survey; Table 12.2b for the 1993-1999 survey, and a summary of the statistical analyses is given in Table 12.2c.

Table 12.2a Attitudes and removals reported during the baseline 1991-1993 survey

Variable	n farmers asked	% response (n)	Response	% for each response (n)	% responding to variable and cheetah problem questions (n)	% of respondents that have a cheetah problem (n) *	% of respondents with no cheetah problem (n) *	% responding to variable and cheetah removal question (n)	% of respondents that remove cheetahs (n) *	% of respondents that do not remove cheetahs (n) *
Have a cheetah problem	241	93.8% (226)	Yes	22.1% (50)	-	-	-	100% (50)	84.0% (42)	16.0% (8)
			No	77.9% (176)	-	-	-	97.7% (172)	59.3% (102)	40.7% (70)
Have a leopard problem	241	83.0% (200)	Yes	36.0% (72)	94.4% (68)	32.4% (22)	67.6% (46)	100% (72)	72.2% (52)	27.8% (20)
			No	64.0% (128)	96.1% (123)	15.4% (19)	84.6% (104)	96.9% (124)	64.5% (80)	35.5% (44)
Have a caracal problem	241	78.8% (190)	Yes	48.4% (92)	97.8% (90)	32.2% (29)	67.8% (61)	100% (92)	72.8% (67)	27.1% (25)
			No	51.6% (98)	95.9% (94)	16.0% (15)	84.0% (79)	95.9% (94)	63.8% (60)	36.2% (34)
Have a jackal problem	241	85.5% (206)	Yes	67.5% (139)	96.4% (134)	26.9% (36)	73.1% (98)	97.8% (136)	73.5% (100)	26.5% (36)
			No	32.5% (67)	95.6% (64)	12.5% (8)	87.5% (56)	98.5% (66)	59.1% (39)	40.9% (27)
Cheetah problem seasonal	50	72.0% (36)	Yes	36.1% (13)	-	-	-	100% (13)	92.3% (12)	7.7% (1)
			No	63.9% (23)	-	-	-	100% (23)	82.6% (19)	17.4% (4)
Remove cheetahs	241	98.3% (237)	Yes	64.1% (152)	94.7% (144)	29.2% (42)	70.8% (102)	-	-	-
			No	35.9% (85)	91.8% (78)	9.4% (8)	89.7% (70)	-	-	-
Mean no. cheetahs removed per year**	152	100% (152)	-	-	94.7% (144)	29.1 (42)	14.3 (102)	-	-	
Cheetah problem compared to the 1980s	241	51.5% (124)	Greater now	43.5% (54)	96.3% (52)	32.7% (17)	67.3% (35)	98.1% (53)	83.0% (44)	17.0% (9)
			Less now	53.2% (66)	100% (66)	13.6% (9)	86.4% (57)	97.0% (64)	53.1% (34)	46.9% (30)
			Same	3.2% (4)	100% (4)	0% (0)	100% (4)	100% (4)	75.0% (3)	25.0% (1)

* = mean value for variables marked **

Table 12.2b Attitudes and removals reported during the 1993-1999 survey

Variable	n farmers asked	% response (n)	Response	% for each response (n)	% responding to variable and cheetah problem questions (n)	% of respondents that have a cheetah problem (n) *	% of respondents with no cheetah problem (n) *	% responding to variable and cheetah removal question (n)	% of respondents that remove cheetahs (n) *	% of respondents that do not remove cheetahs (n) *
Have a cheetah problem	713	75.2% (536)	Yes	47.2% (253)	-	-	-	28.1% (71)	77.5% (55)	22.5% (16)
			No	52.8% (283)	-	-	-	16.3% (46)	41.3% (19)	58.7% (27)
Have a leopard problem	713	64.8% (462)	Yes	41.8% (193)	94.8% (183)	61.2% (112)	38.8% (71)	20.2% (39)	69.2% (27)	30.8% (12)
			No	58.2% (269)	97.8% (263)	36.1% (95)	63.9% (168)	18.6% (50)	50.0% (25)	50.0% (25)
Remove cheetahs	713	23.6% (168)	Yes	72.6% (122)	60.7% (74)	74.3% (55)	25.7% (19)	-	-	-
			No	27.4% (46)	93.5% (43)	37.2% (16)	62.8% (27)	-	-	-
Mean no. cheetahs removed per year**	122	100% (122)	-	-	60.7% (74)	3.47 (55)	1.95 (19)	-	-	-

Table 12.2c Statistical analyses of the attitudes and removals between the 1991-1993 and 1993-1999 surveys.

	91-93 baseline survey results								**93-99 follow-up survey results**							
	Test for relationship with cheetah problem	Test statistic	df	*P*	Test for relationship with cheetah removals	Test statistic	df	*p*	Test for relationship with cheetah problem	Test statistic	df	*p*	Test for relationship with cheetah removals	Test statistic	df	*p*
Cheetah problem	-	-	-	-	3	10.27	1	0.001**	-	-	-	-	3	15.70	1	0.000**
Leopard problem	3	7.42	1	0.006**	3	1.23	1	0.267	3	27.29	1	0.000**	3	3.34	1	0.068
Caracal problem	3	6.69	1	0.010*	3	1.74	1	0.187	-	-	-	-	-	-	-	-
Jackal problem	3	5.17	1	0.023*	3	4.32	1	0.038*	-	-	-	-	-	-	-	-
Cheetah problem seasonal	-	-	-	-	3	0.65	1	0.419	-	-	-	-	-	-	-	-
Remove cheetahs	3	10.37	1	0.001**	-	-	-	-								
Mean no. cheetahs removed/yr	2	-1.89	52	0.064	-	-	-	-	-	-	-	-	-	-	-	-
Cheetah problem compared to 80s	3	7.42	2	0.025*	3	11.83	2	0.003**	-	-	-	-	-	-	-	-

1 = Independent samples t-test, equal variances assumed (test statistic = t)
2 = Independent samples t-test, equal variances not assumed (test statistic = t)
3 = Pearson's chi-squared test for association (test statistic = χ^2)

* denotes significance at the $p<0.05$ level
** denotes significance at the $p<0.01$ level

(a) Problems with cheetahs, leopards, caracals and jackals

The baseline survey revealed a significant association between cheetah problems and removals, with 84% of farmers with a cheetah problem removing cheetahs, compared to 59% of those without a problem. The same trend was seen in the 1993-1999 survey, where 78% of farmers who had a cheetah problem removed cheetahs, compared to 41% of those without a problem. Both the initial and the follow-up surveys showed significant association between having a leopard problem and having a cheetah problem, but not between having a leopard problem and removing cheetahs.

The baseline survey also dealt with caracal and jackal problems. It revealed a significant association between caracal and cheetah problems, but not between caracal problems and cheetah removals. Having a jackal problem was related both to having a cheetah problem and to removing cheetahs.

(b) *Seasonality of cheetah problems*

Of the farmers that answered both the questions regarding cheetah problems and seasonality, just over a third of farmers who reported having a cheetah problem considered it to be seasonal. This question was not included in the follow-up surveys.

(c) *Frequency of cheetah removals*

Almost all (98.3%) of the 241 farmers questioned in the baseline survey responded to the question regarding cheetah removals. Of these respondents, 64.1% removed cheetahs, while 35.9% did not. In the follow-up survey, however, less than a quarter (23.6%) of the farmers questioned responded to the question regarding cheetah removals. Of these respondents, 72.6% removed cheetahs, while 27.4% did not. Several typical comments about cheetah removals were noted during the initial interviews and are shown in Table 12.3.

Table 12.3 Comments made by Namibian farmers during the interviews

Comments
"It is a fever to kill/shoot cheetah."
"People live with blinders on and keep killing."
"High prices paid by dealers, plus playtrees, could mean a threat to the cheetah's future."
"Man's ignorance equals cheetah's enemy."
"People did things in the past, because my father did it and my grandfather did it, but maybe it does not have to be that way anymore."
"Several people say that young farmers will help older farmers, who are set in their ways and want to kill cheetah, to understand."

(d) *Number of cheetahs removed annually*

In the baseline survey, the number of cheetahs removed per farmer each year varied from one to 250, with a mean of 19 cheetahs removed per farmer annually. A few farmers skewed this mean, however – more than half (55.3%) of the farmers that replied removed fewer then 10 cheetahs each year. Farmers who considered cheetahs to be a problem removed a mean of 29 cheetahs per year, compared to 14 for farmers who did not consider them to be a problem, a difference that was statistically significant (Table 12.2c).

In the follow-up survey, the number of cheetahs removed per farmer each year had dropped, with a mean of 2.9 cheetahs removed per farmer annually. The number of cheetahs removed ranged from one to 22, with virtually all (99.2%) of the farmers that replied removing fewer then 10 cheetahs each year. Farmers who considered cheetahs to be a problem removed a mean of 3.5 cheetahs per year, compared to 2.0 for farmers who did not consider them to be a problem, a difference that, again, was statistically significant (Table 12.2c).

Overall, therefore, the mean number of cheetahs removed had declined significantly in the follow-up survey when compared to the baseline survey (t = 6.031, $p < 0.001$). Figure 12.2 shows the numbers of cheetahs removed annually during the follow-**up survey compared to the numbers of farmers reporting a cheetah problem.**

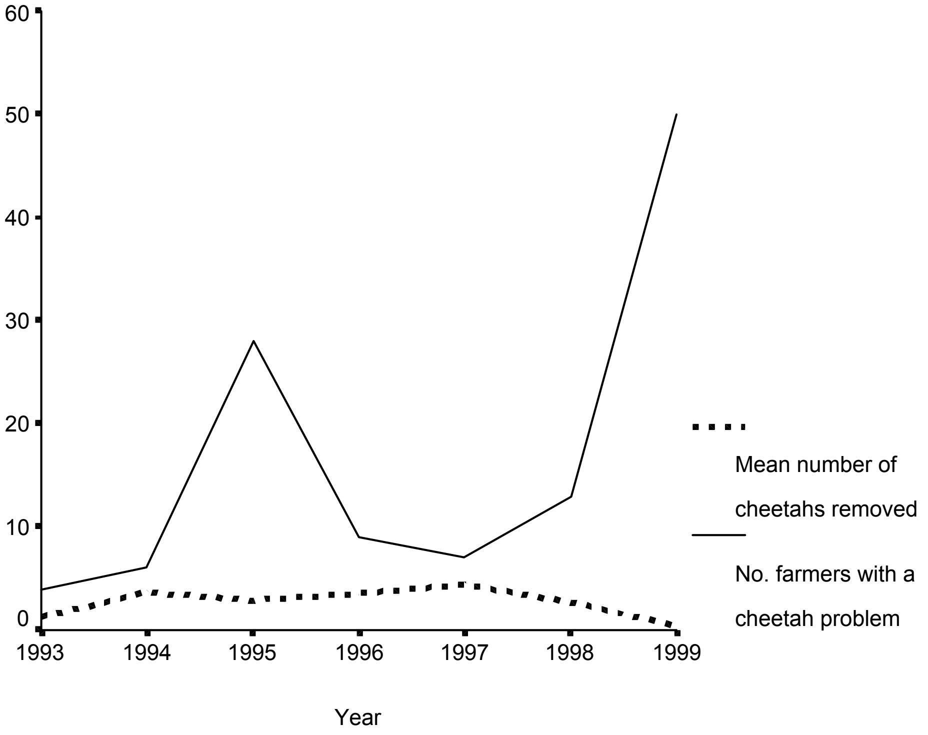


Figure 12.2 Trends in perceived cheetah problems and numbers of cheetahs removed on an annual basis

(e) *Change in cheetah problems since the 1980s*

During the 1980s, the combination of a severe drought and a rabies epidemic led to a huge die-off in Namibia's kudu population, and this in turn led to increased conflict between farmers and predators. The baseline survey questioned farmers regarding whether cheetahs had been more of a problem in the 1980s than they were presently. The respondents were fairly evenly split, with just over half saying that the problem was no greater than in the 1980s.

12.3.2 Characteristics of the farm

Details of subject response for this section are shown in Table 12.4a for the 1991-1993 survey; Table 12.4b for the 1993-1999 survey, and a summary of the statistical analyses is given in Table 12.4c.

Table 12.4a Farmland characteristics reported during the 1991-1993 survey

Variable	N farmers asked	% response (n)	Response	% for each response (n)	% responding to variable and cheetah problem questions (n)	% of respondents that have a cheetah problem (n) *	% of respondents with no cheetah problem (n) *	% responding to variable and cheetah removal question (n)	% of respondents that remove cheetahs (n) *	% of respondents that do not remove cheetahs (n) *
Farm type	241	92.1% (222)	Game farm	25.7% (57)	91.2% (52)	40.4% (21)	59.6% (31)	100% (57)	82.5% (47)	17.5% (10)
			Livestock farm	74.3% (165)	95.2% (157)	15.9% (25)	84.1% (132)	97.6% (161)	58.4% (94)	41.6% (67)
Farm size**	241	100% (241)	-	-	93.8% (226)	9868 (50)	10 813 (176)	98.3% (237)	10 682 (152)	10 153 (85)
Water point density**	241	67.6% (163)	-	-	100% (163)	- (0)	1.50 (163)	98.2% (160)	1.51 (101)	1.47 (59)
Farm camp density**	241	51.9% (125)	-	-	95.2% (119)	3.84 (28)	4.92 (91)	99.2% (124)	4.54 (97)	4.78 (27)
% dense bush**	241	50.2% (121)	-	-	95.9% (116)	24.8 (26)	21.9 (90)	99.2% (120)	24.0 (95)	18.1 (25)
% medium bush**	241	49.4% (119)	-	-	95.8% (114)	34.1 (24)	39.6 (89)	99.2% (118)	33.6 (93)	56.0 (25)
% sparse bush**	241	49.4% (119)	-	-	95.8% (114)	25.5 (27)	28.0 (87)	99.2% (118)	27.5 (93)	22.9 (25)
% grassland**	241	49.8% (120)	-	-	95.8% (115)	17.1 (26)	10.8 (89)	99.2% (119)	15.8 (94)	2.60 (25)
Frequency of tracks**	241	82.6% (199)	-	-	97.0% (193)	47.0 (41)	27.7 (152)	98.0% (195)	39.3 (132)	21.2 (63)
Presence of playtrees	241	100% (241)	Yes	64.7% (156)	94.9% (148)	28.4% (42)	71.6% (106)	97.4% (152)	100% (152)	0% (0)
			No	35.3% (85)	91.8% (78)	10.3% (8)	89.7% (70)	100% (85)	0% (0)	100% (85)

`* = mean value for variables marked **`

Table 12.4b Farmland characteristics reported during the 1993-1999 survey

Variable	n farmers asked	% response (n)	Response	% for each response (n)	% responding to variable and cheetah problem questions (n)	% of respondents that have a cheetah problem (n) *	% of respondents with no cheetah problem (n) *	% responding to variable and cheetah removal question (n)	% of respondents that remove cheetahs (n) *	% of respondents that do not remove cheetahs (n) *
Farm type	713	57.6% (411)	Game farm	19.0% (78)	75.6% (59)	54.2% (32)	45.8% (27)	69.2% (54)	79.2% (19)	20.8% (5)
			Livestock farm	81.0% (333)	79.9% (266)	43.2% (115)	56.8% (151)	23.7% (79)	53.2% (42)	46.8% (37)
Farm size**	713	6.5% (46)	-	-	69.6% (32)	10 078 (23)	13 989 (9)	37.0% (17)	13 123 (14)	7067 (3)
Frequency of tracks**	713	100% (713)	-	-	75.2% (536)	3.4 (253)	1.82 (283)	23.6% (168)	3.48 (122)	1.68 (46)

* = mean value for variables marked **

Table 12.4c Statistical analyses of the farmland characteristics between the 1991-1993 and 1993-1999 surveys.

	91-93 baseline survey results								**93-99 follow-up survey results**							
	Test for relationship with cheetah problem	Test statistic	df	*P*	Test for relationship with cheetah removals	Test statistic	df	*P*	Test for relationship with cheetah problem	Test statistic	df	*p*	Test for relationship with cheetah removals	Test statistic	df	*p*
Farm type	3	13.62	1	0.000**	3	10.68	1	0.001**	3	2.36	1	0.124	3	5.15	1	0.023*
Mean farm size	1	0.62	224	0.534	1	-0.42	235	0.675	2	-0.74	8	0.477	1	-1.65	15	0.121
Water point density	-	-	-	-	1	-0.24	158	0.813	-	-	-	-	-	-	-	-
Farm camp density	1	1.86	117	0.065	1	0.41	122	0.686	-	-	-	-	-	-	-	-
% dense bush	1	-0.50	114	0.619	2	-0.99	118	0.324	-	-	-	-	-	-	-	-
% medium bush	1	0.71	112	0.466	1	3.07	116	0.003**	-	-	-	-	-	-	-	-
% sparse bush	1	0.36	112	0.717	1	-0.66	116	0.514	-	-	-	-	-	-	-	-
% grassland	1	-2.14	113	0.258	2	-2.30	117	0.023*	-	-	-	-	-	-	-	-
Frequency of tracks	1	-1.38	191	0.170	1	-1.43	193	0.153	2	-2.63	404	0.009**	1	1.04	166	0.302
Presence of playtrees	3	9.74	1	0.002**	3	237.00	1	0.000**	-	-	-	-	-	-	-	-

1 = Independent samples t-test, equal variances assumed (test statistic = t)
2 = Independent samples t-test, equal variances not assumed (test statistic = t)
3 = Pearson's chi-squared test for association (test statistic = $\chi 2$)
* denotes significance at the p<0.05 level
** denotes significance at the p<0.01 level

(a) *Farm type*

In the 1991-1993 survey, 7.9% (n = 19) of the farmers failed to answer the question regarding farm type, leaving 92.1% (222 farms) that could be classified as either livestock or game farms. Of these 222, 74.3% (n = 165) were livestock farms while 25.7% (n = 57) were game farms.

In the 1993-1999 follow-up surveys, more respondents (42.4%, n = 302), failed to answer the question regarding farm type. Of the remaining 411 cases, 81.0% of the follow-up respondents (n = 333) were livestock farmers while 19.0% (n = 78) were game farmers.

Table 12.4c shows that in 1991-1993 there was a significant association between farm type and the frequency of reported cheetah problems, with a higher proportion of game farmers regarding cheetahs as a problem. In the follow-up survey there was no relationship between farm type and cheetah problems. Both surveys, however, revealed a significant association between farm type and cheetah removals, with a higher proportion of game farmers removing cheetahs.

In both surveys, a greater percentage of both livestock and game farmers removed cheetahs than considered them to be a problem. The baseline survey showed that only 16% of livestock farmers regarded cheetahs as a problem, but over half (58.4%) removed them. Similarly, just over 40% of game farmers viewed cheetahs as problematic, while over twice that percentage (82.5%) removed them from their farms. It is interesting to note that although a higher percentage of game farmers removed cheetahs, livestock farmers showed a greater disparity between the proportion that reported problems and the proportion that removed cheetahs.

In 1993-1999, a higher percentage (43.2%) of livestock farmers regarded cheetahs as a problem, but a lower proportion (53.2%) actually removed them. Similarly, although more (54.2%) of the game farmers responding viewed cheetahs as problematic, a smaller percentage (79.2%) removed them from their farms than did in the baseline survey.

(b) *Farm size*

Farm size ranged from 1100 to 100 000ha in the initial survey, with a mean of 10 436ha, and from 3000 to 54 500ha in the follow-up, with a mean of 10 961ha. Farm size showed no significant relationship with the incidence of cheetah problems or cheetah removals in either survey.

(c) *Density of water points – only included in baseline survey*

Water point density ranged from 0.3 to 8.2 water points per 1000ha, with a mean of 1.5 per 1000ha. None of the farmers that provided data regarding the density of water points had a cheetah problem. There was no significant difference in the mean density of water points between removing and non-removing farms.

(d) *Density of farm camps – only included in baseline survey*

The number of farm camps per 1000ha ranged from 0.7 to 21.4, with a mean of 4.6, and showed no significant relationship with the number of cheetah problems reported or the frequency of cheetah removals.

(e) *Presence of playtrees – only included in baseline survey*

The presence of playtrees on a farm was strongly related to the reporting of cheetah problems, with 28% of farms that had playtrees reporting a cheetah problem compared to only 10% of farms without playtrees. There was an even more striking relationship between the presence of playtrees and the removal of cheetahs – all the farmers that had playtrees removed cheetahs, while none of the farmers without playtrees on their farms performed removals. Game farmers were aware of significantly more playtrees on their land than livestock farmers (t = -3.622, $p < 0.001$).

Despite the relationships between having a playtree and cheetah problems and removals, there was no significant increase in the percentage of either cattle or smallstock lost on farms that had playtrees compared to those that did not (cattle: t = 1.280, $p = 0.205$; smallstock: t = -1.759, $p = 0.106$).

(f) *Frequency of sighting cheetah tracks*

In the baseline survey, a mean of 27.3 sightings of cheetah tracks were made per year, and this showed no significant relationship with cheetah problems or cheetah removals. In the follow-up survey, the mean number of sightings per year had dropped to 2.3, with significantly more cheetah tracks spotted on farms that reported having a cheetah problem than those without a problem, although there was still no relationship with cheetah removals.

12.3.3 Stocking rates and livestock management techniques

Details of subject response for this section are shown in Table 12.5a for the 1991 - 1993 survey, with a summary of the statistical analyses given in Table 12.5b.These questions were only asked in the baseline survey and the analyses were restricted to livestock farmers.

Table 12.5a 1991-1993 survey stocking rates and livestock management techniques: relationships with cheetah problems and removals

Variable	n farmers asked	% response (n)	Response	% for each response (n)	% responding to variable and cheetah problem questions (n)	% of respondents that have a cheetah problem (n) *	% of respondents with no cheetah problem (n) *	% responding to variable and cheetah removal question (n)	% of respondents that remove cheetahs (n) *	% of respondents that do not remove cheetahs (n) *
No. cattle owned	165	98.2% (162)	-	-	95.7% (155)	840.2 (25)	805.4 (130)	97.5% (158)	840.8 (94)	746.9 (64)
Used calving season	165	88.5% (146)	Yes	89.0% (130)	93.8% (122)	16.4% (20)	83.6% (102)	97.7% (127)	59.1% (75)	40.9% (52)
			No	11.0% (16)	100% (16)	0% (0)	100% (16)	100% (16)	50% (8)	50% (8)
Type of calving season used	146	89.0% (130)	Summer	54.6% (71)	98.6% (70)	15.7% (11)	84.3% (59)	98.6% (70)	64.3% (45)	35.7% (25)
			Winter	0% (0)	-	-	-	-	-	-
			Both	45.4% (59)	94.9% (56)	16.1% (9)	83.9% (47)	96.6% (57)	52.6% (30)	47.4% (27)
No. smallstock owned	165	100% (165)	-	-	95.2% (157)	213.2 (25)	364.9 (132)	97.6% (161)	226.5 (94)	595.3 (67)
Used a dog with smallstock	104	55.8% (58)	Yes	74.1% (43)	97.7% (42)	14.3% (6)	85.7% (36)	95.3% (41)	63.4% (26)	36.6% (15)
			No	25.9% (15)	93.3% (14)	7.1% (1)	92.9% (13)	100% (15)	26.7% (4)	73.3% (11)
Used a herder with smallstock	104	57.7% (60)	Yes	65.0% (39)	100% (39)	7.7% (3)	92.3% (36)	97.4% (38)	55.3% (21)	44.7% (17)
			No	35.0% (21)	95.2% (20)	15.0% (3)	85.0% (17)	95.2% (20)	35.0% (7)	65.0% (13)
Total no. livestock animals owned	165	98.2% (162)	-	-	95.7% (155)	1053.4 (25)	1175.9 (130)	97.5% (158)	1067.3 (94)	1370.2 (64)
Density of livestock	165	98.2% (162)	-	-	95.7% (155)	0.13 (25)	0.14 (130)	97.5% (158)	0.12 (94)	0.16 (64)
Total no. of game animals owned	165	100% (165)	-	-	95.2% (157)	571.6 (25)	531.9 (132)	97.6% (161)	587.5 (94)	437.3 (67)
Density of game	165	98.8% (163)	-	-	95.1% (155)	0.061 (25)	0.063 (130)	96.9% (158)	0.067 (94)	0.053 (64)
Proportion of game animals owned	165	98.2% (162)	-	-	95.7% (155)	0.31 (25)	0.32 (130)	97.5% (158)	0.34 (94)	0.28 (64)

* = mean value for variables marked **

Table 12.5b Statistical analyses of the stocking rates and livestock management techniques: statistical analyses.

	Test for relationship with cheetah problem	Test statistic	df	*p*	Test for relationship with cheetah removals	Test statistic	df	*p*
No. cattle owned	1	-0.36	153	0.721	1	-1.29	156	0.199
Use of calving season	3	2.96	1	0.086	3	0.48	1	0.489
Timing of calving season	3	0.00	1	0.957	3	1.77	1	0.184
No. smallstock owned	1	0.84	155	0.403	2	2.30	159	0.023*
Use of dogs with SS	3	0.49	1	0.484	3	5.96	1	0.015*
Use of herder with SS	3	0.77	1	0.379	3	2.16	1	0.142
Total no. livestock owned	1	0.64	153	0.520	2	1.57	75	0.122
Density of livestock	1	0.23	153	0.820	2	1.88	75	0.064
Total no. game owned	1	0.24	153	0.813	2	-2.40	155	0.018*
Density of game	1	-0.38	155	0.705	1	-1.98	159	0.050
Proportion of game	1	0.40	153	0.688	1	-2.32	156	0.022*

1 = Independent samples t-test, equal variances assumed (test statistic = t)
2 = Independent samples t-test, equal variances not assumed (test statistic = t)
3 = Pearson's chi-squared test for association (test statistic = *X2)*

* denotes significance at the p<0.05 level
** denotes significance at the p<0.01 level

(a) *Number of cattle owned, and timing and use of calving seasons*

The number of cattle owned ranged from 60 to 2850 (mean = 800) and was not significantly linked to the frequency of reported cheetah problems or cheetah removals. Similarly, the use of calving seasons, and the timing of the calving season, had no significant relationship with cheetah problems or removals.

(b) *Number of smallstock owned, and use of dogs and herders with smallstock*

The number of smallstock owned ranged from 10 to 8000, with a mean of 597. There was no relationship between the number of smallstock owned and cheetah problems, but farmers that reported removing cheetahs had significantly more smallstock than those that did not.

Having a dog with the smallstock did not seem to influence the incidence of cheetah problems, but a higher proportion of farmers that had a dog with smallstock removed cheetahs compared to those without a dog. Having a herder with the smallstock bore no relationship to cheetah problems or cheetah removals.

(c) *Number and density of livestock owned*

The total number of livestock owned (range 100-8300; mean 1183) was not significantly linked to cheetah problems or cheetah removals, and the same was true for livestock density.

(d) *Number and density of game owned*

The estimated number of game animals on a livestock farm showed no relationship with either cheetah problems or cheetah removals. Game density was not related to the frequency of reported cheetah problems, although farmers that removed cheetahs had a significantly greater density of game on their farms than those that did not remove cheetahs. There was also a relationship between playtree abundance and game density on livestock farms: livestock farms with playtrees had a significantly higher density of game than those without playtrees (t = 2.52, p = 0.013).

(e) *Proportion of game animals*

The proportion of game on livestock farms was not linked to cheetah problems, but there was a significantly higher proportion of game on farms where cheetah removals occurred than on those where they did not.

12.3.4 Livestock losses

Details of subject response for this section are shown in Table 12.6a for the 1993-1999 survey; Table 12.6b for the 1993-1999 survey, and a summary of the statistical analyses is given in Table 12.6c. This section dealt with livestock farmers only.

Table 12.6a Livestock losses reported during the 1991-1993 survey

Variable	n farmers asked	% response (n)	% respondents answering cheetah problem question (n)	Mean for respondents that have a cheetah problem (n)	Mean for respondents that have no cheetah problem (n)	% respondents answering cheetah removal question (n)	Mean for respondents that remove cheetahs (n)	Mean for respondents that do not remove cheetahs (n)
No. cattle lost to cheetahs	165	27.3% (45)	97.8% (44)	8.20 (10)	3.18 (34)	97.8% (44)	5.33 (24)	3.10 (20)
No. cattle lost to other predators	165	75.2% (124)	98.4% (122)	6.95 (19)	3.92 (103)	97.6% (121)	4.82 (78)	3.53 (43)
No. cattle lost overall	165	20.0% (33)	96.7% (32)	16.67 (6)	6.77 (26)	96.7% (32)	12.16 (19)	4.92 (13)
% cattle lost to cheetahs	165	27.3% (45)	97.8% (44)	1.05 (10)	0.55 (34)	97.8% (44)	0.78 (24)	0.53 (20)
% cattle lost to other predators	165	75.2% (124)	98.4% (122)	0.99 (19)	0.64 (103)	97.6% (121)	0.69 (78)	0.69 (43)
% cattle lost overall	165	20.0% (33)	97.0% (32)	2.00 (6)	1.26 (26)	97.0% (32)	1.64 (19)	1.08 (13)
No. smallstock lost to cheetahs	104	26.0% (27)	70.4% (19)	9.00 (2)	4.71 (17)	66.7% (18)	3.82 (11)	6.29 (7)
No. smallstock lost to other predators	104	67.3% (70)	98.6% (69)	8.80 (10)	6.00 (59)	95.7% (67)	5.49 (39)	7.93 (28)
No. smallstock lost overall	104	16.0% (16)	100% (16)	18.00 (1)	11.47 (15)	93.8% (15)	10.40 (10)	12.40 (5)
% smallstock lost to cheetahs	104	18.3% (19)	100% (19)	3.28 (2)	1.71 (17)	94.7% (18)	1.47 (11)	2.31 (7)
% smallstock lost to other predators	104	67.3% (70)	98.6% (69)	4.87 (10)	2.14 (59)	95.7% (67)	2.26 (39)	3.14 (28)
% smallstock lost overall	104	15.4% (16)	100% (16)	5.29 (1)	4.34 (15)	93.8% (15)	4.91 (10)	2.93 (5)
No. livestock lost to cheetahs	165	17.6% (29)	100% (29)	10.40 (5)	4.25 (24)	96.6% (28)	5.47 (15)	4.46 (13)
No. livestock lost to other predators	165	64.8% (107)	99.1% (106)	12.38 (16)	7.33 (90)	97.2% (104)	7.84 (64)	8.50 (40)
No. livestock lost overall	165	13.3% (22)	100% (22)	21.33 (3)	10.42 (19)	95.5% (21)	14.00 (13)	6.50 (8)
% livestock lost to cheetahs	165	17.6% (29)	100% (29)	1.38 (5)	0.53 (24)	96.6% (28)	0.76 (15)	0.48 (13)
% livestock lost to other predators	165	64.8% (107)	99.1% (106)	1.21 (16)	0.80 (90)	97.2% (104)	0.85 (64)	0.90 (40)
% livestock lost overall	165	13.3% (22)	100% (22)	2.42 (3)	1.30 (19)	95.5% (21)	1.85 (13)	0.51 (8)

Table 12.6b Livestock losses reported during the 1991-1993 survey.

Variable	n farmers asked	% response (n)	% respondents answering cheetah problem question (n)	Mean for respondents that have a cheetah problem (n)	Mean for respondents that have no cheetah problem (n)	% respondents answering cheetah removal question (n)	Mean for respondents that remove cheetahs (n)	Mean for respondents that do not remove cheetahs (n)
No. cattle lost to cheetahs	333	52.6% (175)	94.3% (165)	2.19 (63)	0.14 (102)	30.3% (53)	1.06 (17)	2.11 (36)
No. cattle lost to other predators	333	77.2% (257)	94.6% (243)	4.81 (106)	1.25 (137)	25.7% (66)	4.90 (29)	0.51 (37)
No. cattle lost overall	333	51.7% (172)	95.3% (164)	5.81 (63)	2.15 (101)	30.8% (53)	3.94 (17)	1.58 (36)
No. smallstock lost to cheetahs	333	46.5% (155)	92.9% (144)	2.64 (53)	0.46 (91)	36.1% (56)	3.58 (19)	2.16 (37)
No. smallstock lost to other predators	333	74.2% (247)	92.3% (228)	8.05 (98)	9.87 (130)	26.3% (65)	4.14 (28)	5.47 (37)
No. smallstock lost overall	333	45.6% (152)	94.1% (143)	8.46 (53)	12.09 (90)	34.9% (53)	6.25 (16)	6.64 (37)
No. livestock lost to cheetahs	333	44.7% (149)	94.0 (140)	4.92 (51)	0.49 (89)	34.9% (52)	3.94 (16)	2.31 (36)
No. livestock lost to other predators	333	69.4% (231)	94.4% (218)	12.90 (94)	10.44 (124)	27.7% (64)	8.11 (27)	5.99 (37)
No. livestock lost overall	333	44.1% (147)	94.6% (139)	14.50 (51)	13.47 (88)	35.4% (52)	10.25 (16)	8.40 (36)

Table 12.6c Statistical analyses of livestock losses.

	91-93 baseline survey results								**93-99 follow-up survey results**							
	Test for relationship with cheetah problem	Test statistic	Df	*p*	Test for relationship with cheetah removals	Test statistic	df	*p*	Test for relationship with cheetah problem	Test statistic	df	*p*	Test for relationship with cheetah removals	Test statistic	df	*p*
No. cattle lost to cheetahs	1	-4.078	42	0.000**	1	-1.9	42	0.064	2	-5.261	64	0.000**	1	0.08	51	0.937
No. cattle lost to other predators	1	-3.021	120	0.003**	1	-1.664	119	0.099	2	-4.473	126	0.000**	2	-2.971	29	0.006
No. cattle lost overall	1	-3.413	30	0.002**	1	-2.529	30	0.017*	2	-5.466	69	0.000**	2	-1.661	19	0.113
% cattle lost to cheetahs	1	-1.889	42	0.066	1	-2.128	42	0.266	-	-	-	-	-	-	-	-
% cattle lost to other predators	1	-1.626	120	0.107	1	0.005	119	0.996	-	-	-	-	-	-	-	-
% cattle lost overall	1	-1.016	30	0.318	1	-0.974	30	0.338	-	-	-	-	-	-	-	-
No. SS lost to cheetahs	1	-1.219	17	0.240	1	2.115	16	0.281	2	-2.744	59	0.008**	2	-2.086	24	0.048*
No. SS lost to other predators	1	-1.709	67	0.092	1	2.076	65	0.042*	1	0.598	226	0.550	1	0.427	63	0.671
No. SS lost overall	1	-0.643	14	0.531	1	0.376	13	0.713	1	0.783	141	0.435	1	0.083	51	0.934
% SS lost to cheetahs	1	-0.922	17	0.370	1	0.753	16	0.463	-	-	-	-	-	-	-	-
% SS lost to other predators	2	-1.015	9	0.336	1	0.819	65	0.416	-	-	-	-	-	-	-	-
% SS lost overall	1	-0.131	14	0.898	1	-0.503	13	0.624	-	-	-	-	-	-	-	-
No. LS lost to cheetahs	1	-2.574	27	0.016*	1	-0.508	26	0.616	2	-5.063	55	0.000**	2	-2.193	21	0.246
No. LS lost to other predators	2	-2.297	18	0.034*	1	0.499	102	0.619	1	-0.753	216	0.452	1	-0.612	62	0.543
No. LS lost overall	1	-1.59	20	0.127	1	-1.552	19	0.137	1	-0.215	137	0.830	1	-0.382	50	0.704
% LS lost to cheetahs	1	-2.39	25	0.024*	1	-0.965	26	0.344	-	-	-	-	-	-	-	-
% LS lost to other predators	1	-1.849	104	0.067	1	0.286	102	0.776	-	-	-	-	-	-	-	-
% LS lost overall	1	-2.141	20	0.268	2	-2.62	14	0.020*	-	-	-	-	-	-	-	-

1 = Independent samples t-test, equal variances assumed (test statistic = t)
2 = Independent samples t-test, equal variances not assumed (test statistic = t)
3 = Pearson's chi-squared test for association (test statistic = *X2)*

* denotes significance at the $p<0.05$ level
** denotes significance at the $p<0.01$ level

(a) *Number and percentage of cattle lost to cheetahs, other predators and overall*

The number of cattle reported lost to cheetahs in the baseline survey ranged from zero to 12, with a mean of 4.3 annually, while in the later survey cattle losses to cheetahs ranged from zero to 15, with a mean of 0.9 per year. Those farmers reporting cheetah problems did lose significantly more cattle to cheetahs than those farms without a problem. The farmers that removed cheetahs also lost more cattle to cheetahs, although the difference was not statistically significant. These trends were the same in both the baseline and follow-up surveys.

The number of cattle taken by cheetahs was not significantly correlated with the number of cheetahs removed in the baseline survey ($r = 0.257$, $p = 0.135$), but it was significantly correlated in the later survey ($r = 0.248$, $p = 0.017$).

In the initial survey, reported cattle losses to other predators ranged from zero to 12, with a mean of 4.4, while in the later survey the range was from zero to 46, with a mean of 2.8 lost annually. In both surveys, farmers reporting cheetah problems had significantly more cattle lost to other predators than farmers without a problem, and the same was also true for farmers that removed cheetahs compared to those that did not. Overall, in both surveys, the mean number of cattle lost overall was significantly related to the incidences of both reported cheetah problems and removals.

The stocking rate information allowed the losses to be considered as a percentage of the total for the 1991-1993 dataset. When analysed this way, the percentage of cattle lost to cheetahs (range 0 – 3.3%, mean 0.67%)was not related to cheetah problems or cheetah removals. The percentage of cattle owned lost to other predators (range 0 – 6.0%, mean 0.7%) was not related to cheetah problems or removals, and overall the percentage of cattle lost in total was not found to be significantly linked to cheetah problems or cheetah removals.

(b) *Number and percentage of smallstock lost to cheetahs, other predators and overall*

The mean annual number of smallstock lost to cheetahs in the baseline survey was 5.2, and was not significantly related to the incidence of cheetah problems or cheetah removals. In the follow-up survey, an average of 1.3 smallstock were lost annually and showed a significant relationship both with cheetah problems and removals.

In the baseline survey, the number of smallstock lost to other predators (mean 6.5 losses per year) was not significantly linked to cheetah problems but did show a significant relationship with cheetah removals, with more smallstock being lost on farms that removed cheetahs. The later survey revealed no significant relationship between the number of smallstock lost to other predators (mean = 8.9) and either cheetah problems or cheetah removals.

The number of smallstock lost overall was not correlated with the number of cheetahs removed in the initial survey ($r = 0.408$, $p = 0.117$), but a relationship was evident in the later survey ($r = 0.320$, $p = 0.002$).

Overall, neither survey showed a significant relationship between the number of smallstock lost in total, to both cheetahs and other predators, and either cheetah problems or cheetah removals.

When, in the baseline survey, the number of smallstock lost was considered as a percentage of the total owned, no significance was found with cheetah problems or removals. This was true both for losses to cheetahs, losses to other predators and overall losses.

(c) *Number and percentage of livestock lost, to cheetahs, other predators and overall*

Farms reporting cheetah problems had significantly more livestock lost to cheetahs than farms that reported no cheetah problems. Although farms that removed cheetahs also had more livestock taken by cheetahs than those that did not, the difference was not statistically significant. These trends were found to be the same in both the baseline and the follow-up surveys.

In both surveys, the number of livestock killed by other predators was not significantly linked to either cheetah problems or removals. There was also no significant difference in the number of total livestock killed between problem and non-problem farms, or between removal and non-removal farms in either survey.

As expected from the patterns seen with smallstock and cattle losses, no correlation was evident between the number of livestock lost and the number of cheetahs removed in the initial survey ($r = 0.133$, $p = 0.586$), but there was a relationship in the later survey ($r = 0.344$, $p = 0.001$).

When considered as a percentage, the amount of livestock lost to cheetahs in 1991-1993, which ranged from zero to three percent with a mean of 0.7%, was not related to cheetah problems or removals. This was also true for the percentage of livestock lost to predators (range 0-6%, mean = 0.9%) and the percentage of livestock lost overall (range 0-6%, mean = 1.4%).

12.3.5 Perception and Tolerance Indices

As shown in Figure 12.3, the mean perception score of farmers who believed they had cheetah problems increased slightly from 1.6 in the baseline survey to 2.4 in 1999, while the level of tolerance also showed a slight increase from 2.7 to 3.3.

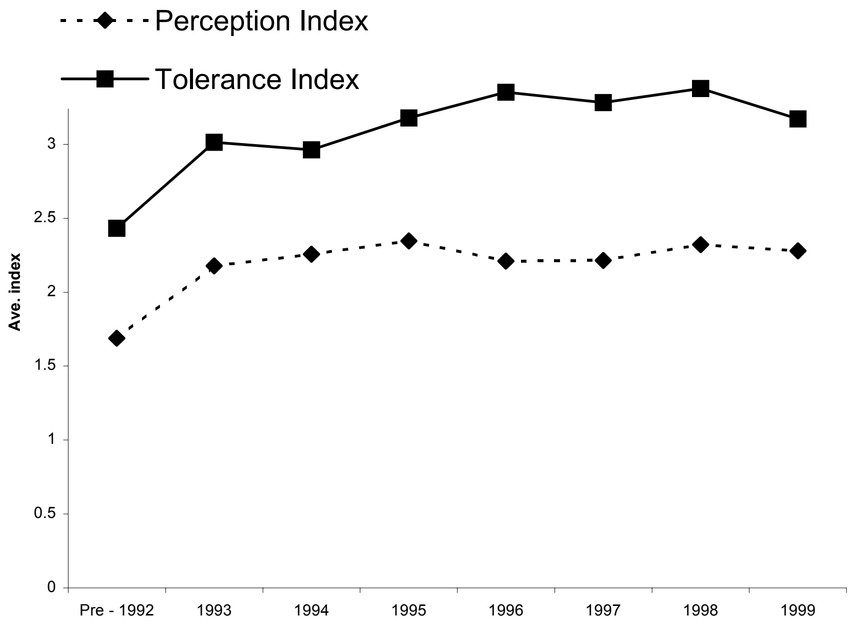


Figure 12.3 Trends in perception and tolerance indices through the study

Despite there being a significant increase in the perception of cheetah problems between the baseline and the follow-up survey (t = -8.218, $p < 0.001$), the tolerance level did not decrease significantly (t = 2.118, $p = 0.265$).

12.4 DISCUSSION

12.4.1 Attitudes and removals

Cheetah removals were found to be associated with perceived cheetah problems in both surveys, indicating that many farmers do not just eradicate them without at least believing them to be a problem. However, it was evident that many indiscriminate removals do seem to occur, as almost sixty percent of the farmers that did not consider cheetahs problematic still removed cheetahs. This percentage decreased in the later survey, but it was still a substantial proportion. This leads to the obvious question: Why remove something if it really isn't a problem? A logical explanation deals with traditional predator control attitudes common worldwide. Predators are often eliminated whether they are perceived as a problem or not. This same scenario is seen worldwide with other predators and reinforces the fact that inclusion and understanding of the human dimension must become one of the central tenets of carnivore conservation biology (e.g., Sillero-Zubiri and Laurenson 2001).

Relationships were found between cheetah problems and other predator problems, indicating that management practices on farms that have a cheetah problem may be relatively poor and more likely to suffer problems from other carnivores too. In general, however, the perception of having problems with other carnivores did not seem to influence cheetah removals, for instance by removing cheetahs as a reaction to losses by predators in general. The only exception to this was for jackals, as the incidence of jackal problems was found to be related to the removal of cheetahs.

A higher proportion of farmers reported removing cheetahs in the follow-up study compared to the baseline survey. It is difficult to gauge the extent to which this is an accurate reflection of later situation, however, due to the fact that over three quarters of the farmers did not answer this question in the 1993-1999 survey. If the farmers that removed cheetahs were the ones least keen to answer this question, it may be assumed that the proportion of farmers still removing cheetahs is indeed high. Alternatively, it may be that respondents left the answer blank for the number of cheetahs removed if they did not remove any, and in that case the numbers of removing farmers would have been relatively low in the later survey. Nevertheless, removals do continue, so there is a pressing need for continued education on the value of predators in the farmland ecosystem and ways of managing to farm alongside them.

Greater numbers of cheetahs were removed on farms where the farmer perceived having a cheetah problem, in both the initial and the follow-up surveys. This indicates that removals are not entirely indiscriminate, and that if work is done to reduce the perception of problems through proper management techniques, it is likely that removals could drop substantially. Indeed, the number of cheetahs removed annually per farmer had dropped considerably by the end of the follow-up survey, which may be attributable to the years of predator education presented to the Namibian farmers.

12.4.2 Characteristics of the farm

In the baseline survey, more game farmers considered that they had a cheetah problem compared to livestock farmers. This is to be expected given that hunting game is natural behaviour for cheetahs, whereas our examinations have revealed that cheetahs that resort to habitual livestock predation often show some physical or behavioural problem. Cheetah removals were also higher on game farms, revealing the importance of working with game farmers to find workable strategies that can reduce this level of removal. Well-maintained electric fencing can be effective at excluding predators from certain areas, such as game camps, but this is an expensive and high-maintenance solution. Research is currently underway into alternative strategies, including the potential use of ‘swing-gates’ in game fencing, to reduce the predator entry points being dug by warthogs, and encouraging the formation of conservancies for the shared, sustainable use of game rather than relying on isolated game camps.

It is striking that a greater percentage of both livestock and game farmers remove cheetahs than actually consider them to be a problem. The proportion of farmers removing cheetahs despite reporting no problem had declined in the follow-up survey, however, and this was true for both farm types. Again, this may be a result of greater awareness of conservation issues as a result of sustained predator education programs conducted by CCF across Namibia.

One of the most important characteristics of the farmland ecosystem influencing cheetah problems and removals was the presence of so-called ‘playtrees’. These are particular trees used as scent-marking locations, predominantly by territorial adult males (Marker-Kraus et al. 1996). Playtrees represent a vulnerable location for cheetahs, as they are often located where several cheetahs’ home ranges overlap (Gaerdes 1974, McVittie 1979, Morsbach 1987, Marker-Kraus and Kraus 1995, Marker-Kraus et al. 1996). The fact that many cheetahs come to such trees may be a reason for the increased level of perceived problems on farms with playtrees, although there was no evidence here for an actual increase in the level of livestock loss. Farmers tend to be aware of the presence of such trees on their land, and they are often used as opportunistic capture sites (Marker-Kraus and Kraus 1995), explaining the relationship with cheetah removals.

12.4.3 Stocking rates and livestock management techniques

The most evident factor here influencing cheetah removals was the density of game, with more cheetahs being removed on livestock farms with a high density of game. This may be linked to the fact that the livestock farms with playtrees had a higher game density, and on such farms the awareness of cheetah presence is likely to be higher, while the removal of cheetahs is also easier. The fact that there are more playtrees both on game farms, and on livestock farms with higher densities of game, indicates that cheetahs may be using the density of game as a selecting factor for determining which trees are favoured above others as ‘playtrees’.

Cheetah removals were also higher on farms that had large numbers of smallstock, and those that had dogs with the herds of smallstock. This may indicate a tendency towards using removal as a preventative measure, as neither factor was related to actually having a cheetah problem.

12.4.4 Livestock losses

The greater numbers of cattle lost on livestock farms where the farmer reported having a problem showed that there is often some basis for the perception of a problem. The lack of relationship with cheetah removals, however, suggests that removals may be on a more opportunistic basis rather than in direct response to losses. Livestock farmers that had cheetah problems also suffered more cattle losses from other predators, and these were related to cheetah removals. Especially on farms with playtrees, cheetahs are relatively easy to catch, and it appears that on livestock farms they may be captured in response to losses from other predators. It is interesting to note that although in the initial survey smallstock losses to other predators were also linked to cheetah removals, this was no longer the case in the later survey. This, again, may be a result of increased awareness of conservation issues amongst farmers, and possibly a greater ability to accurately determine the cause of livestock loss and address the factor that is actually responsible rather than removing cheetahs as a reactionary measure.

When examined as a percentage of the stock owned, there was no significant relationship between either cattle or smallstock losses and cheetah problems and removals.

This suggests that there may be some ‘threshold’ level of loss, e.g. 15 or 20 animals, which the farmer finds unacceptable, regardless of the size of his herd overall.

The fact that cheetah removals were actually correlated with the level of loss in the later survey may indicate that as awareness increases, removals become more closely linked to actual problems rather than done purely on an indiscriminate and opportunistic basis

12.4.5 Perception and Tolerance Indices

The perception and tolerance indices, along with the problem and removal trends in Figure 12.2, show that although cheetahs are increasingly perceived as a problem on the Namibian farmlands, the tolerance level for them has not decreased. This may be a result of effective conservation education, but, ultimately, farming is a commercial venture and financial incentives must be provided if such tolerance is to be sustained in the longer term.

To alleviate some of the problems with cheetahs associated with livestock and game-fenced farming in Namibia, we suggest the development of conservancies. Conservancies consist of adjacent farms that are joined together in broad units where natural resources are cooperatively managed using ecosystem-sensitive management plans. A constitution outlines conservation and management strategies, including sustainable utilisation of natural resources in conjunction with agricultural aims. Conservancy constitutions may include utilization of game for trophy hunting, meat, ecotourism, etc., and provide guidelines to assist farmers in coordinating the management and utilisation of species on the farms. Namibia’s constitution is one of the first in the world to encourage conservancies and sustainable utilization (Namibian Government 1990).

Another potential economic incentive would be to market ‘cheetah- or predator-friendly’ Namibian beef to the European Union and South African export markets. Farmers using non-lethal predator control methods could be certified as such and could charge a higher price for their livestock products.

The cheetah is recognized as a sustainable resource in Namibia (CITES 1992), where trophy hunting offers another opportunity to encourage tolerance toward cheetahs. For a fee, many farmers allow cheetahs on their land to be hunted. In 2000, cheetahs commanded approximately US$2000 each, whereas the average value of a cow was US$200. By increasing the cheetah’s value, they would become more valuable to farmers, who might then be less likely to kill them indiscriminately. Of course, a scientifically rigorous cheetah census and monitoring program is a prerequisite for responsible management of trophy hunting. Namibia has tried to encourage the implementation of a national carnivore census, but, due to farmers’ or hunters’ reluctance to participate and methodological difficulties, limited data have been collected to date.

Additionally, we have encouraged the development of ecotourism focusing on the Namibian farmland cheetahs. Due to the economic pressures of the past few years, most cattle farmers now have both hunting and ecotourism guests. The occurrence of playtrees on farms provides an ecotourism opportunity for visitors, as they often show signs of cheetahs, which increases the awareness both of the presence and ecology of an elusive and rare species. Several tour companies in Namibia are now marketing this opportunity. Encouraging such ecological awareness amongst tourists is an important component of predator conservation, both in Namibia and in other countries such as Kenya, where the tourist pressure on cheetahs and other carnivores can be intense.

12.5 CONCLUSIONS

Extensive livestock and game farming is the backbone of Namibia's agriculture, and the farmlands are home to the majority of the country's wildlife. Under these circumstances, seeking to isolate cheetahs from farmers and to conserve them in large numbers off farmlands in Namibia seems to be unrealistic. Therefore, our goal is a land-use strategy that integrates the requirements of agriculture with those of conservation, through which farmers become custodians, rather than adversaries, of the cheetah and its prey. While there are widespread perceptions that farmers are hostile to cheetahs, and that cheetahs are highly problematic to farmers, our questionnaires suggest that neither view is intractable. First, we have presented evidence that farmers are open to new information and approaches, leading them to change their behaviour and attitudes. Second, some aspects of the cheetah's reputation as a pest appear to be more imagined than real; for those problems that are real, we have found an encouraging number of farmers who are receptive to management proposals to mitigate the damage (for example the use of stock-guarding dogs: Marker-Kraus et al. 1996, Chapter 13). One particular difficulty in Namibia is that commercial farmers must face a drought cycle, which brings with it fluctuating densities of livestock and corresponding variation in the value of, and pressure on, game populations. Plans to conserve cheetahs must take into account such situations when financial strictures might make farmers less likely to be tolerant. As gaps in biological knowledge are plugged and conservation thinking is decreasingly constrained, the reality is that the human dimension is likely to be the determining ingredient of the success of any plan for conserving cheetahs in Namibia.

CHAPTER 13

EVALUATING THE EFFECTIVENESS OF USING LIVESTOCK GUARDING DOGS AS A METHOD OF CONFLICT RESOLUTION

This thesis chapter has been submitted as the following papers:

Evaluating the effectiveness of livestock guarding dogs as a method of conflict resolution. L.L. Marker, A.J. Dickman, R. Coppinger & D.W. Macdonald. Submitted to the *Journal of Wildlife Management.*

Survivorship of livestock guarding dogs: implications for human-predator conflict resolution. L.L. Marker, A.J. Dickman, R. Coppinger & D.W. Macdonald. Submitted to the *Journal of Wildlife Management.*

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CHAPTER 13: EVALUATING THE EFFECTIVENESS OF USING LIVESTOCK GUARDING DOGS AS A METHOD OF CONFLICT RESOLUTION

ABSTRACT

Evaluations were conducted on 117 livestock guarding dogs placed on Namibian farms between January 1994 and November 2001, as part of a study into methods of reducing conflict between humans and cheetahs outside protected areas. The dogs were scored for attentiveness, trustworthiness, protectiveness, care given and farmer satisfaction. Data regarding mortality, age at death and causes of death were also collected on all dogs placed, to investigate whether any action could be taken to reduce the level of mortality, thereby increasing the cost-effectiveness of this conflict resolution technique.

The dogs were very successful in terms of reducing livestock losses, with 76% of responding farmers reporting a large decline in losses since acquisition of a guarding dog. The dogs exhibited high levels of protectiveness and attentiveness, although trustworthiness was relatively low. Farmer satisfaction with the dogs was high, and the care given was also good. Attentiveness and trustworthiness declined with the age of the dog, as did the level of care given, while protectiveness and farmer satisfaction showed some increase with the age of the dog. There were no obvious differences in effectiveness between the sexes, while dogs placed on communal farms scored slightly better than those on commercial farms, and the dogs were most attentive when placed with mixed flocks of goats and sheep. The majority of dogs exhibited behavioural problems at some stage, particularly chasing game, staying at home and playing roughly with the livestock, but corrective training solved 61% of the reported problems.

During the study period, 42.7% of the dogs placed were removed from working situations. Deaths accounted for 80.3% of removals, while the remaining 19.7% were transfers out of the program. The most common cause of death for working dogs, especially young ones, was accidental, which accounted for 44.9% of reported deaths. Causes of death varied by farm type, and killing of the dog by the owner was relatively prevalent on commercial farms, being given as the reason for 24.5% of working dog deaths. The mean survival time as a working dog was 4.3 years, and dogs were removed at a significantly higher rate from commercial farms than communal farms. There was no significant difference regarding the survival distributions between the sexes, although farm type had some influence.

We conclude that with the correct training and care, livestock guarding dogs can be a successful and cost-effective method of livestock protection and could be a valuable tool in reducing human-predator conflict.

13.1 INTRODUCTION

Livestock guarding dogs have been used in Europe for centuries with the aim of reducing livestock losses from large carnivores (Laurans 1975, Sims and Dawydiak 1990). Many breeds have originated across Europe that share the same basic characteristics but have been selectively bred for efficiency under local conditions (Sims and Dawydiak 1990).

These different breeds share not only physical traits such as large size and a threatening bark, but also important behavioural characteristics, showing attentive, trustworthy and protective behaviour to the livestock with which they were raised. They are not bred to herd or move the stock, which can trigger a predator to attack, but instead place themselves between the stock and the threat and bark loudly. In extremis, the dog will attack, but often the mere presence of an intimidating guardian is enough to make the predator leave.

Human-carnivore conflict, however, occurs not just in Europe but worldwide wherever large predators exist in areas of human habitation (Frank and Woodroffe 2001, Sillero-Zubiri and Laurenson 2001). Such conflicts have often been resolved by attempting to eradicate the carnivore, and the success of this strategy has led to the local extirpation of many predators from areas that were once strongholds for the species, e.g. brown bears (*Ursus arctos)*, lynx (*Lynx lynx*) and wolves in Britain; wolves, grizzly bears and mountain lions (*Felis concolor*) in parts of the U.S.; and lions, wild dogs and spotted hyaenas in much of Africa. Today, however, many of the large carnivores causing conflict are locally or globally threatened, and alternative solutions must be found that reduce conflicts without endangering the predator population further. This is the case in

Namibia, where the only hope for maintaining a viable cheetah population in the long term is to develop and implement conflict resolution strategies that reduce livestock losses without resorting to the elimination of predators.

The Cheetah Conservation Fund (CCF) began a livestock guarding dog program in 1994, using the Anatolian Shepherd dog, which has been used in Turkey for over 6,000 years to protect sheep from wolves (Ancona 1985). Anatolian Shepherds were chosen in preference to the other livestock guarding dog breeds available as they are short-coated, well adapted to working in a hot, arid climate, and are heavy, imposing dogs that outweigh the majority of Namibian farmland predators (Richardson 1994). The objectives of the program were to evaluate how well these dogs could adapt to the Namibian environment and to examine their effectiveness in terms of reducing livestock losses.

It is important, however, that the dogs placed are not only efficient but also cost-effective. Farmers will only use a technique that has economic benefits, and for guarding dogs, the ability to deter predators and the longevity of the dogs used are key factors in determining success (Green et al. 1984). Previous studies have shown that dogs placed on farmlands tend not to live very long (Lorenz et al. 1986), and maximizing the lifespan of a working guardian is vital in order to provide farmers with the most economic benefit. I evaluated the survivorship of livestock guarding dogs placed on Namibian farms, and investigated the causes of death and removal, so that factors leading to the removal of these guardians could be better understood and prevented. The ultimate aim of this programme was to develop an appropriate method for diminishing the level of conflict with farmland predators, thus fostering a sustainable co-existence of predators and people.

13.2 STUDY AREA

The arid environment and the encroached bush in the study area meant that farmers had to use extensive farming methods, allowing their stock to range over large areas in the day before bringing them into a corral at night. The average number of goats on a livestock farm in the study region was 118, with an average of 78 sheep, and an overall mean of 198 head of smallstock per farm (Sartini 1994). The mean flock size in the study area was 134 head of smallstock, with 1.6 dogs accompanying each flock (Sartini 1994). The majority of communal farmers used an open grazing system with no fences except a livestock kraal near the homestead. Wildlife on the Eastern Communal lands occurs at low density, and the land has deteriorated through the communal farming system (Katzoa et al. 1993) changing from open savannah to thornbush savannah (Joubert & Mostert 1975).

13.3 METHODS

The study was started in 1994 with ten purebred Anatolians from the Birinci line that were imported to Namibia from the United States, while 145 dogs were subsequently bred on selected farms in Namibia in working environments. Two additional males were later imported for breeding purposes. All the dogs bred in-country were kept with their mother for 6-8 weeks, in a kraal with livestock in the vicinity of the puppies. Overall, 143 dogs were placed as working livestock guardians during the study period.

Farmers applied to us if they were interested in receiving a livestock guarding dog, and were then asked to complete a Potential Owner's Questionnaire to allow us to select the most appropriate farms on which to place dogs, with the aim of placing dogs on farms where livestock losses to predators occurred. Dogs were donated to farmers without a set charge, although some contribution towards the cost of breeding and care of the puppy was requested. The farmers signed a formal agreement before taking the puppy, but we retained ownership so that dogs could be removed if the care given was inadequate, and so that breeding and transfer of the dogs could be regulated. Farmers were given both written and verbal guidelines on the recommended care and training of the dog, what they should expect from the dog, and were encouraged to contact us if they had any subsequent problems or questions. Following placement, dogs were periodically monitored throughout their lives, using farmer questionnaires that were conducted either in person or over the phone, and regular visits were made to the farms to check on the condition of the dogs and provide advice. When behavioural problems were identified, more intensive follow-up studies were done to investigate the type of problem, its likely causes and potential solutions. Placements began on commercial farms in January 1994 and on communal farms in February 1997, and were ongoing at the time of analysis.

The performance of the dogs was evaluated on the basis of 334 questionnaires conducted on 117 dogs between August 1995 and January 2002, and the questions asked are shown in Appendix X. Following Coppinger & Coppinger (1980), three main indicators of performance were calculated: attentiveness, trustworthiness and protectiveness of the livestock guarding dog. Attentiveness was determined by examining whether the dog stayed with the herd all the time, whether it bonded with the livestock, if it appeared to be a part of the flock and if it showed suitably attentive and investigative behaviours towards the flock. Trustworthiness was evaluated through observations of whether the dog showed the expected guarding-dog behaviours, such as submission towards the stock, and whether it exhibited undesirable behaviour such as playing with and chasing the stock. Assessing protectiveness involved examining whether the dog showed protective behaviour, showed a capability to guard effectively, displayed an aggressive reaction towards intruders and investigating the level of impact that the dog had on stock losses since joining the herd.

The evaluations contained questions relating to each of these topics, and the responses were all scored on a scale from 2 (excellent) to –2 (very poor). Attentiveness, protectiveness and trustworthiness scores were then calculated by adding up the relevant scores, determining the number of questions asked on each topic, and the score obtained converted to a percentage of the maximum possible score. A care score was calculated from questions regarding the diet given, healthcare provided and access to water. Finally, a percentage satisfaction score was determined, based on whether the farmer thought that the dog was performing well, whether it was behaving as expected, whether there was a perceived economic benefit to having the dog, and whether the farmer would recommend the program. Not all the farmers answered all the questions, so there is some variation in the number of respondents for different variables.

Puppy aptitude tests were conducted on 39 of the puppies (23 males and 16 females) from three litters born since 1998, all of which later entered the program as working dogs. These tests were conducted at 6-9 weeks of age and each puppy was scored using the protocol defined by Sims and Dawydiak (1990). A score of 1 indicated submissive behaviour, 2 indicated intermediate behaviour and 3 indicated dominant behaviour, and these scores were examined in relation to the later performance of the working dog.

When removals from a working situation occurred, all possible attempts were made to determine the reason for the removal, and, in the case of death, the cause of death. Accidental deaths included drowning, snakebite, being killed by baboons, or hit by vehicles. Calculations of survivorship referred to the end of a dog's working life, regardless of whether the dog was removed to become a pet, education or breeding animal, or actually died. Survivorship analyses were restricted to dogs that had been placed as working guardians, and excluded other cases such as infant mortality.

Statistical analyses were performed using SPSS version 10.0 software (SPSS Inc. Chicago, USA). Normality of variables was tested using the Kolmogorov-Smirnov and Shapiro-Wilk tests, and where there was significant deviation from normality, non-parametric tests were used. These included the Kruskal-Wallis and Mann-Whitney U tests, while departures from expected ratios were analysed using chi-squared tests. For normally distributed variables, means analyses were conducted using the independent samples t-test, using Levene's test to determine the equality of variances. Correlations were investigated using Spearman's correlation coefficient, unless there was known to be a confounding variable, in which case partial correlations were calculated instead. Breslow's test (generalized Wilcoxon's) was used to examine the equality of survival distributions, and all tests were two-tailed unless otherwise stated.

13.4 RESULTS

13.4.1 Sample population

During the study, 12 dogs were imported while 145 were born in 15 litters to 6 sires and 7 dams. Overall, 143 were placed as guarding dogs and 65 died. The sample population on which the 334 questionnaires were conducted is shown in Table 2.3.1.

Table 13.1 The sample population of Namibian livestock guarding dogs that the 334 questionnaires were conducted on during the study, separated by farm type, age group and sex.

	Commercial				Communal				Unknown	
	Puppy (< 1yr)	Juvenile (1-2yrs)	Adult (≥2yrs)	Unk	Puppy (< 1yr)	Juvenile (1-2yrs)	Adult (≥2yrs)	Unk	Juvenile (1-2yrs)	Total
Female	44	29	47	5	22	3	3	1	0	154
Male	30	22	46	8	51	11	11	0	1	180
Total	74	51	93	13	73	14	14	1	1	334

13.4.2 Attentiveness

The dogs evaluated were highly attentive, with an overall mean attentiveness score of 85.9% (Figure 13.1).

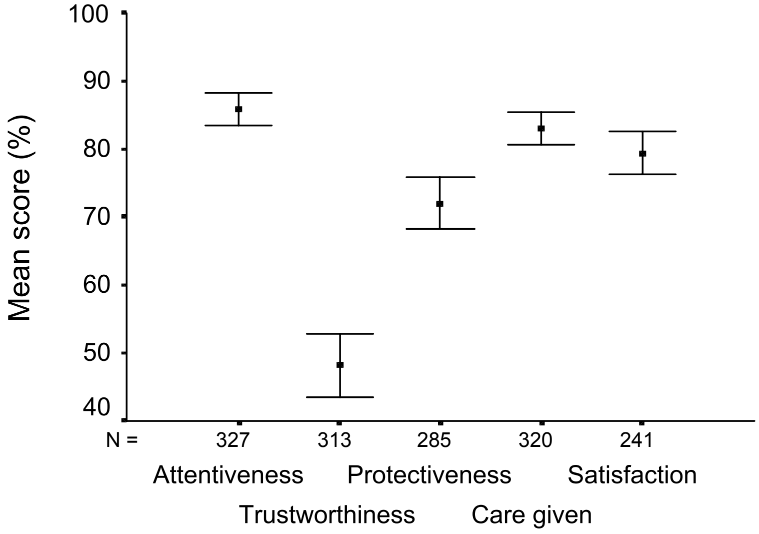

Figure 13.1 Mean scores for attentiveness, trustworthiness, protectiveness, care given and farmer satisfaction, calculated for livestock guarding dogs placed on Namibian farms. Error bars indicate 95% confidence intervals.

Over two-thirds of the responding farmers (69.9%, *n* = 114) claimed that their dogs stayed with the stock 24 hours a day, 89.1% (*n* = 188) reported that the dog appeared to be part of the stock, and 83.8% (*n* = 109) stated that the dog had bonded with the stock. In addition, 77.3% of respondents (*n* = 51) described the dog as attentive to the stock, 86.9% (*n* = 33) rated the attentiveness of their dog as good or excellent, and 98.3% (*n* = 59) reported that the dog had been accepted by the stock.

13.4.3 Trustworthiness

The trustworthiness of the dogs showed the most variation, and the mean trustworthiness score, at 48.2%, was substantially lower than the other scores attained (Figure 13.1). This reflected the fact that 22.5% (*n* = 27) of farmers reporting problems said that their dogs showed a tendency to chase, play with, or bite the livestock (see below). Despite this, over two-thirds of responding farmers (68.1%, *n* = 81) reported that their dog did show submissive behaviour towards the stock.

13.4.4 Protectiveness

The dogs scored highly on protectiveness, with an average score of 72.0% (Figure 13.1). Almost eighty percent of responding farmers (79.8%, *n* = 95) reported seeing effective guarding behaviour such as barking at or confronting predators, with 12.6% (*n* = 15) not being sure. Nearly half (45.9%, *n* = 73) of the farmers rated their dog's protectiveness as excellent, with a further 37.7% (*n* = 60) classifying it as good.

13.4.5 Care given

The care provided to the dogs was very high, with a mean care score of 83.0% (Figure 13.1). The diet given to 75.1% (*n* = 151) of the dogs was excellent, with a further 7% (*n* = 14) being fed diets of good quality. The most common diet was a mixture of maize meal, dog pellets and milk, which was the option chosen by 25% (*n* = 49) of the responding farmers. The next most common diet was as above but supplemented with cooked meat, and this was provided in 13% (*n* = 25) of the cases. Only 6.5% of the farmers (*n* = 13) fed their dogs unsatisfactory or poor diets, for example plain maize meal with no additional protein (3.6%, *n* = 7), or diets that included raw meat (2.6%, *n* = 5).

Almost all of the dogs (93.9%, *n* = 124) were fed at least twice a day and 82.4% (*n* = 14) had water freely available. The high level of care given was reflected in the condition of the dogs: 93.0% of the dogs (*n* = 159) were classified as being in good or excellent health.

13.4.6 Farmer satisfaction

The level of farmer satisfaction was high, with an overall mean score of 79.4% (Figure 13.1). Farmers' expectations of the program were usually met, with the majority of respondents (79.9%) reporting that the dog behaved as expected. In addition, 32.2% of responding farmers reported their dog's performance as excellent, with a further 43.9% classifying it as good. Almost 80% of respondents with herders said that the dog was working well with the herder, and overall, 90.4% of respondents said that they were confident with the behaviour of their livestock guarding dog.

13.4.7 Interactions between different variables

The variables described above are unlikely to be independent of one another (Table 13.2).

Table 13.2 Relationships (determined using Spearman's correlations) between the attentiveness, trustworthiness, protectiveness, farmer satisfaction and care given for the livestock guarding dogs studied on Namibian farms.

		% attentiveness	% trustworthiness	% protectiveness	% satisfaction	% care given
% attentiveness	r_s	1.00	0.27	0.28	0.48	0.20
	P	-	0.000**	0.000**	0.000**	0.000**
	N	327	308	283	236	317
% trustworthiness	r_s	0.27	1.00	0.23	0.36	0.99
	P	0.000**	-	0.000**	0.000**	0.084
	n	308	313	269	224	304
% protectiveness	r_s	0.28	0.23	1.00	0.41	0.09
	P	0.000**	0.000**	-	0.000**	0.132
	n	283	269	285	199	275
% satisfaction	r_s	0.48	0.36	0.41	1.00	0.21
	P	0.000**	0.000**	0.000**	-	0.002**
	n	236	224	199	241	228
% care given	r_s	0.20	0.10	0.09	0.21	1.00
	P	0.000**	0.084	0.132	0.002**	-
	n	317	304	275	228	320

** Correlation is significant at the 0.01 level (2-tailed).

Attentiveness, trustworthiness, protectiveness and farmer satisfaction were all linked to one another and showed some statistically significant relationships. The care given also showed positive relationships with all the behavioural traits, but the only statistically significant relationship was with attentiveness.

13.4.8 Changes in the level of livestock loss

The change in the level of reported livestock loss since acquiring a livestock guarding dog is shown in Figure 13.2. The dogs appeared to have a substantial impact on the level of livestock losses, as the majority of the farmers had high levels of losses before getting a dog, but after the placement almost three-quarters of farmers reported that they suffered no losses.

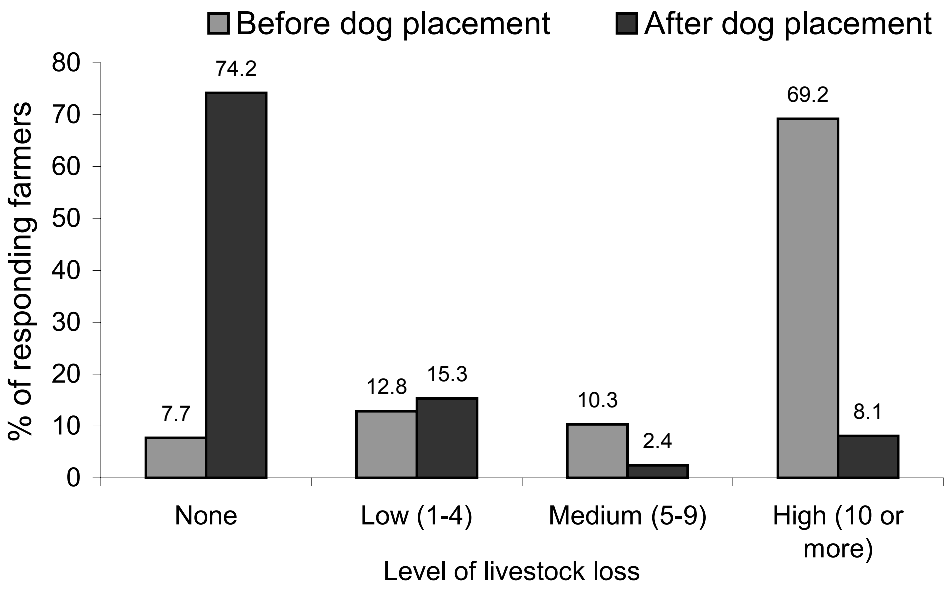

Figure 13.2 Change in the level of livestock loss reported by Namibian farmers, both communal and commercial, since acquiring a livestock guarding dog.

Overall, 76% of responding farmers reported a large decrease in the level of livestock loss since receiving a livestock guarding dog. Before placement of the dogs, the level of loss was greater on communal farms than commercial farms (z = -3.39, P = 0.001), but after placement there was no significant difference between the farm types. The change in loss, therefore, was significantly greater on communal than commercial farms (z = -2.52, P = 0.012), with almost all of the responding communal farmers reporting a large decrease in the level of livestock loss since placement of the dog (Figure 13.3).

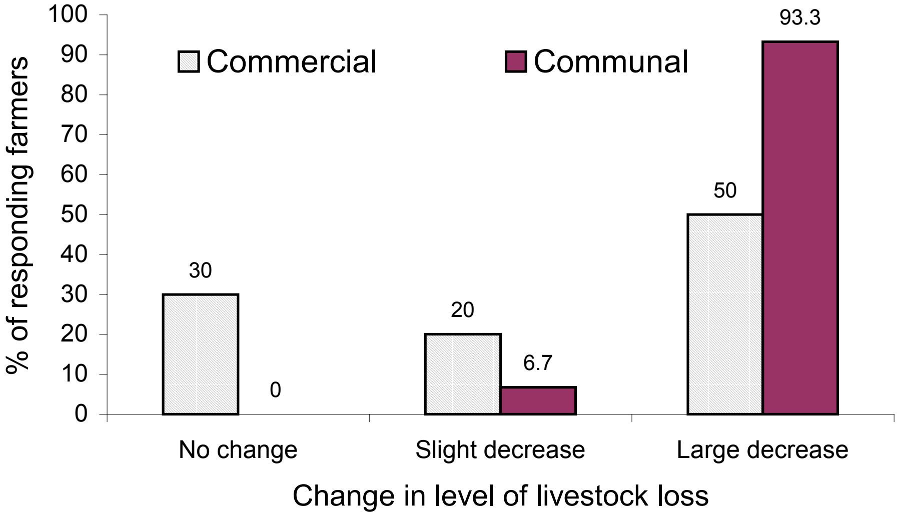

Figure 13.3 Magnitude of the change in level of livestock loss reported by commercial and communal Namibian farmers since acquiring a livestock guarding dog. A slight decrease was defined as changing by one category, e.g. from suffering a medium level of loss to a low level of loss, while a large decrease was defined as changing by two categories or more, e.g. from a high level of loss to low or no losses.

13.4.9 Factors influencing the success of the dogs

13.4.9.1 Age

The relationships between age and the variables scored are shown in Figure 13.4.

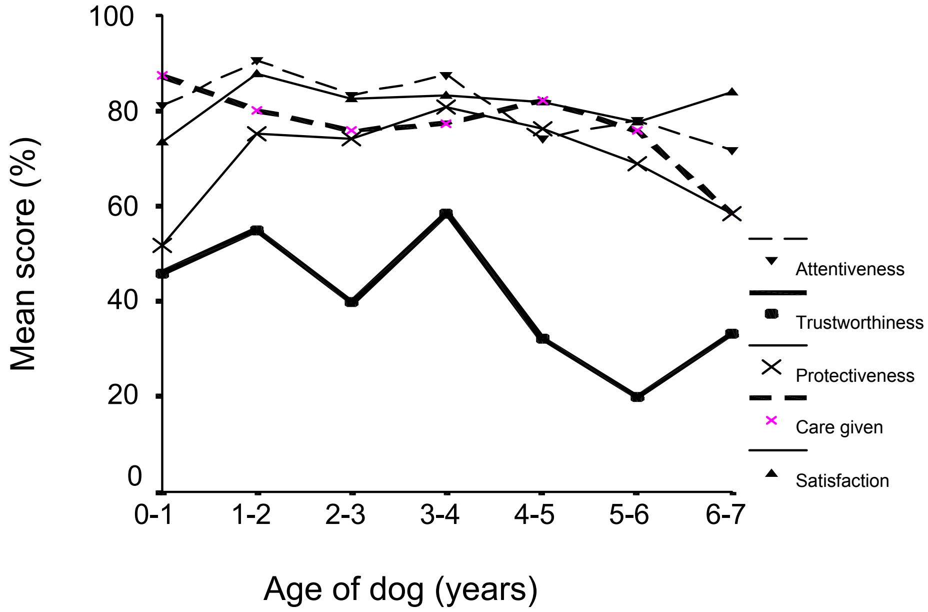

Figure 13.4 Changes in the mean scores for attentiveness, trustworthiness, protectiveness, care given and farmer satisfaction with age for livestock guarding dogs placed on Namibian farms.

Age of the dogs showed a negative relationship with attentiveness (r_s = -0.19, *n* = 314, *P* = 0.001), trustworthiness (r_s = -0.18, *n* = 300, *P* = 0.001) and care given (r_s = -0.31, *n* = 309, *P* < 0.001). The protectiveness of the dogs also decreased slightly with age, although the relationship was not statistically significant (r_s = -0.34, *n* = 273, *P* = 0.574) and the only factor that increased significantly with the age of the dog was farmer satisfaction (r_s = 0.16, *n* = 229, *P* = 0.013).

13.4.9.2. Farm type

The scores attained by farm type are shown in Figure 13.5. Whether a dog was placed on a commercial or communal farm had a significant bearing on its performance, with the dogs placed on communal farms showing greater levels of attentiveness (z = -2.71, P = 0.007) and trustworthiness (z = -3.33, P = 0.001), and the communal farmers being more satisfied with their dog's behaviour (z = -2.04, P = 0.041). The communal farmers also gave their dogs higher levels of care and their dogs were slightly more protective, although these differences were not statistically significant (care: z = -1.74, P = 0.083; protectiveness: z = -1.40, P = 0.163).

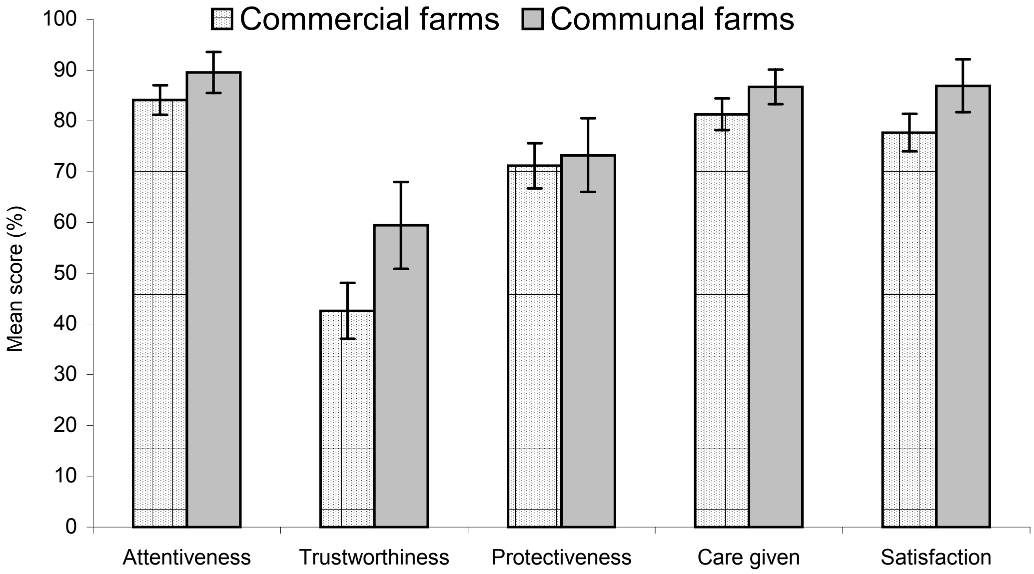

Figure 13.5 Mean scores for attentiveness, trustworthiness, protectiveness, care given and farmer satisfaction for dogs placed on commercial and communal farms in Namibia. Error bars indicate 95% confidence intervals.

The dogs on communal farms, however, were significantly younger at the time of the study than on commercial farms ($t = 8.35$, df = 315, $P < 0.001$), and, as shown above, age had a significant bearing on the dogs' performance. To account for this, performance was compared between farm types for puppies, juvenile and adult dogs (Table 2.3.3). The only significant differences once age was accounted for were that farmer satisfaction with puppies was higher on communal than commercial farms, and that the juvenile dogs were more attentive on communal farms. The puppies on communal farms also appeared to be more trustworthy than their commercial counterparts, although the difference was not quite statistically significant.

Table 13.3 Mean scores for attentiveness, trustworthiness, protectiveness, care given and farmer satisfaction, for livestock guarding dogs of different ages on commercial and communal farms. Mean scores for each trait were compared between farm types using two-tailed Mann-Whitney U tests.

		Commercial			Communal				
		Mean score	SD	*n*	Mean score	SD	*n*	*Z*	*P*
Puppy	Attentiveness	87.0	20.7	71	91.7	14.4	73	-1.06	0.289
	Trustworthiness	48.9	37.0	67	61.2	40.0	72	-1.90	0.057
	Protectiveness	65.6	38.2	53	71.0	39.2	70	-1.01	0.313
	Care given	87.7	20.8	70	91.2	13.9	73	-0.69	0.488
	Satisfaction	65.2	30.1	42	89.7	12.0	16	-3.47	0.001**
Juvenile	Attentiveness	84.9	19.1	49	100.0	0.0	14	-3.56	0.000**
	Trustworthiness	47.0	40.2	47	64.3	49.7	14	-1.51	0.131
	Protectiveness	76.8	27.6	37	83.3	25.7	13	-0.19	0.852
	Care given	78.4	24.9	46	77.9	21.7	13	-0.37	0.715
	Satisfaction	81.9	21.7	50	90.1	11.9	14	-0.95	0.344
Adult	Attentiveness	82.1	23.2	92	74.3	33.3	14	-0.58	0.559
	Trustworthiness	36.5	42.5	85	50.0	51.9	14	-0.80	0.422
	Protectiveness	72.6	27.4	86	77.9	23.2	13	-0.62	0.538
	Care given	78.7	23.2	92	72.3	19.7	14	-1.55	0.121
	Satisfaction	82.5	23.7	93	84.4	21.0	14	-0.11	0.913

**denotes significance at the $p < 0.01$ level

13.4.9.3 Sex

There were no significant differences between the sexes on either farm type for any of the three behavioural traits scored, or for farmer satisfaction, although better care was given to female dogs (Table 13.4).

Table 13.4 Mean scores for attentiveness, trustworthiness, protectiveness, care given and farmer satisfaction for male and female livestock guarding dogs on Namibian farms. Comparisons between the sexes were made on commercial and communal farms separately, and were calculated using Mann-Whitney U tests.

Farm type	Variable	Male	Female	*z*	*P*
Commercial	Attentiveness	85.0	83.4	-0.30	0.767
	Trustworthiness	40.1	44.7	-0.77	0.441
	Protectiveness	66.9	74.5	-1.71	0.086
	Care given	74.8	86.7	-3.20	0.001**
	Satisfaction	76.3	79.1	-1.67	0.096
Communal	Attentiveness	89.4	89.9	-0.06	0.950
	Trustworthiness	57.2	64.9	-0.76	0.447
	Protectiveness	73.3	73.1	-0.30	0.767
	Care given	85.2	90.2	-0.62	0.535
	Satisfaction	87.0	86.5	-0.15	0.883

**denotes significance at the $p < 0.01$ level

13.4.9.4 Stock guarded

Just over half of the surveys (50.2%, *n* = 115) were conducted on dogs placed with herds of goats, while 26.2% (*n* = 60) were placed with mixed flocks and 23.6% (*n* = 54) were placed with flocks of sheep. The attentiveness of the dogs on both farm types varied depending on the type of stock guarded (commercial: $\chi^2 = 8.89$, df = 2, *P* = 0.012; communal: $\chi^2 = 6.74$, df = 2, *P* = 0.034). In both cases, the dogs were least attentive when guarding flocks of sheep, and most attentive with mixed herds of goats and sheep. There were no significant differences, however, in trustworthiness, protectiveness or farmer satisfaction regarding the type of stock guarded.

13.4.9.5 Age at placement

The age at placement ranged from zero (in cases where the dog was bred and kept at the same farm) to 2.7 years old, with 91.8% of the dogs (*n* = 301) placed by 12 weeks of age. Dogs were placed at a younger age as the program progressed ($r_s = -0.259$, *n* =

328, $P < 0.001$) so the age of the dog at the time of the survey was controlled for during statistical analyses to remove any confounding effect. Age at placement appeared to have no effect on the resulting attentiveness, trustworthiness, protectiveness, farmer satisfaction or care given to the dogs on either farm type. Previous studies have suggested 16 weeks as a critical age to place a dog by, but no statistically significant differences were found here in performance between dogs placed under 16 weeks old and those placed over 16 weeks old.

13.4.9.6 Time with farmer

Again, older dogs are likely to have spent more time with the responding farmer, so age of the dog was controlled for in this analysis. Time spent with the responding farmer was not related to attentiveness, trustworthiness, protectiveness, farmer satisfaction or care given on either farm type.

13.4.9.7 Moving owners

Only a few (7.5%, $n = 25$) of the evaluations involved dogs that had been transferred between owners. Moving dogs between owners on communal farms had no significant effect on the performance of the dog for any of the variables measured, although on commercial farms transferred dogs were significantly less trustworthy than others ($z = -2.27$, $P = 0.023$). The dogs that had been transferred between owners exhibited a slightly higher frequency of behavioural problems than expected, although the difference was not statistically significant ($\chi^2 = 2.85$, df = 1, $P = 0.091$).

13.4.9.8 Presence of a herder

Over two-thirds of responding farmers (69.1%, $n = 85$) had a herder working with the dog at the time of the survey. Having a herder did not affect the performance of the dogs for any of the variables. The dogs that had been accompanied by a herder only for part of their working lives were slightly less trustworthy than other dogs ($z = -2.081$, $P = 0.037$), while having a herder throughout the dog's working life made no difference to performance.

13.4.9.9 Presence of other dogs

On both farm types, over a third of farmers had another dog with the same flock as the livestock guarding dog – on commercial farms the proportion was 42.6% ($n = 52$), and on communal farms it was 39.0% ($n = 23$). Having other dogs made no significant difference to the effectiveness of the livestock guarding dog on either farm type. The presence of other dogs negatively affected the attentiveness of commercial dogs, but the effect was not statistically significant ($z = -1.81$, $P = 0.071$).

13.4.9.10 Changes through the programme

As the program has evolved, more knowledge has been gained about how to work more successfully with the dogs placed. The litters born were numbered and placed in sequence, so the litter number reveals how early on in the program the dog was placed. Partial correlations, controlling for the age of the dogs, revealed that on commercial farms the protectiveness, attentiveness, trustworthiness and farmer satisfaction all increased with litter number, although none of the relationships was statistically significant. On communal farms, however, litter number was negatively related to protectiveness, attentiveness, trustworthiness and farmer satisfaction, although only the relationship with attentiveness was statistically significant ($r = -0.32$, $P = 0.041$).

13.4.10 Puppy Aptitude Tests

Thirty-nine dogs had puppy aptitude tests conducted on them and all were subsequently placed on farms, with a mean age at placement of 9 weeks. Twenty dogs (51.3%) were placed on commercial farms, 18 (46.2%) were placed on commercial farms and one was initially placed on a communal farm but was later moved to a commercial farm.

The mean test score attained by the puppies overall was 2.0, indicating that most of the dogs did not react in a particularly submissive or dominant way to the situations presented to them. Just over half of the dogs tested (51.3%, $n = 20$) were scored as intermediate on the majority of their tests, with 25.6% ($n = 10$) being scored as dominant in most situations, and the remaining 23.1% ($n = 9$) usually exhibiting submissive behaviour. Using the most common score attained, each puppy was categorized as being primarily submissive, intermediate or dominant. When the evaluations as working dogs were examined, there were no statistically significant differences regarding trustworthiness, attentiveness, protectiveness, care given or farmer satisfaction between the three groups, although the dominant puppies appeared to be slightly less trustworthy. There was no significant difference in age at evaluation between the three groups of dogs ($\chi^2 = 0.69$, df = 2, $P = 0.708$).

13.4.11 Behavioural problems

Almost all of the respondents (94.4%, *n* = 186) reported having had some sort of behavioural problem with their dog at some stage. The majority of farmers (68.1%, *n* = 113) had regular contact with their dogs, which makes identifying and correcting behavioural problems easier. Three-quarters of farmers with problems reported them to CCF, although the majority (68.6%, *n* = 48) waited until some time later rather than reporting them immediately. Thirty-nine farmers responded to the question regarding methods of correction used, and the majority of these (76.9%, *n* = 30) used the methods of correction advocated by CCF. Corrective training was found to be effective in 61% of cases, and 39.5% of farmers (*n* = 120) were having some sort of behavioural problem with their dogs at the time of the survey.

The problems reported at the time of the survey are shown in Figure 2.3.6. The most common problem reported overall was chasing game, which was cited as a problem in almost half the cases (44.1%, *n* = 53). Staying at home was reported in 37.5% of cases (*n* = 45), while 25% (*n* = 30) of the problems reported involved dogs that were harassing or killing livestock.

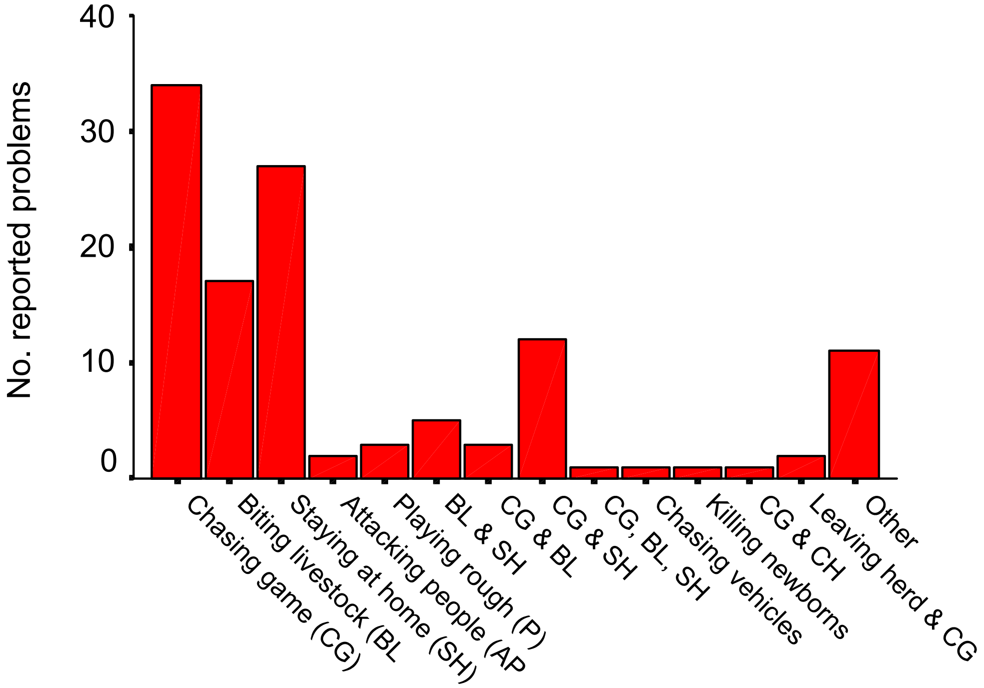

Figure 13.6 Frequency of behavioural problems reported by Namibian farmers as being exhibited by their livestock guarding dogs.

The behavioural problems varied by age group – the most common problem exhibited by dogs under a year old was harassing livestock, which was reported in 48% (n = 14) of cases. This harassment was also the most common reported problem in juvenile dogs, cited in 40.7% (*n* = 11) of cases, with chasing game being the next most prevalent complaint (33.3%, *n* = 9). Chasing game became more of a problem in adult dogs, where it was cited as the reason for 63.3% (*n* = 36) of the problems reported. The same overall patterns of behavioural problems were seen on both farm types, with chasing game accounting for most complaints, followed by the dogs biting livestock and staying at home.

When the dogs exhibiting behavioural problems were compared to the overall population, there was no significant deviation from the expected sex ratio ($\chi^2 = 0.10$, df =

1, $P = 0.758$), and transferring dogs did not seem to have a discernible influence either ($\chi^2 = 3.00$, df = 1, $P = 0.083$). Farm type did seem to be important, however, with dogs on commercial farms showing more behavioural problems than expected ($\chi^2 = 5.39$, df = 1, $P = 0.020$). This may be affected by the age of the dogs – as seen above, communal dogs were significantly younger than their commercial counterparts at the time of the survey, and adult dogs did show significantly more behavioural problems than subadults ($\chi^2 = 14.75$, df = 1, $P < 0.001$).

13.4.12 Mortality

During the study period, 65 (41.4%) of the 157 livestock guarding dogs involved in the program were reported to have died. The most common cause of death overall was accidents, which accounted for 35.4% ($n = 23$) of reported deaths. Just over a fifth of deaths (21.5%, $n = 14$) involved dogs being killed by their owner, while a further 9.2% of deaths ($n = 6$) were of dogs that were killed either by a neighbour or by another farmer. Infant mortality accounted for 20% ($n = 13$) of reported deaths, while poisoning and disease were both cited in 1.5% ($n = 1$) of cases.

When the analysis was restricted to the 143 dogs that were placed as working dogs, 52 (36.4%) of the dogs were reported to have died. Three of these deaths, however, involved dogs that had already been removed from the program, so overall, 49 (34.3%) of the dogs that entered the program were reported to have died while they were still active as guarding dogs. The sex ratio of reported deaths did not differ significantly from the sex ratio of dogs placed ($\chi^2 = 0.728$, df = 1, $P = 0.323$), or from a 1:1 ratio ($\chi^2 = 1.653$, df = 1, P = 0.199).

13.4.12.1 Age at death

Age at death was known for 46 (93.9%) of the dogs that died as working dogs, and ranged from 2.5 months to 5.8 years, with a mean of 1.7 years. Over a third of the deaths (39.1%, n = 18) involved dogs that were under a year old, while a further 30.4% (n = 14) of the deaths occurred in the second year of life. Overall, therefore, over two-thirds (69.6%, n = 32) of the reported ages for working dog deaths in the program involved dogs less than two years old. Figure 13.7 shows the age at death for working dogs, split by sex.

Figure 13.7 The percentage of deaths reported in yearly age groups, for male and female livestock guarding dogs that died while still active in Namibia as working dogs.

Age at death for male working dogs ranged from 3.4 months to 5.8 years old, with a mean of 2.0 years (*n* = 27), while for females the range was from 2.5 months to 3.0 years, with a mean of 1.2 years (*n* = 19). There was no significant difference between the sexes regarding age at death for working dogs (*z* = -1.51, *P* = 0.132).

On commercial farms, the age at death ranged from 2.5 months to 5.8 years old, with a mean of 1.8 years ($n = 41$). By comparison, the age at death on communal farms ranged from 3 months old to 1.7 years old, with a mean of 0.9 years old at the time of death ($n = 5$). This difference was not statistically significant, either overall ($z = -1.41$, $P = 0.158$) or when the analysis was restricted to dogs placed since 1997 ($z = -0.87$, $P = 0.384$).

13.4.12.2 Causes of death

Causes of death for working dogs, separated by farm type, are shown in Figure 2.3.8. Almost ninety percent of the deaths reported (89.8%, $n = 44$) were on commercial farms, which was a higher percentage than expected in relation to the proportion of dogs placed on commercial farms ($\chi^2 = 6.29$, df = 1, $P = 0.012$). However, communal placements began later than the commercial ones, so the older dogs were on commercial farms. When the analysis was restricted to dogs placed since 1997, when the communal placements began, commercial farms still accounted for a higher number of deaths than would be expected ($\chi^2 = 3.98$, df = 1, $P = 0.046$).

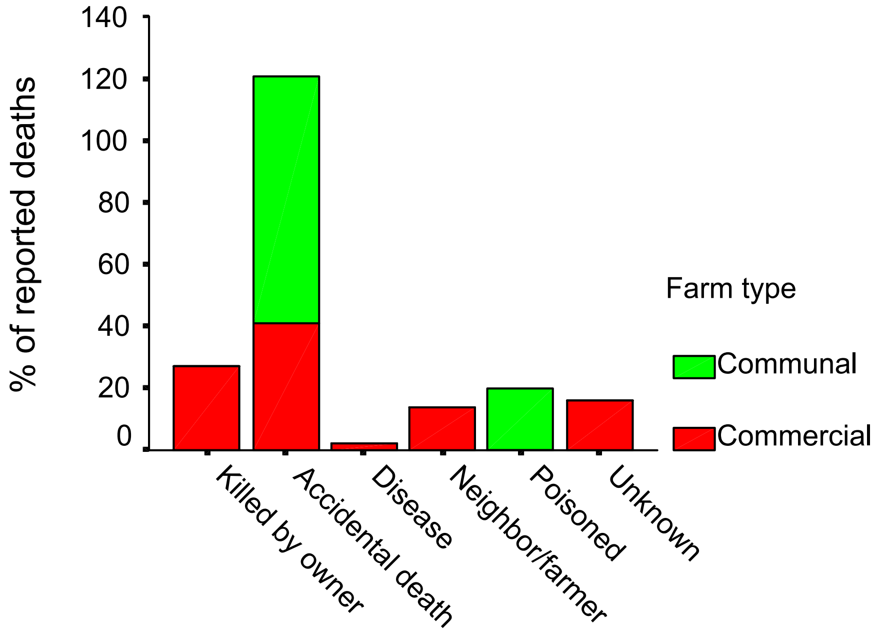

Figure 13.8 Reported causes of death for livestock guarding dogs that died while still active in Namibia as working dogs. Dogs that died on commercial farms are shown separately from those on communal farms, so the cumulative percentage of deaths attributed to one cause may exceed 100%.

Accidents were the single most common cause of death for working dogs, accounting for 44.9% (*n* = 22) of the deaths reported overall, and for 80% (*n* = 4) of the deaths on communal farms. A quarter of deaths (24.5%, *n* = 12) were due to the owner killing the dog (all of which occurred on commercial farms), and a further 12.2% of deaths (*n* = 6) involved dogs that were shot by a neighbour or another farmer, again all on commercial farms.

Figure 13.9 shows the breakdown of causes of death by age group. Accidents were the most common cause of death in young dogs, accounting for 55.6% (*n* = 10) of the reported deaths for dogs under a year old, and for 57.1% (*n* = 8) of the juvenile deaths. The proportion of accidental deaths had dropped to 28.6% (*n* = 4) for adult dogs, which was equal to the percentage of adult dogs that were killed by their owners.

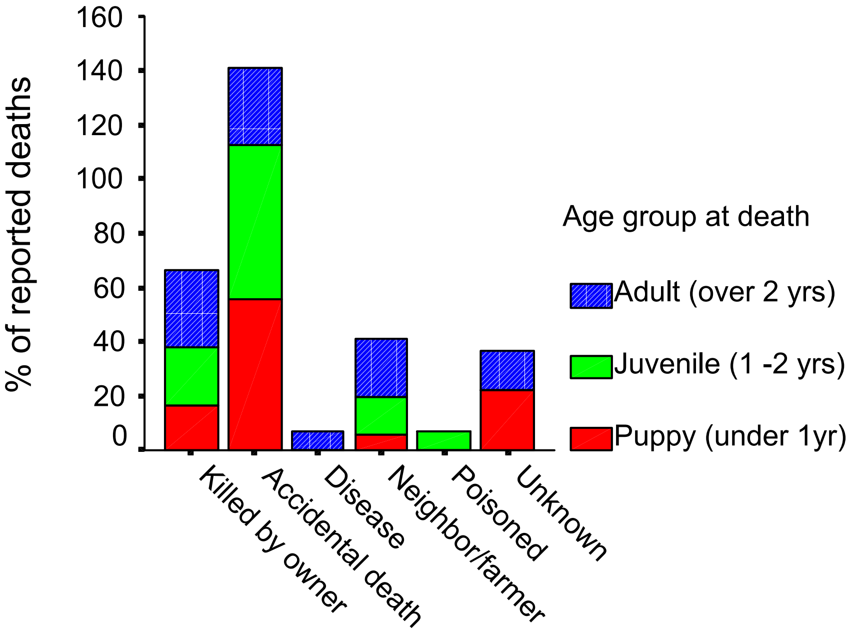

Figure 13.9 Reported causes of death for puppy (under 1 year old), juvenile (1-2 years old), and adult (over 2 years old) livestock guarding dogs that died while still active in Namibia as working dogs.

13.4.12.3 Overall survivorship of working dogs

In addition to the 49 dogs that died as working dogs, 12 dogs were removed from the working population (8.4% of those placed) and were transferred, either into pet situations, for breeding purposes or to be used as education animals. Combining the mortality data with these removals provides an overview of the average time that dogs spent in the program as effective working guardians. These deaths and removals of working dogs mean that almost half (42.7%, *n* = 61) of the 143 dogs that were placed as working dogs were ultimately removed during the study period. Just over 80% of removals were due to death, while 19.7% were due to transfers.

Time in the program could be calculated for 57 of the removed dogs, and this ranged from three weeks to 5.6 years, with a mean of 1.5 years. Although males spent slightly longer in the program before removal than females (means of 1.8 years for males and 1.1 years for females) the difference was not statistically significant ($z = -1.77$, $P = 0.077$). The mean time in the program before removal for dogs on commercial farms was 1.6 years ($n = 51$), while on communal farms it was 0.9 years ($n = 6$), a difference that again was not statistically significant ($z = -1.18$, $P = 0.237$).

Overall, the dogs placed had spent between 3 days and 7.6 years working as livestock guardians by the end of the study period, and 82 dogs (57.3% of those placed) were still working by the end of the study period. Male dogs placed worked on average for 2.4 years (n = 73), while the mean for females was slightly shorter at 2.2 years ($n = 66$). Overall, however, this difference was not statistically significant ($z = -0.871$, $P = 0.384$), and the overall mean for all dogs placed was 2.3 years ($n = 139$).

By the end of the study period, dogs placed on commercial farms had worked for an average of 2.5 years ($n = 102$). This was longer than those placed on communal farms, where the mean working lifespan was 1.8 years ($n = 37$), but the difference was not statistically significant ($z = -1.48$, $P = 0.139$). The first communal dogs were only placed in 1997, however, and if just dogs placed since this date were examined, the same trend was evident: although dogs on commercial farms survived slightly longer as working dogs than their communal counterparts (commercial: mean = 1.9 years, $n = 70$; communal: mean = 1.8 years, $n = 37$), the difference was not statistically significant ($z = -0.46$, $P = 0.644$).

These figures are obviously skewed by the fact that by the end of the study period many dogs had not been in the program for long, and those dogs may spend many more years as effective livestock guardians. The life table (Table 13.5), in which dogs that were transferred out of the population are treated in the same way as those that died, reveals the probable 'survival' as working dogs of those dogs placed during the program.

Table 13.5 Life table for livestock guarding dogs placed on Namibian farms, using one-yearly intervals. For this table, the 'death' of a working dog included removal from the program for other purposes, such as for a pet, breeding or exhibition animal, and was not solely restricted to actual mortality.

Interval (years)	No. entering interval	No. withdrawn during interval	No. exposed to risk	No. terminal events	Proportion terminating	Proportion surviving	Cumulative proportion surviving at end (A)	SE (A)	Probability density (B)	SE (B)	Hazard rate (C)	SE (C)
0	139	22	128.0	23	0.18	0.82	0.82	0.03	0.18	0.03	0.20	0.04
1	94	10	89.0	17	0.19	0.81	0.66	0.04	0.16	0.03	0.21	0.05
2	67	10	62.0	11	0.18	0.82	0.55	0.05	0.12	0.03	0.19	0.06
3	46	24	34.0	2	0.06	0.94	0.51	0.05	0.03	0.02	0.06	0.04
4	20	3	18.5	3	0.16	0.84	0.43	0.06	0.08	0.04	0.18	0.10
5	14	4	12.0	1	0.08	0.92	0.39	0.07	0.04	0.03	0.09	0.09
6	9	4	7.0	0	0.00	1.00	0.39	0.07	0.00	0.00	0.00	0.00
7	5	5	2.5	0	0.00	1.00	0.39	0.07	0.00	0.00	0.00	0.00

13.4.12.4 Survival distributions

The dogs had a 43% chance of making it to the fifth year of working life, and their overall survival distribution is shown in Figure 13.10.

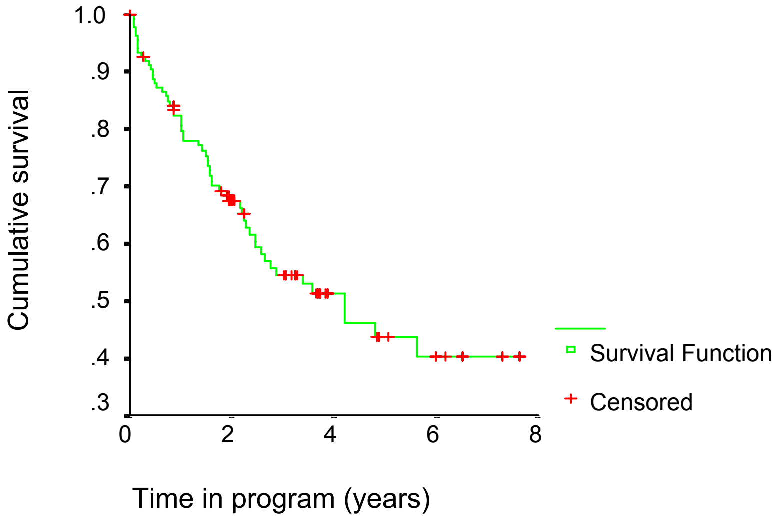

Figure 13.10 Kaplan-Meier survival function for all livestock guarding dogs that died while still active as working dogs on Namibian farms. Censored cases are shown on the survival curve.

This model predicted that the mean survival time for a dog placed into the programme would be 4.3 years, and there was no statistically significant difference in the survival distributions of males and females (Breslow's test = 0.26, df = 1, *P* = 0.612). When all dogs were included, the difference in survival distributions between dogs placed on commercial and communal farms was just statistically significant (Breslow's test = 3.86, df = 1, *P* = 0.049). When the analysis was restricted to dogs placed from 1997 onwards, when dogs were being placed on both farm types, the difference was not quite at the level of statistical significance (Breslow's test = 3.80, df = 1, *P* = 0.051). The survival distributions of dogs placed on commercial and communal farms since 1997 is shown in Figure 13.11, and reveals that the survival of adult dogs is better on communal farms, with the mortality rate dropping dramatically at around two years of age.

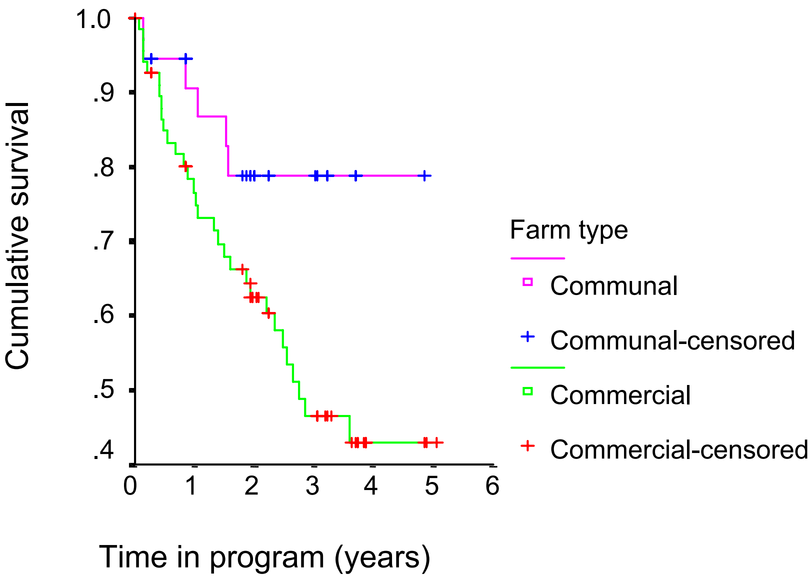

Figure 13.11 Survival distributions for livestock guarding dogs placed on commercial and communal farms in Namibia. Data were restricted to dogs placed in 1997 or later, to remove the confounding effect of earlier placements on commercial farms. Censored cases for each farm type are shown on the relevant survival curve.

13.4.13 Factors affecting the removal of dogs

Partial correlations, accounting for the age of the dog, revealed that the time spent in the program as a working guardian was significantly linked to the attentiveness of the dog ($r = 0.27$, $n = 89$, $P = 0.010$), as well as its trustworthiness ($r = 0.34$, $n = 89$, $P = 0.001$), and the satisfaction of the farmer ($r = 0.25$, $n = 89$, $P = 0.016$). Time in the programme was also positively related to protectiveness, although the trend was not statistically significant ($r = 0.19$, $n = 89$, $P = 0.079$). As expected, therefore, evaluations performed on dogs that were eventually removed showed that they were less attentive, protective and trustworthy than dogs that were not removed, had less care given and the farmer was less satisfied. The only differences that proved to be statistically significant, however, were the differences in trustworthiness ($z = 2.02$, $P = 0.043$) and farmer satisfaction ($z = -2.52$, $P = 0.012$).

Farm type had an important influence on the likelihood of removal – overall, dogs were removed from commercial farms significantly more often than expected ($\chi^2 = 8.72$, df = 1, $P = 0.003$). Even when the analysis was restricted to dogs placed since 1997, the level of removal was still significantly higher on commercial farms ($\chi^2 = 6.59$, df = 1, $P = 0.010$). The sex ratio of the removed dogs, however, did not differ significantly from that of the placed population ($\chi^2 = 0.45$, df = 1, $P = 0.503$).

13.5 DISCUSSION

13.5.1 Attentiveness

A high level of attentiveness is a key component of effective, successful guarding (Lorenz and Coppinger 1986, Coppinger et al. 1988). Inattentiveness has been linked both to the high level of mortality in juvenile livestock guarding dogs and to a reduction in protectiveness (Lorenz and Coppinger 1986, Lorenz et al. 1986). The dogs in this survey were highly attentive relative to those in most previous studies. In a 1983 study, Coppinger et al. found that only 37% of the Anatolians rated in the U.S. were described as being excellent or good in terms of attentiveness, although high levels of attentiveness were reported by shepherds using the same breeds of dogs in Old World countries.

In this study, attentiveness reached a peak at 1-2 years of age, and then declined with age. Livestock guarding dogs are expected to be attentive by around 1 year old (Coppinger and Coppinger 1980), as seen here, but the drop after 2 years is unexpected. The most likely explanation is the lower level of care provided to older dogs – care given was significantly linked to attentiveness, and a dog that is not cared for properly, for instance being fed an inadequate diet, may start wandering off from the flock and displaying other inattentive behaviours.

13.5.2 Trustworthiness

Trustworthiness proved to be the lowest-scoring of the behavioural traits, and also showed a large amount of individual variation. Other studies have reported higher degrees of trustworthiness for Anatolians than we found here (see Coppinger 1992a), although as a breed they have been scored as relatively untrustworthy (Green and Woodruff 1990). Trustworthiness was closely linked to other behavioural traits such as attentiveness and protectiveness, both here and in other studies (Lorenz and Coppinger 1986, Coppinger et al. 1988).

Livestock guarding dogs have been selectively bred to lack the ancestral sequence of operative predatory behaviour (Coppinger 1993a; Coppinger et al. 1988), and trustworthiness of livestock guardians has been defined as the absence of such behaviour (Lorenz and Coppinger 1986). In many cases, however, predatory behaviours are manifested initially as play, and can become reinforced into a problem if not corrected immediately (Coppinger 1991b). This type of predatory play behaviour was one of the most common problems reported to us, and has also been described in numerous other studies (Linhart et al. 1979). One proposal is for herders or handlers to accompany dogs, especially subadults, to enforce training (Coppinger 1991b), but in this study the presence of a herder was linked to a drop in the trustworthiness of the dog. This may be a result of unscrupulous herders encouraging the dog to chase game for meat, leading to the dog habitually leaving the stock and chasing wildlife.

Untrustworthy behaviour has been linked to a diet too high in calories for the dog, leading to the surplus energy being utilized in excessive play behaviour that can result in stock being harmed or killed (Muller-Schwartz et al. 1982, cited in Lorenz et al. 1986). Indeed, diet was proposed as a contributory factor to the low level of play observed amongst livestock guarding dogs in Italy compared to those in the U.S. (Langeloh 1991). The Namibian dogs, however, were often fed a low-calorie diet; yet still exhibited a high frequency of problems associated with excessive playing with the stock. The high-calorie commercial foods commonly available in the U.S. are seldom used for working dogs in Namibia, and the dogs tend to range over large areas on a daily basis, often in the heat, making excess energy an unlikely basis for the behavioural problems exhibited.

The trustworthiness of the dogs studied here increased from the first to the second year of life, slowed during the second year and then peaked at 3-4 years old. This increase in trustworthiness after the first 12 months has been described in several other studies, as dogs under a year old are particularly prone to exhibiting the type of rough play with the livestock that can lead to harm (Coppinger and Coppinger 1980, Lorenz and Coppinger 1986). The decline in the second year may be attributable to the fact that some dogs mature more slowly than others and exhibit ‘puppy’ play behaviour later in life. Despite reaching full height by around 18 months old, livestock guarding dogs mature slowly, with Anatolians having been estimated to reach behavioural maturity only at 18-30 months old (Green and Woodruff 1990). The later decline in trustworthiness of older dogs may be linked, again, to the decline in care given as dogs aged.

Dogs moved between owners on commercial farms were less trustworthy than those that had not been moved, and exhibited slightly more behavioural problems.

Careful selection should be made when choosing a second home for a livestock guarding dog, as the new owner may experience a higher frequency of problems, and close monitoring should be undertaken after any such transfers. Overall, however, moving owners had no negative influence on the performance of the dog in terms of protectiveness or farmer satisfaction, with transferred dogs proving to be as effective as those that had not moved. This strengthens the finding of other studies that moving dogs between owners can be a workable strategy, and that such dogs can still be successful guardians (Green and Woodruff 1990).

13.5.3 Protectiveness

The dogs studied here proved to be very protective, with almost all farmers having witnessed effective guarding behaviour. The mean protectiveness rating here (72%) was very similar to the 74% found by Coppinger et al. in 1988 for various breeds, with over eighty percent of responding farmers in this study rating their dog's protectiveness as good or excellent. Protectiveness reached a peak at 3-4 years of age, reflecting the finding that although dogs can show the precursors of effective guardianship earlier in life, the majority of dogs do not reach their true potential until they are fully mature (Lorenz and Coppinger 1986, Sims and Dawydiak 1990).

The high level of protectiveness was reflected in the large decrease in livestock losses reported by farmers after placement of the dog, a trend that has also been observed in numerous other studies (Coppinger et al. 1988, Green and Woodruff 1988, Andelt 1992, Hansen and Smith 1999). Despite their effectiveness, however, livestock guarding dogs are unlikely to eliminate losses entirely, and may be most effective when used as a part of a broader, mixed livestock management strategy.

13.5.4 Care given

Overall, the care given to the dogs was high, particularly on communal farms, which is probably because communal farmers reported suffering greater losses before getting the dog, and may therefore be more committed to the dog as a potential solution. The care given was positively linked to all the behavioural traits, and the concomitant declines in attentiveness, trustworthiness and care as the dog aged highlights the fact that all the desirable traits of a livestock-guarding dog are linked. The decline in the level of care given as the dogs aged is a cause for concern. It is critical that farmers do not become complacent once their dog has reached adulthood, as sustaining a high level of care is important for maintaining the long-term effectiveness of adult dogs.

13.5.5 Farmer satisfaction

Regardless of the calculated performance of the dog, the farmer must perceive a benefit to having a livestock guarding dog for the program to be truly successful. This seemed to be the case in this study, with over three-quarters of responding farmers classifying their dog's performance as very good or excellent. This was similar to the ratings given to livestock guarding dogs by Green and Woodruff in their 1980 study and higher than that reported by Coppinger in 1992 (Coppinger 1992a). This high level of satisfaction, coupled with the dramatic decline in livestock losses, may result in farmers regarding predators as less of a threat on their land and make them less inclined to remove them.

13.5.6 Interactions between different variables

The behavioural traits of the livestock dogs being attentive, trustworthy and protective were not independent (Coppinger and Coppinger 1980, Coppinger et al. 1983).

Traditionally, the literature has defined a successful livestock guardian as one that scores highly in all three areas, although this study shows that even dogs that exhibit behavioural problems and do not score highly on trustworthiness can be effective in reducing losses.

The importance of the level of care given highlights the fact that although livestock guarding dogs have long been selectively bred for certain specific behavioural traits, the environment must be adequate in order for these traits to be expressed fully. This interaction between a genetic predisposition to guarding and the local environment has been noted previously (McGrew and Blakesley 1982, Coppinger and Smith 1983) and is a very important factor in the development of a useful guarding dog.

13.5.7 Factors influencing the success of the dogs

13.5.7.1 Sex

We found no significant differences between the sexes regarding performance. This supported the findings of previous studies (Coppinger 1990, Sims and Dawydiak 1990).

13.5.7.2 Stock guarded

There was no statistically significant difference in effectiveness between dogs associated with different types of livestock, despite the fact that they were significantly less attentive when kept with flocks of sheep. Livestock guarding dogs have been successfully bonded to a wide variety of species, however, including donkeys, llamas, alpacas, turkeys, chickens, emus and ostriches (Coppinger 1991a, Coppinger 1992a), so the management and raising of the dog, rather than the species to be guarded, seems to be the most important factor in determining the eventual success of the guardian.

13.5.7.3 Age at placement

There has been much debate about the best age at which to place a dog with the livestock it is assigned to guard. Many authors assert that placing a dog with stock while it is still a young puppy (usually between 6-8 weeks old) is a key component of future success (Lorenz and Coppinger 1986, Coppinger 1993b, Hansen and Smith 1999). Some people believe that for maximal effectiveness a future sheep guarding dog should be suckled on ewes, but a study by Arons in 1981 found that this was not a critical stage for bonding.

In her 1991 report, Coppinger identified the 8-16 week old stage as being vital for 'secondary socialisation', when a livestock guarding dog will bond most successfully to other species and make firm attachments to them. She indicated that this 'critical window' closes at 16 weeks old, and that if a dog has not been socialized to livestock by then, it is unlikely to make a well-bonded guardian. Socialization to people during this stage detracts significantly from the dog's effectiveness (Hansen and Smith 1999).

Other studies, however, have shown that dogs introduced to stock later in life can be effective guardians (Coppinger and Coppinger 1980, Flamholtz 1986). Arons (1981) found that exposure to stock before 16 weeks old was not essential to success, while McGrew and Blakesley reported in 1982 that the ideal age for exposure of Komondor guarding dogs to livestock was 6-10 months old. We found no significant effect of age at placement on the resultant effectiveness of dogs.

13.5.7.4 Presence of other dogs

The effect of contact between livestock guarding dogs and other dogs has also been a source of some debate. Traditional use of the Old World breeds of livestock guarding dog often involved using more than one dog with the stock, and this is still the practice in many areas (Sims and Dawydiak 1990, Coppinger 1993b, Hansen and Smith 1999), with an older dog sometimes used to help train a younger dog (Lorenz and Coppinger 1986). It has been reported, however, that the presence of other dogs can cause the livestock guarding dog to develop undesirable tendencies such as roaming, leaving the flock, and exhibiting aggressive or predatory behaviour (Coppinger et al. 1983, Green and Woodruff 1990).

In this study, having other dogs working alongside the livestock guarding dog did not have a significant influence on performance. Working effectively despite the presence of other dogs is an advantage, because many farmers had several dogs working with the flock, although the negative impact upon the attentiveness of dogs on commercial farms highlights the need for close monitoring.

13.5.8 Puppy Aptitude Tests

Categorising the puppies as showing predominantly submissive, intermediate or dominant behaviour at a young age did not prove to be a useful indicator of later success as working dogs, although previous authors have suggested that the more submissive puppies may be the best suited to livestock guarding (Sims and Dawydiak 1990).

13.5.9 Behavioural problems

Behavioural problems were very prevalent amongst the dogs placed, although they still acted as effective guardians. The tendency to chase wildlife has been reported in other studies (Coppinger et al. 1988, Hansen and Smith 1999) and may be exacerbated on farms with an unreliable herder. The situation in Namibia is unusual in that there is a high density of wildlife on the farmlands, and an overzealous guardian may regard them as a threat to the stock and learn to chase them. An attentive herder can be very effective in recognising any such behaviour early and teaching the dog that game and other stock animals are not threats.

Harassment of livestock is also a well-reported problem with livestock guarding dogs, particularly subadults, where it is a damaging manifestation of play behaviour. The higher frequency of behavioural problems amongst adult dogs contrasted with the results of other studies (Coppinger and Coppinger 1980, Lorenz and Coppinger 1986, Coppinger 1992b), but may be linked to the declining level of care through time.

The use of a cumbersome ‘dangle stick’ attached to a dog’s collar has proved effective in curbing the desire to leave the herd and chase wildlife (Coppinger 1991b), while young dogs in particular must be closely monitored while with stock to ensure that any rough behaviour is noticed immediately and the dog sternly reprimanded.

Use of the suggested correction methods proved effective in the majority of cases, although the majority of farmers waited some time before reporting the problems they were observing. This time lag before seeking advice with behavioural problems is of concern, as rapid action is critical for successful correction (Coppinger 1992b).

13.5.10 Mortality

Although the mortality rate in this study is lower than the 48% reported for livestock guarding dogs used in the United States (Lorenz et al. 1986), it is still high, with over a third of the dogs placed dying during the study period, and almost half the working dogs being removed. Accidents and culling were both important causes of death, with factors such as disease being virtually insignificant. This is very different from the situation seen with domestic dogs but is similar to what was found in the American population of livestock guarding dogs (Lorenz et al. 1986). Accidents were found to be an important mortality factor, which was to be expected under the dangerous circumstances that working dogs are exposed to in Namibia, especially for young dogs, which are likely to be relatively inattentive (Lorenz and Coppinger 1986, Lorenz et al. 1986). Inattentive dogs were found to be more likely to be lost or killed in the U.S. study by Lorenz et al. (1986), and a similar relationship was found here, with dogs that were ultimately removed, by either death or transfer, being significantly less attentive than other dogs.

13.5.11 Factors affecting the removal of the dogs

It is important to note that the working lifespan of a guardian in this study was linked in particular to the farmer's rating of its trustworthiness and attentiveness, as well as its protectiveness and the farmer's overall satisfaction. However, research conducted on the dogs placed in Namibia showed that dogs do not tend to reach their full potential until they are fully mature, which in Anatolians can often take around 3 years (Green and Woodruff 1980). This reflects the findings of other studies, which have emphasized the fact that although livestock guarding dogs may show some precursors of effective guardianship while they are young, the full range of operative behaviour only manifests itself with adulthood (Lorenz and Coppinger 1986, Sims and Dawydiak 1990).

13.5.12 Causes of death

Culling accounted for almost a quarter of working dog deaths, lower than the 33% reported by Lorenz et al. (1986), or the 27% by Green and Woodruff (1990). Our research in Namibia revealed that the vast majority of dogs placed exhibited behavioural problems at some stage. Similar problems, especially with young dogs, have been reported in previous studies (Coppinger and Coppinger 1980, Lorenz and Coppinger 1986, Coppinger 1992b). The high level of culling suggests that farmers may be getting frustrated with such problems, and resort to culling the dog rather than investing time and energy in attempting to remedy the problem. This is supported by the fact that culling became more significant with adult dogs, the age group that in Namibia appears to give most problems. Our data indicate, however, that the majority of problems can be solved with suitable corrective training, and this fact, combined with the evidence that even dogs that exhibit some unwanted behaviours are usually very effective in reducing losses, should discourage farmers from readily culling a problematic dog.

Culling was only reported on commercial farms, which is probably due to the fact that dogs placed on commercial farms were perceived as being significantly less attentive and trustworthy than their communal counterparts, with their owners being significantly less satisfied. Culling by neighbours also accounted for several deaths on commercial farms, and this has been reported as a problem by previous authors (Green and Woodruff 1988). Neighbouring farmers may not realize that the dog is meant to be with the stock, and shoot it to prevent it causing problems. Dogs may also cause problems by being overly protective and becoming aggressive towards any neighbour's stock that they encounter, chasing game onto a neighbour's farm or visiting a neighbour's farm if one of their domestic dogs was in season.

13.5.13 Survival distributions

Survival distributions proved to differ slightly by farm type, with low adult mortality evident on communal farms. This reflected the different causes of mortality: accidents, which mainly affected young dogs, were the predominant cause of death on communal farms, while the culling of adult dogs influenced the survival distribution on commercial farms. This result was the opposite of that described by Lorenz *et al.* in 1986, as they found that survival distributions became very similar after 30 months of age, regardless of the farm management system used. Overall, we found that an Anatolian Shepherd livestock-guarding dog placed in Namibia was likely to survive as a guardian for just over four years, with farm type but not sex influencing the working lifespan. The dogs had a 43% chance of reaching 5 years of working age, which was better than in the U.S., where 50% of the dogs died by 18 months old if they were placed on ranches, and by 38 months on farm/ranches, the farming system most similar to that in Namibia (Lorenz et al. 1986).

13.6 CONCLUSIONS

Questioning farmers regarding the performance of their dogs is clearly a subjective way of collecting information, as the responses often depend as much on the perception of the farmers as the actual efficacy of the dogs. For a successful conflict resolution method, however, the perceptions of the people involved are more important than any objective calculation of performance, and therefore, even using these subjective responses, the placement of livestock guarding dogs proved successful in Namibia. Effective guarding is challenging in situations where the dog guards stock that ranges unaccompanied over large tracts of land (Hansen and Smith 1999), and this is often the case on the Namibian farmlands. Unlike breeds such as the Komondor, which tends to show site fidelity to a particular area (Linhart et al. 1979), the dogs used here proved their efficacy at protecting livestock even in circumstances where they often move several kilometres on a daily basis. Although livestock guarding dogs do require care, attention and training, the time spent investing in them is usually outweighed by the time saved in terms of livestock protection and predator control (Andelt 1992), and they have proved to be economic assets (Coppinger et al. 1988, Green and Woodruff 1990).

The decline in livestock losses reported since obtaining a guarding dog, and the high levels of protectiveness, attentiveness and farmer satisfaction, demonstrate that the dogs placed have worked well in Namibia. For a conflict resolution technique to be successful, it needs to be both efficient and cost-effective, and farmers will only use these techniques if there is a clear economic benefit in doing so. A working lifespan of 4.3 years, combined with the low initial outlay cost due to donation of the dogs by the Cheetah Conservation Fund and the resultant decline in livestock losses, mean that the livestock guarding dogs placed on Namibian farms are likely to be a substantial economic asset for recipient farmers. However, almost half of the dogs placed were removed during the study period, and this proportion must be reduced in order to make this management technique truly viable for farmers. The high level of culling and accidental deaths could be prevented with more farmer education and better care of the dogs, and with such changes, the use of livestock guarding dogs could prove to be a useful and economically viable conflict resolution technique. This strategy has valuable potential in terms of conflict resolution, diminishing livestock losses while still maintaining predators as an integral part of the ecosystem.

CHAPTER 14

GENERAL DISCUSSION AND CONSERVATION IMPLICATIONS

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CHAPTER 14: GENERAL DISCUSSION AND CONSERVATION IMPLICATIONS

14.1 Conservation strategies for Namibian cheetahs

The research findings in this thesis have provided detailed insight into various aspects of the Namibian cheetah, including its biology and ecology, and the major threats to its survival, within the complex arid farmland system it inhabits. Understanding the human/predator conflict problems within this system and identifying effective conflict resolution strategies are key elements to the cheetah's future in Namibia.

The need to conserve the cheetah does not come into the mind of most Namibian farmers who have lost livestock or game through cheetah predation. The farmer's interests are in economic gain, be it through the sale of livestock, or selling game as trophies to foreign hunters. This is the harsh reality for the cheetah today in many areas of Africa and in particular southern Africa and Namibia, its last major refuge (Marker and Schumann 1998, Nowell and Jackson 1996). Can the economic needs of the people be provided for, while at the same time the biological and ecological requirements of the cheetah be met? In this chapter, I consider how certain strategies can fulfil both cheetah and human needs, and whether Namibia can continue to maintain the necessary habitat for long-term cheetah conservation. While the questions I pose are interesting purely from a scientific standpoint, insights gained from such research may have conservation applications, and lessons learnt in Namibia may be applicable to cheetahs facing similar conflict elsewhere.

14.2 Habitat pressures

Namibian cheetahs have the largest home ranges of any cheetah population studied to date (Chapter 11) and this factor will affect their long-term survival on farmlands. Home ranges often cover over 10 farms (averaging 8,000 ha each), and the large home ranges are likely to be due to the increase in the bush encroachment from livestock overgrazing, exacerbated by drought cycles, which has reduced the density and changed the distribution of the prey (Chapter 11). Therefore, cheetahs need to cover larger areas in order to find prey. Bush encroachment is also responsible for reducing the carrying capacity of the farmland for livestock and wild game, which reduces farmers' economic gains (Bester 1996). Droughts also play a role in the reduction of game, as farmers catch or kill more of the game during these times to save pastures for livestock, and are also less tolerant of any conflict with predators if they resort to preying upon livestock (see Figure 1) (Marker-Kraus et al. 1996). In addition to these factors, native Namibians want greater access to land ownership, through land redistribution, while other farmers want exclusive rights to their game. The continued practice of game fencing farms reduces the movement of cheetahs through the farmland and, although increasing their potential for appropriate prey, game farmers have little tolerance for cheetahs on their farms (Chapter 3 and Chapter 12). This scenario will in the short-term place greater pressure on the habitat needs for cheetahs as well as reducing the prey available for cheetahs, thus increasing possible depredation of livestock by cheetahs, and therefore increasing the level of farmer-cheetah conflict.

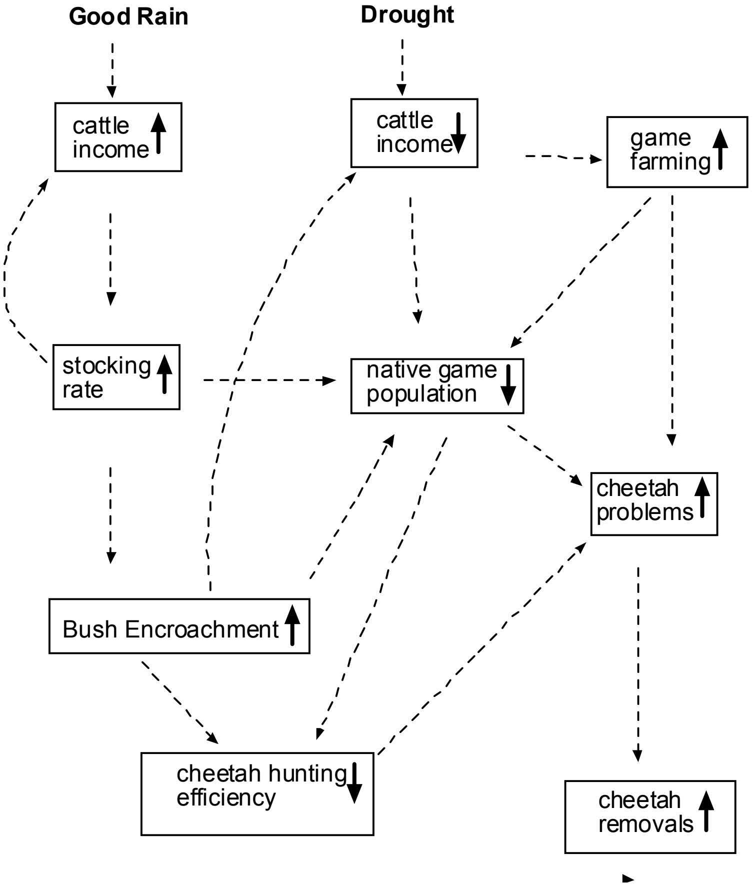

Figure 14.1 Conceptual model illustrating some of the linkages between rainfall cycles, bush encroachment and cheetah problems and removals on commercial farmland in Namibia.

In order to improve this situation, opportunities for Namibians to benefit from the land without compromising the survival of the cheetah must be developed. For successful conservation, cheetahs require large areas of intact habitat encompassing suitable and available prey, and there must be mechanisms that allow movement of cheetahs between regions to encourage gene flow (Chapter 5). Both the development of game farms and land redistribution will have negative effects on the cheetah's survival, and therefore require programmes and policies that will increase the chances of long-term species survival.

Countries surrounding Namibia have undertaken socio-political developments to redistribute existing farmlands (Johnson 2002), which, if copied by Namibia, mean that the available cheetah habitat will become fragmented and exacerbate the conflict that already exists between farmers and cheetahs. The pressures placed on the arid Namibian environment if redistribution without guidelines takes place will be detrimental to not only the cheetah, but also the Namibian economy as a whole. These increased pressures will increase bush encroachment, thereby reducing even more the productivity of the land and further impacting upon wildlife populations. In addition, as more settlement occurs on the farmlands, the potential for disease transmission increases, as cheetahs are increasingly likely to encounter domestic pets (Chapter 6 and Chapter 7).

Research from this thesis has shown that cheetahs and farmers can coexist if suitable strategies are employed (Chapter 12). The objectives of cheetah conservation must be to encourage practices that tolerate predators through restored habitat and healthy management of wild game populations, via a reduction in both game fencing and the stocking of non-native game species, as well as through the establishment of conservancies.

Strategies for cheetah survival on Namibian farmlands must include two important aspects, education and economic development. A multi-disciplined and integrated approach to educate the population and alleviate poverty is necessary and this may be done through training and creating entrepreneurship opportunities.

14.3 Education and training

Chapter 12 showed that the perceived threat to livestock or game from cheetahs was much greater than the actual threat they posed. Furthermore, there was no relationship between the percentages of livestock owned, livestock losses and cheetah problems and removals. The data suggested that there might be some ‘threshold’ level of loss, e.g. 15 or 20 animals per year to any cause, above which the farmer finds the situation unacceptable, regardless of the size of his herd overall, or reason for the loss. Changing the perception that cheetahs are a significant threat to livestock and game is clearly of vital importance if indiscriminate removal is to be reduced. An indication that the levels of tolerance towards cheetahs can be increased through awareness-building and education was shown by the increased proportion of tagged and radio-collared cheetahs farmers allowed to be released during the study (Chapter 3). Most of the releases were facilitated through long-term contact and work with farmers.

Recent findings (Orford 2002) support the findings in this thesis and indicate that extension-training programmes have positive effects and that continuing such programmes, and expanding them, would be beneficial. Therefore, opportunities for local Namibian capacity building must be encouraged, with the primary goal of showing how the linkage of sustainable practices provide direct and indirect benefits to communities. Programmes should be developed that train land managers in the environmental value of appropriate range management, which optimises the economic value of a sustainable, mixed wildlife-livestock system designed to avoid land degradation. Such programmes should focus on the benefits of natural resource management, attaching economic and cultural values to these resources, and raising awareness of ecological issues (Wildt and al. 2002). Educating Namibians about both consumptive and non-consumptive use through hunting and tourism and empowering local people so that they can be instrumental in responsible decision-making is of great importance.

A range of programmes are currently being developed through cooperation with the Namibian university and agriculture training colleges in connection with non-government organisations such as Cheetah Conservation Fund (CCF), World Wildlife Fund for Nature (WWF), the Smithsonian Institution's National Zoo and the Namibian Environmental Educators Network (NEEN) (Knausenberger et al. 1996, Marker et al. 2002, Wildt and al. 2002). They provide a means for students and new farmers to gain an understanding of business opportunity development through methods other than small plot management. Such investment in local people will promote sustainable farming practices, as well as developing alternative jobs (e.g. tour guides, arts and crafts manufacturers and other entrepreneurships) that will reduce the effects of habitat fragmentation in Namibia**.** Successful examples of local conservancies and trans-boundary land management planning are providing a basis for developing large-scale land management plans for the future.

14.4 Game-fenced farms and Conservancies

The availability of a wild prey base for the cheetah is critical in the issue of predator conflict in Namibia (Chapter 3 and Chapter 12). According to many Namibian farmers, maintaining a substantial population of wild game is the most important feature in reducing livestock predation in the survey area (Marker-Kraus et al. 1996).

The relationship between prey availability, livestock predation and feeding behaviour in cheetahs has important management implications. Scat analysis (Chapter 10) indicated that cheetahs preferentially take wild game species over domestic livestock.

Although domestic stock were evident in 6.4% of the scats, confirming that cheetahs do prey upon livestock, two-thirds of the available prey base on these farmlands is livestock (Marker-Kraus et al. 1996), suggesting that cheetahs appear to preferentially select game species. Farmers' reported information supports this finding (Marker-Kraus et al. 1996).

One of the biggest arguments against allowing cheetahs on game farms is the risk of them predating upon expensive, exotic game animals. Many game farmers stock exotic game species on their land for trophy hunters, and these animals are not only more valuable than indigenous game but may also be more liable to predation than the better-adapted indigenous species (Marker and Schumann 1998, Marker-Kraus et al. 1996). Although results presented from scat analysis suggest that cheetahs prey mainly upon indigenous game species, even a relatively low level of predation upon expensive, introduced game can have economic impacts upon farmers that they are unwilling to tolerate (Oli et al. 1994). Therefore, strategies to mitigate such economic losses could include fencing sections of farms, which contain expensive game animals. These initiatives should be a part of a game farm management plan and linked to permitting regulations as a part of government policy, as most game fenced areas are not conservation areas but are private businesses. Proposed game laws do stipulate that game fenced areas cannot eliminate wildlife indiscriminately for private gain (MET, 2002).

A longer-term, more sustainable strategy than fencing in small portions of land for game, might be the removal of game fencing and, instead, the development of cooperative game management areas in the form of conservancies (Marker-Kraus et al. 1996). Conservancies consist of adjacent farms that are joined together in broad units where natural resources are cooperatively managed using ecosystem-sensitive management plans. A constitution outlines conservation and management strategies, including the sustainable utilisation of natural resources in conjunction with agricultural aims. Conservancy constitutions may include utilisation of game for trophy hunting, meat, ecotourism, etc., and provide guidelines to assist farmers in coordinating the management and utilisation of species on the farms.

Namibia's constitution is one of the first in the world to encourage conservancies and sustainable utilisation (Namibian Government 1990). Presently there are a number of commercial and communal conservancies in Namibia. Proposed wildlife laws will provide incentives to farmers cooperating in conservancies to encourage large unfenced areas that will promote movement of game species, especially during droughts. Objectives for conservancy development should also include the connectivity of conservancies throughout the country therefore providing corridors for movement of wildlife (game and cheetahs) to ensure gene flow. Strategies such as these, whereby the sustainable utilisation of natural resources is encouraged, will be critical components of cheetah conservation outside protected areas.

14.5 Economic benefits

To reduce the levels of conflict between people and cheetahs in an unpredictable environment such as Namibia, there must be some economic advantages to maintaining cheetahs on private land. Potential economic benefits, as outlined below, include ecotourism, trophy hunting and incentives for predator-friendly meat. In addition, the benefits of habitat restoration could potentially benefit farmers, prey, livestock, and the Namibian economy as a whole.

14.5.1 Ecotourism

One of the most important characteristics of the farmland ecosystem influencing cheetah problems and removals was the presence of so-called ‘playtrees’ (Chapter 12). These particular trees are used as scent-marking locations, predominantly by adult males (Marker-Kraus et al. 1996). Playtrees represent a vulnerable location for cheetahs, as they are often located where several cheetah home ranges overlap (Gaerdes 1974; McVittie 1979; Morsbach 1987; Marker-Kraus & Kraus 1995; Marker-Kraus et al. 1996). Farmers tend to be aware of the presence of such trees on their land, and they are often used as opportunistic capture sites (Marker-Kraus & Kraus 1995) (Chapter 3). The fact that many cheetahs come to such trees may be a reason for the increased level of perceived problems on farms where they occur, although there was no evidence for an actual increase in the level of livestock loss (Chapter 12).

Over the last few years, the development of ecotourism focusing on the Namibian farmland cheetahs has increased with the world recognition of Namibia harbouring the largest population of cheetahs (Time 2000). Due to continued economic pressures, especially during years of drought, most cattle farmers now have both hunting and ecotourism guests. The occurrence of playtrees on farms provides an ecotourism opportunity for visitors, as they often show signs of cheetahs, which increases the awareness both of the presence and ecology of this elusive and rare species. Encouraging such ecological awareness amongst tourists is an important component of predator conservation, both in Namibia and in other countries such as Kenya, where the tourist pressure on cheetahs and other carnivores is very intense (Burney 1980, Wykstra-Ross and Marker 2001).

14.5.2 Trophy hunting

The cheetah is recognised as a sustainable resource in Namibia, and Namibia is one of three countries where a quota exists for the trophy hunting of cheetahs (CITES 1992). It has been proposed that trophy hunting offers an economic incentive for landowners to increase tolerance toward cheetahs.

Since the most common reported cause of death for wild cheetahs was shooting by livestock farmers, which accounted for over a third of all deaths, and human-caused mortality appeared to outweigh natural causes of death (Chapter 3 and Chapter 9), finding economic incentives to reduce indiscriminate killing of cheetahs is significant. Of the necropsies reported on cheetahs in this study, only seven (11%) were of trophy hunted animals (Chapter 3). The limited number of cheetahs trophy hunted can be of only minimal consequence to the population, especially when compared to the large numbers of cheetahs killed indiscriminately. For a fee, many farmers allow cheetahs on their land to be hunted. In 2000, cheetahs commanded approximately US$2,000 each, whereas the average value of a cow was US$200 (M.E.T. 1999).

The United States is the only country that does not endorse the CITES quota because of the rules of their Endangered Species Act (Marker-Kraus et al. 1996). However, Namibian and United States hunting organisations are placing increasing pressure on the United States to allow the import of trophies into their country (Marker and Schumann 1998). The United States Fish and Wildlife Department, however, has stipulated that without a scientifically rigorous cheetah census and monitoring programme, and incentives that actually prove that economic benefits for trophy hunting cheetahs will actually ‘enhance’ the survival of the species they will not issue import permits (Marker and Schumann 1998). The data in this thesis will be scrutinised by both countries' wildlife departments and will provide long-term base-line data for population monitoring.

14.5.3 Predator friendly meat

Despite the reduction in cheetah removals by Namibian farmers over the years and an increased tolerance towards them (Chapters 3 and 12), this trend could easily be reversed if economic conditions worsened in Namibia. Environmental fluctuations such as droughts affect the farmers' economic income and can create hardship due to losses from predation, resulting in an increase in predator removal rates. Providing economic incentives to farmers who practice livestock management that does not rely upon lethal predator control should be tied into a farmer certification process. One such incentive currently being researched is to provide a stable and profitable beef market to farmers who choose to manage their lands using predator-friendly management techniques that might include conservancy membership, limited stocking rates and habitat restoration. The certification of farmers and marketing of 'predator-friendly beef' would also increase the influx of foreign currency, which is important to the Namibian government, as these 'predator -friendly' certified farmers could charge a higher price for their livestock products.

14.5.4 Habitat restoration

Bush encroachment may cause additional conservation problems for cheetahs in Namibia as human-caused mortality is the primary source of mortality for Namibian cheetahs as discussed in Chapters 3 and 9, and the tolerance of landowners for predators may be further reduced due to the economic impact of the less productive, bush-encroached farmland.

The thickening and multiplication of endemic bush species is a desertification process that is a major environmental and economic concern for the Namibian government, as cattle farming is one of the main industries for the country: however it continues to lose over US$100 million a year from reduced grazing lands from bush encroachment (Bester 1996). In addition, bush encroachment creates problems for cheetah populations since it causes eye injuries because of thorns (Bauer 1998), generates changes in prey species abundance and distribution (see Appendix III) and reduces the tolerance of cheetah by farmers. As such, bush encroachment represents a major threat to cheetah existence on commercial farmland, as if left unchecked it is likely to result in the increased scarcity of preferred habitat patches, a reduction in prey biomass and a concomitant increase in human-caused mortality (Chapter 11 and Chapter 12).

A recently sponsored project in Namibia by the United States Agency for International Development (USAID), the Cheetah Bush Project of Namibia (2002), aims to address the Namibian bush encroachment problem by developing an eco-friendly industry that will selectively harvest invasive bush. Biodiversity measures of sustainable harvest, as predicted by the Forest Stewardship Council (FSC), will be used and the encroaching bush will be converted into clean burning wood fuel that can be marketed in the UK, Europe, Namibia and South Africa. Project FUEL aims to restore cheetah habitat, empower Namibians through capacity building and provide political leverage to implement sound conservation strategies.

Farmers participating in the project will profit by having their land harvested, thus opening land for grazing of both game species and livestock. In addition, farmers will be certified and monitored so that over-grazing does not take place. If the project is successful, it will provide eco-friendly jobs, restore habitat, increase the prey base for cheetahs, and increase the revenue for farmers. Through wood product marketing, the cheetah habitat needs will be highlighted, along with the certification of conservation farmers, and the economic benefits to the country will include foreign currency and job creation (Schumann and Marker 2002).

14.6 Modifying husbandry to reduce livestock loss

Livestock management world-wide draws heavily upon traditional methods of livestock husbandry of which removal of predators versus living with them was the accepted practice (Sillero-Zubiri and Laurenson 2001). Over the years many farmers are changing their views as predator species become increasingly endangered (Metzger 2002, Orford 2002). Providing alternative management strategies for farmers has become a major component of predator conservation strategies worldwide (Landry 1999, Marker-Kraus et al. 1996).

Namibian farmers have presented a variety of farm management techniques that have worked to reduce conflict with cheetahs and other Namibian predators. Some of these techniques include synchronising calving seasons within and between farms, using calving corrals, farming with more aggressive breeds of cattle, observing heifer's closer during calving times, and maintaining high concentrations of wild game species, and the use of livestock-guarding animals (Marker-Kraus et al. 1996, Metzger 2002, Orford 2002). Methods suggested for use by the farmers are inexpensive and easy to incorporate into farm management plans. The introduction of livestock guarding dogs in Namibia expanded upon an already existing livestock management practice (Marker-Kraus et al. 1996) which, however, had not proved to be as effective as using Anatolian Shepherds, from our finding in Chapter 13.

14.6.1 Use of Livestock Guarding Dogs

Anatolian Shepherds proved to be very protective, with over 76% of the responding farmers reflecting nearly a 90% decrease in livestock losses reported after placement of the dogs, which was also seen in other studies (Coppinger et al. 1988, Green and Woodruff, Andelt 1992, Hansen and Smith 1999). Despite their effectiveness, however, livestock guarding dogs are unlikely to eliminate losses entirely, and may be most effective when used as a part of a broader, mixed livestock management strategy.

The situation in Namibia is unusual in that there is a high density of wildlife on the farmlands, and an untrained guarding dog may regard them as a threat to the stock and learn to chase them. However, as with any management technique, the use of Livestock Guarding Dogs must be monitored and the dogs socialised with wildlife and other livestock by the farmer, so the dogs do not chase game or other livestock from the livestock that is in their care. In addition, proper care is critical for the dogs to withstand the harsh environment and lifestyle necessary to be an effective guardian. Increased education with farmers in proper care and training of the dogs could increase the working life-span of the dogs from the 4.3 years reported in Chapter 13, thus providing greater benefit to the farmer. The high level of satisfaction (over 90%) by the farmers towards the dogs, coupled with the dramatic decline in livestock losses, may result in Namibian farmers regarding predators as less of a threat on their land and making them less inclined to remove them. This study has provided evidence that the use of livestock guarding dogs can prove to be useful and economically viable as a conflict resolution technique in Namibia.

Although Livestock Guarding Dogs have been used in Eurasia for thousands of years, this practice has been all but forgotten (Ancona 1985). The use of the dogs since the 1970's has been studied in both North America and Europe with good success (Ancona 1985, Andelt 1992, Andelt 1999, Andelt and Hopper 2000, Coppinger 1990, Coppinger 1992, Coppinger 1993a, Coppinger 1993b, Coppinger et al. 1988) – and this first African study also provides evidence for their use as a conservation tool for other countries where predators are in conflict with humans.

14.7 Ongoing research

Long-term research presented in this thesis on Namibian cheetahs has provided fundamental insights into the species' population biology, and farmland ecology, as well as genetic health, disease risks and human impacts. Studying the Namibian cheetah has been difficult because of the limited availability of viewing it naturally in the wild. Studies have been opportunistic and at the whims of the farming community, highlighting the fact that conservation problems are not biological but have more to do with humans. However, on-going research is necessary to continue monitoring the species and the effects of conservation initiatives.

Biomedical research must continue to monitor the wild cheetah population's genetic and overall health. In addition, all opportunities should be taken to collect samples (blood, tissue and sperm) for a Genome Research Banking (GRB) programme that will provide important materials not only for captive breeding but long-term biomedical research (Bartels and al. 2001). Standardised methodologies identified in this thesis (Chapter 3 and Chapter 4) will assist other researchers in other countries to safely and effectively develop similar programmes to that developed in Namibia so that data are comparable. The opportunistic collection of bio-samples will allow both genetic and disease comparisons between regions to be analysed and the assessment of risks evaluated between and within countries. Genetic analysis of cheetahs from other range country's will provide necessary information for developing management recommendations (Breitenmoser and Breitenmoser 2001).

Of vital importance for the future of cheetah conservation must be the development of an objective population census technique to check the presence, and estimate the abundance, of cheetah. This is critical for monitoring and assessment of conservation measures. A proper methodology may include photo traps and hair snares, which may work with different kinds of olfactory lures and would include the use of genetic markers present in hair or faeces. Data from this thesis provides base-line genetic analysis of the Namibian cheetah population (Chapter 5) and their spatial movement (Chapter 11), which will prove valuable to continued research in Namibia and in other areas of the cheetahs' range.

As human land-use has the greatest impact on the distribution and abundance of cheetahs, monitoring several parameters, including population fragmentation, health, and habitat loss will be necessary so as to not miss important elements, which may affect species survival. Although maintaining cheetahs in protected areas will provide long-term habitat stability and, as such, are critical areas for the cheetah, conflict resolution between people and cheetahs will be a significant determinant for cheetahs in the future on private lands. As such, management of ‘problem’ animals will continue and necessary strategies must be implemented. Such strategies may include placing individuals in captivity, translocating animals, or re-introduction; each provides opportunities for species conservation but should be conducted under international guidelines (Marker-Kraus et al. 1996, Nowell and Jackson 1996). Overall, through collaborative research and multi-disciplined approaches, both within protected areas and on private lands, it should be possible to maintain large intact ecosystems for the cheetah, which is the most critical aspect of future conservation, both for cheetahs and for other large carnivores.

APPENDIX I

CURRENT STATUS OF THE CHEETAH

This Appendix has been published as the following paper:

Current status of the cheetah (*Acinonyx jubatus)*. L. Marker. 1998. In: Cheetahs as Game Ranch Animals. B.L. Penzhorn (editor). Onderstepoort, South Africa.

Appendix I: Current Status of the Cheetah

By: Laurie Marker, Director, Cheetah Conservation Fund, August 1998

ABSTRACT

The status of the cheetah, (*Acinonyx jubatus*), varies widely in the 32 countries listed in this report. All populations are classified as vulnerable or endangered by the World Conservation Union (IUCN) and are regulated by the Convention for International Trade in Endangered Species of Wild Fauna and Flora (CITES) as Appendix I. There are 13 countries listed in this report where the cheetah has become extinct during the past forty years. The wild cheetah is nearly extinct in Asia, with approximately 100 cheetahs surviving in small pocketed areas through Iran. Free-ranging cheetah inhabit a broad section of Africa including areas of North Africa, Sahel, eastern, and southern Africa. The two strongholds remain in Kenya and Tanzania in East Africa and Namibia and Botswana in southern Africa. Although there has not been a comprehensive survey of African cheetahs since 1975, there is a consensus that the cheetah population is declining throughout Africa. Since 1991, and up-dated regularly, Cheetah Conservation Fund has made contact with researchers in cheetah range countries and has tried to keep communication open about cheetah populations in those countries. From the information gathered, it is approximated that less than 15,000 cheetahs are found throughout their range, with a low estimate of 9,000 animals and an optimistic estimate of 12,000 animals. Perhaps for the cheetah, though, individual numbers of animals may not be the important point, but the numbers of viable populations still existing. Viable populations may be found in only half or less of the countries where cheetahs still exist. The cheetah has suffered a devastating decline of available habitat and prey, both necessary for its survival. In addition, the species does not do well in protected game reserves due to competition with other large predators, and the captive population is not self-sustaining but is maintained through imports of cheetahs from the wild population.

CURRENT STATUS

The status of the cheetah, (*Acinonyx jubatus*), varies widely in the 32 countries listed in this report. All populations are classified as vulnerable or endangered by the World Conservation Union (IUCN) and are regulated by the Convention for International Trade in Endangered Species of Wild Fauna and Flora (CITES) as Appendix I[16], which bans international commerce and sporting trophies. There are 13 countries listed in this report where the cheetah has become extinct during the past forty years. Only in two or three countries are cheetah populations considered only threatened and are killed legally if found to be in conflict with human interests. In 1992, at the CITES meeting, quotas were set for export of 150 animals from Namibia, 50 animals from Zimbabwe, and 5 animals from Botswana, as live animals or as trophies[16].

Five subspecies are considered valid by most taxonomists[80]. But this should be changed or condensed in the future, as the validity of the existence of sub-species is questionable. Genetic research has shown the genetic distance between two subspecies *A. j. jubatus* and *A. j. raineyi*, is trivial, 10 to 100 times less, for example, than the genetic distance between human racial groups[69].

The recognized subspecies are as follows:

NORTH AFRICA AND ASIA:

Acinonyx jubatus venaticus (Griffith, 1821): Algeria, Djibouti, Egypt, Mali (northern), Mauritania (northern), Morocco, Niger (northern), Tunisia, Western Sahara.

On the Asian continent: Afghanistan, India, Iran, Iraq, Israel, Jordan, Oman, Pakistan, Saudi Arabia, Syria, Russia and the Commonwealth of Independent States.

WEST AFRICA

Acinonyx jubatus hecki (Hilzheimer, 1913): Benin (northern), Bukina Faso, Ghana, Mali (southern), Mauritania (southern) , Niger, and Senegal.

CENTRAL AFRICA

Acinonyx jubatus soemmeringii (Fitzinger, 1855): Cameroon (northern), Chad, Central African Republic (northern), Ethiopia, Nigeria (northern), Niger (southern), and Sudan .

EAST AFRICA

Acinonyx jubatus raineyii: (Heller, 1913) Kenya, Somalia, Tanzania (northern), and Uganda.

SOUTHERN AFRICA

Acinonyx jubatus jubatus: (Schreber, 1976): Angola, Botswana, Democratic Republic of Congo (southern), Mocambique, Malawi, South Africa, Tanzania (southern), Zambia, Zimbabwe,

HISTORIC DISTRIBUTION

The cheetah was widely distributed throughout Africa and Asia. Cheetahs were originally found in all suitable habitats from the Cape of Good Hope to the Mediterranean, throughout the Arabian Peninsula, and the Middle East, from Israel to India and Pakistan, and through the southern provinces of the Russia and the former Commonwealth of Independent States.

Cheetahs have become extinct in at least 13 countries over the past 50 years. These countries and the year of extinction are as follows:

1. **Djibouti**: Believed to be extinct (not a party to CITES). Although in 1990 private people could still buy cheetah skins and live cheetah cubs in the market place. These skins and live cheetahs are thought to be coming from Somalia and possibly eastern Ethiopia[81]. Skins are still available in large numbers.

2. **Ghana**: Believed to be extinct. The Mole National Park had a small population in the reserve as of 1975[93].

3. **India:** Extinct in 1952. Last known cheetah found in Hyderadad in 1951 and Chitoor in 1952. Indians were importing cheetahs from Africa to be used as hunting leopards in 1929 due to the rarity of local cheetahs[29, 93, 18]. There has been talk of reintroducing cheetah back to India, but availability of prey

species and unsuitable habitat are limiting factors. A captive breeding effort may be launched.

4. **Iraq:** Extinct (not a party to CITES). Last sighting in 1950.

5. **Israel:** Extinct. Last report of cheetah was in 1956[47, 57]. There have been thoughts of re-introduction of cheetahs into the Biblical Wildlife Reserve of the Negev Desert[47, 57].

6. **Jordan:** Extinct. In 1935 many skins were still sold in Be'er Sheva'. May still have been found in Negev Desert, the Palestine Mountains, Sinai Desert, and Trans Jordan until the late 1940's[29].

7. **Morocco:** Extinct. Were still found up to 40 years ago in the mountainous regions of the country bordering the Sahara[93].

8. **Nigeria:** Extinct[20]. Skins are found for sale in the public market in Lagos which are probably coming from the countries north of Nigeria[87].

9. **Oman:** Extinct (not a party to CITES). Last sighting in 1968[93], probably lived on until the early 1970’s on the Jiddat al Harasis Plateau, Dhofar province[71].

10. **Russia and the former Commonwealth of Independent States**: Considered extinct as of 1989. No confirmed sightings in the past few years, a small expedition looked for cheetahs during the summer of 1989 but no animals or tracks were seen[22]. Cheetahs existed in many areas until the 1940's and 1950's when their prey, the goitered gazelle, was reduced drastically from over-hunting. Some cheetahs were believed to have moved down into Afghanistan when the goitered gazelles conducted a permanent move southward. In the 1960's and 1970's the last cheetahs existed in parts of Turkmenia and Uzbekistan (east and west of Murgab, east of the Caspian sea, and in the Badkhyz Preserve). In these areas they lived mostly on remnant populations of goitered gazelle and arkhar sheep, saiga antelope, kopet-dag sheep and hares[43, 73, 34, 22, 84, 17, 83]. In 1972 it was suggested that the cheetah be listed as a living monument and very strict international laws be proposed to save the last of the Asian cheetahs. The Commonwealth would like to reintroduce cheetahs into areas with sufficient prey populations such

as the Ustyurt Plateau of Uzbekistan. We have suggested that before they introduce African cheetahs they wait until the genetics have been run on the Asian cheetahs in Iran.

11. Saudi Arabia: Extinct (not a party to CITES).

Four cheetahs shot in 1950 near Saudi, Jordan, Iraq border intersection[29], last cheetah in the country probably lived on until the 1970's in the remote parts of Rubrquote Al-Khali desert[71].

12. Syria: Extinct (not a party to CITES). Oil pipeline worker killed one of the last cheetahs in the Syrian Desert in 1950 [29], the last cheetahs lived on until the 1960's in the eastern temperate Syrian steppe (Badiyat ash-sham) near Khabur river[71].

13. Tunisia: Believed to be extinct. Formerly found in the region of Chott el Djerid and the desert south of Tatahoume[93]. Last cheetah sighted and killed was in 1968 near Bordj Bowrgiba in the extreme south[19], 1990. Last Tunisian cheetahs lived until the 1970's in the Alfalfa-endash Acacia steppes at the North of the Hammada El Homra, near the Libyan border[71]. Re-introduction of cheetahs back into Tunisia may occur in the next few years in Bou Hedma National Park, which has good prey diversity[71].

CURRENT DISTRIBUTION

Reports on the status of cheetahs in the following countries are included in this document.

In Africa, Algeria, Angola, Benin, Bukina Faso, Botswana, Cameroon, Central African Republic, Democratic Republic of Congo, Egypt, Ethiopia, Gambia, Kenya, Libya, Malawi, Mali, Mauritania, Mozambique, Namibia, Niger, Senegal, Somalia, South Africa, Sudan, Tanzania, Tunisia, Uganda, Western Sahara, Zambia, and Zimbabwe.

On the Asian continent, Iran and possibly Pakistan.

POPULATION CENSUS

Censusing such an elusive species as the cheetah is very difficult, particularly since it is largely diurnal and widely roaming. Current information about the status of the cheetah in many countries, especially countries that have been engaged in long civil wars, is lacking. The following material is taken from recent literature, and where noted, from recent communications originating from researchers in the field.

From the information gathered, it is estimated that there are less than 15,000 cheetahs throughout their range, with a low estimate of 9,000 animals and an optimistic estimate of 12,000 animals. Perhaps for the cheetah, though, individual numbers of animals may not be the important point, but the numbers of viable populations still existing. Viable populations may be found in only half or less of the countries where cheetahs still exist.

ASIA

The wild cheetah is nearly extinct in Asia. Once widely distributed throughout Asia, the cheetah has suffered a devastating decline of available habitat and prey. A small number of Asian cheetahs still survive in small pocketed areas through Iran, and possibly in the boarding areas of Pakistan.

AFRICA

Free-ranging cheetahs inhabit a broad section of Africa including areas of North Africa, Sahel, eastern, and southern Africa. The two remaining strong-holds are Kenya and Tanzania in East Africa, and Namibia and Botswana in southern Africa.

There has not been a comprehensive survey of African cheetahs since 1975, when Norman Myers calculated the African population of cheetahs to be between 7,000 and 23,000 animals in 25 countries. The population of cheetahs in Africa had decreased by half since the 1960's[62]. On the basis of his research, he estimated that there would be less than 10,000 cheetahs by 1980. No new information is available to validate or refute this prediction, although there is a consensus that the cheetah population is declining throughout Africa.

Since 1991, and up-dated regularly, Cheetah Conservation Fund has made contact with researchers in range countries and has tried to keep communication open about cheetah populations in those countries[42, 71].

Until more recently, the cheetah has been generally considered to be an animal of open country and grasslands. This impression is probably due to the ease of sighting the cheetah in the shorter grass, and the long-term studies conducted on cheetahs in East Africa[14]. However, cheetahs use a wider variety of habitats and are often found in dense vegetation, ie. the Kora Reserve in Kenya, Botswana's Okavango Delta, and the Namibian farmlands[54].

As reported throughout Africa, cheetahs are not doing well in protected wildlife reserves due to increased competition from other, larger predators such as lion and hyenas[44, 61, 59, 54, 67]. Therefore, a large percentage of the remaining, free-ranging cheetah populations are outside of protected reserves or conservation areas.

There has been limited information from North or West Africa in the form of personal correspondence with field researchers and the cheetah's future in these areas is questionable[76, 19, 64, 26, 71]. Cheetahs continue to survive in small, pocketed groups in isolated areas throughout the Sahel. Most of these populations though can not be considered viable for long-term survival. Controlling factors are small populations, restricted habitats with a limited prey base, conflict with nomadic herders and wars that have supplied guns and ammunition to the populace, which then poach all forms of wildlife for food and profit.

A few regional studies do exist: David Burney reported on cheetahs in Kenya in 1980; P.H. Hamilton did a survey on the cheetah in Kenya in 1981; Norman Myers reported on the status of cheetahs in Africa, 1981; Dieter Morsbach reported on the cheetah in Namibia, 1986; Marker-Kraus et al, followed up on the Namibian cheetah in 1996; Vivian Wilson on the status of cheetah in Zimbabwe, 1985; and Christopher Stuart and Vivian Wilson on the status of cheetahs in southern Africa, 1988, and

Paula Gross conducted surveys in several African countries from 1989-1996.

In East Africa both Burney and Hamilton found the cheetah adapting in the agriculture land in the Masai Mara region outside the national parks and were co-existing with the Narok Masai, whose stock they left alone[12, 30]. In Southern Africa, it has been reported that cheetahs are killed regularly in farming areas due to their raiding of livestock and the attitudes of the farmers[61,91, 82, 11, 45, 53, 54].

Hamilton predicted that cheetah prospects in Kenya in the 1981-2000 period looked reasonable in the vast arid and semi-arid rangelands (primarily in the north) which would be the last areas to be developed. Hamilton's premise seems to be that the cheetah is a "remarkably successful predator...supremely adapted to surviving at low densities over large expanses of often waterless arid and semi-arid lands. Elsewhere the spread of commercial and group ranching is likely to bring the cheetah into greater conflicts with man. The spread of illegal and legal firearms is also likely to pose a threat so long as the cheetah's skin has any value[30].

Myers believes the cheetah is less adaptable. He says, "if its ecological circumstances start to experience persistent perturbation, the specialized nature of the species ecology and behavior, and its genetic make-up, could leave it little able to adapt to the disruptive conditions imposed by human communities in emergent Africa"[62].

In fact, the ability of the cheetah to adapt to a changing ecological system brought about principally by conversion of its preferred habitat to farmland is perhaps the critical question in estimating the population's survivability in Africa. In several studies over the last decade, the cheetah was reported to suffer declining numbers as land was developed and suitable habitat converted to farmland[93, 30, 62, 13, 91,, 61, 52, 54]. In Namibia, the population of cheetahs was halved by farmers from 1975-1987[61], and conflict with the farming community continues[54]. In 1996, the Cheetah Conservation Fund hosted a Population and Habitat Viability Analysis Workshop (PHVA), for Namibian cheetahs, in cooperation with the IUCN's Conservation and Breeding Specialist Group (CBSG), the Ministry of Environment and Tourism (MET) and local Namibia farmers. A working strategy was developed and formed the basis for MET's conservation strategy for cheetahs[66]. In 1997, a working group of MET and Namibian NGO's formed the Large Carnivore Management Forum. In 1998, a country-wide census for cheetahs will commence.

Wild cheetahs in Africa need help. Suitable prey is becoming scarce and habitat is disappearing. They are suffering from the consequences of human encroachment, from competition with other large predators in game reserves, and not least, from the complication of a limited genetic make-up. The wild population continues to sustain the captive population[49].

HISTORY OF THE CAPTIVE CHEETAH

The similar experiences of the world's zoos have reaffirmed the traditional difficulties of breeding cheetahs in captivity. Despite the capturing, rearing and public display of cheetahs for thousands of years, one litter was reported in the 16th century by the son of Akbar the Great, an Indian mogul. The next documented captive reproduction did not occur until 1956[55].

The history of the captive population of cheetahs as of 1955, when it became one of the major animals exhibited throughout the world, is presented in Table A1.1. From 1955 to 1994, the number of world zoos holding cheetahs increased from 29 to 211, and the number of animals during this 40-year period increased from 33 to 1218. Since 1955, 1440 cheetahs have been imported from the wild and there have been 2517 births and 3436 deaths[55].

Table A1.1 History of the captive cheetah population[55]

	1955-64	1965-74	1975-84	1985-94	Total
No. Facilities	29-92	87-80	87-150	152-211	
No. Cheetahs	33-206	215-401	423-848	856-1218	
No. Imports	142	491	419	388	1440
No. Births	16	178	967	1356	2517
No. Deaths	121	382	1244	1689	3436

The captive population as of 31 December 1996, was 1217 (608 males, 602 females, 7 unknown) animals in 240 facilities in 50 countries[49]. Of the 1217 animals, 27% were wild-caught and 73% captive born[49]. The captive population is currently maintained by a combination of imports and captive breeding[49].

The breeding programmes of our world's zoos, though, are not self-sustaining. Data indicates that a high proportion of cheetah propagation has occurred in a handful of the zoos with a majority of these facilities having only limited success; and half of the successful breeding facilities have had only a single breeding pair, or a single male or female. The captive population has had a low effective breeding size (N_e), 17% in 1994[55]. The fecundity of wild-caught versus captive-born animals is higher than captive-born animals and both are low, 17% and 9% respectively

STATUS OF THE CAPTIVE SOUTH AFRICAN CHEETAH POPULATION

As of 31 December 1996, the southern African cheetah population represented 30% of the captive world population[51]. South Africa has the only recognized breeding facilities in Africa. The progress achieved in acquisitions and breeding, as well as the incidence of mortality and sales for the South African captive cheetah population from 1970 to 1996 are presented in Table A1.2.

Table A1.2 History of the South African captive cheetah population[51].

	1970-975	1976-1980	1981-1985	1986-1990	1991-1996	Total
No. Imported	29	26	31	82	76	244
No. Births	37	184	127	133	291	772
No. Deaths	23	88	78	111	197	497
No. Exports	0	29	49	83	116	277
No. Sales	0	5	16	17	57	95
No. Facilities	4	5	9	12	11	
No. Alive at end of Period	46	143	204	166	221	

The number of facilities holding cheetahs has varied between 4 in 1970 to 11 in 1996. A summary of the numbers of imports and captive births from 1970 to 1996 is presented in Table A1.2. In total, 244 animals have been imported from the wild into South Africa, 29% have come from South Africa and 71% have come from Namibia. There have been 772 captive births in 254 litters, 497 deaths occurred and 277 animals were exported out of the country's recognized South African population. Within South Africa, 95 animals were transferred, primarily due to the creation of the new Hoedspruit cheetah breeding facility[51].

Examination of Table A1.2 shows that the majority of the increase in the captive population prior to 1985, when the population reached 204 animals, can be attributed to captive births. Prior to 1985, deaths and exports remained relatively low in comparison to births. From 1986 to 1996 deaths and exports increased to off set the population growth from births during those same years. Therefore, from 1986 to 1996 the captive population increased primarily due to imports, as during this time 65% of the total wild-caught animals (primarily from Namibia) were imported into South African facilities. As of 31 December 1996, the population was 262 (124.138) animals in 12 facilities, of which 30% were wild caught and 70% were captive born[51].

REGIONAL BREEDING PROGRAMMES AND GLOBAL CAPTIVE MANAGEMENT

Regional breeding success is important to monitor as the need for cooperation increases in order to facilitate movement of animals within the regions. The success of the individual regions is important in relation to the number of animals actually living in the population. In 1996, 30% of the world's captive population was in southern Africa, of which 41% were wild-caught animals[49]. By comparison, 26% percent of the 1996 population was in North America and 2% of these were wild-caught animals. A larger percentage of the North American facilities were reproductively successful in part due to the American Zoo Association's (AZA) Species Survival Plan (SSP) cooperative management programme which was developed in 1984.

Internationally, fourteen facilities (15%) have had continuous breeding success and have produced 63% of all cubs born in captivity[55]. Thus, a relatively small number of cheetahs have made a disproportionately large contribution to the captive population gene pool, for example 8 males have sired 21% of all cubs born and 12 females have produced 24% of all cubs born[55]. Several of these breeding animals are from breeding facilities in South Africa and they have produced 28% of the captive births in the world[55].

There is a substantial need to continue enhancing captive management to ensure optimal captive breeding. The implementation of management programmes such as the African Preservation Programme (APP) within the Pan African Association of Zoos, Aquariums, and Botanical Gardens (PAAZAB) are designed to facilitate cooperative management to the benefit of the population as a whole. As free-ranging populations of cheetahs continue to decline, and a large amount of genetic diversity of the wild population is lost, the captive and wild populations should be managed in cooperation. In the future, in the absence of further imports from the wild, the size of the world's captive population could be expected to decline, unless there is continued improvement in captive breeding efficiency. This trend, coupled with the continuing decline of the wild population, leaves the species extremely vulnerable.

CONSERVATION

No one knows what constitutes a minimum viable population for wild cheetahs. Unquestionably, the larger the population and the more broadly it is dispersed, the better placed it will be to avoid genetic failings and to endure localized epidemic mortality or widespread episodic catastrophe.

An important factor that must be taken into account, when considering the long-term conservation of the cheetah, is its lack of genetic variation. In 1981 an extensive genetic and physiological analysis of captive and free-ranging cheetahs revealed that the cheetah appears to be unique among felids and other mammals in having an extreme paucity of genetic variation[68]. The combined genetic, reproductive, and morphological data places the cheetah in a status similar to deliberately inbred mice or livestock, and prompted the hypothesis, that in its recent natural history (perhaps dating back 10,000 years), the species had probably suffered a demographic contraction or population bottleneck necessarily followed by inbreeding[69, 70, 88, 55]. The consequences of this lack of genetic variation include reproductive abnormalities[89, 90], high infant mortality, morphological abnormalities, and a weakened immune system[69, 48, 56, 32, 38], making the species more susceptible to ecological and environmental changes.

Although the species tolerates a broad range of habitat types, its essential requirements for long-term survival is for suitable prey and the reduction of conflict with humans and other large predators. These components are essential to its conservation.

CURRENT STATUS, COUNTRY BY COUNTRY

1. Afghanistan:

Population. No information at this time. Possibly still a few animals in the south-west above Baluchistan, Pakistan and the Iranian border region. There is no protection for cheetahs.

2. Algeria:

***Population*.** Still to be found in a few areas of south-east Algeria, between 3 1/2 E to the Libyan border and between 27 1/2 N to 20 1/2 N, with possible concentrations in Tassili N'Ajjer Range, Tassili Attoggar, and Tassili Teffedest. Females with two cubs are seen regularly by tribesman complaining that cheetahs attack their camels. Rainfall was good from 1987-1990 in these areas, and there were increasing populations of Dorcas gazelle and Barbary sheep for cheetahs to prey upon[19]. It is thought that the majority of the remaining Algerian cheetahs are living in Tassili nr'Azger, because this plateau is far more rich in water and vegetation[71]. It is difficult to see the last Algerian cheetahs, native people know their presence only through their traces[71]. This country could be a very important area for saving the North African cheetah.

Principal Threats. Restricted habitat, effects of drought on prey, and conflict with nomadic herders.

3. Angola (Not a party to CITES):

Population. No recent information due to the long-standing civil war. Estimate of 500 with a range of 200- 1000 animals[62]. Range was confined to the drier, arid areas in the central and southern parts of the country. In 1975 cheetahs were reported in the following parks and protected areas: Iona National Park (14,500 Km2), Bicuar National Park (7,900 Km2), Cameia National Park (14,450km2), Luando National Park (8,280 km2), Quicama National Park[93]. The cheetah was declared protected game in 1957, but legislation is difficult to enforce, and the military community is exempt from these provisions of the law[62].

Principal Threats. Large scale poaching which has helped support the long, civil war, cultivation and over grazing of cattle in the arid areas will contribute to the elimination of cheetah habitat.

4. Benin:

Population. Thought to be extinct outside of the tri-country national park in the north of Benin, the Park Nationale du W, which adjoins Niger, Burkina Faso and Benin. In this park, a very small population of 2 or 3 pairs may exist[26, 23]. A few cheetahs exist in and around the Pendjari complex of protected areas in northwestern Benin[23].

Principal Threat. Insufficient numbers of cheetahs to sustain a viable population and lack of habitat.

5. Botswana:

Population. Estimates vary between 1,000 and 1,500[11, 52,27,53]. Cheetahs have a wide distribution throughout Botswana, but are absent from areas of dense human settlement in the extreme south. In the northern districts of Ngami West, Ngami East, and Tutume areas, the cheetah is found throughout and is often in conflict with communal farmers who graze livestock and the commercial farmers of the Botswana Livestock Development Corporation[11]. Freehold lands make up a small percentage of the overall land base in Botswana, but appear to harbour relatively large cheetah populations[53]. This is especially true in the commercial farming areas of Ghanzi district and the Tuli Block and communal livestock areas in the south central Ghanzi district[45, 53]. Cheetahs have been reported in the following protected parks and reserves: Chobe National Park (11,000 km2), Moremi Wildlife Reserve (3,880 km2), Nxai Pan National Park (2,100 km2), Makgadikgadi Pans Game Reserve (3,900 km2), Kalahari Game Reserve (24,800 km2). Cheetahs have been protected game since 1968 but can be shot for livestock defense even before any damage has been noted. Recent quotas set by CITES in 1992 allows for 5 animals for export.

Principal Threats. Livestock farming and poaching.

6. Burkina Faso:

Population. Extremely low. Estimated at 100[62]. Perhaps only found, now, in the complex of national parks and protected areas and the tri-country national park in the eastern point of the country that borders Niger and Benin where 2 or 3 pairs exist[26, 23]. A few cheetahs exist in the Singou Fauna Reserve and the adjacent proposed Arlin National Park[23]. Cheetahs may now be extinct in the vicinity of Kabore Tambi National Park and the Natinga Game Ranch in southern Burkina Faso[23]. The cheetah is totally protected but enforcement is likely to be inadequate.

Principal Threats. The country is under growing invasion by large numbers of nomads from the north, which has increased the pressure on the cheetah's range. Loss of habitat, poaching and insufficient numbers of cheetahs to sustain a viable population.

7. Cameroon:

Population. Population very small. In 1975, small populations of cheetahs were still found in Benoue National Park[93, 62]. Between 1974 and 1976, a census was carried out in Bouba Nr'dijida National Park, which resulted in finding no cheetahs[62].

Principal Threats. Decline of prey species, poaching and environmental degradation[62].

8. Central African Republic:

Population. Still found in the south-eastern area of the country, bordering Sudan and in the southern middle of the country, bordering Democratic Republic of Congo[85, 71]. A small population still existed in Saint Floris National Park boarding Chad and the hunting domains in the north[93, 9, 71].

Principal Threats. Extensive poaching and limited prey species.

Taxonomy. North Central African Republic listed as *A.j. soemmeringii*, there is no listing for southern Central African Republic.

9. Chad:

Population. Possibly a small population still exists in the Tibesti Highlands where prey species still are abundant, and there may also be a small population in Ennedi mountains[71]. As of 1975, there was a small population of cheetahs in the Zakouma National Park93.

Principal Threats. Changing climate conditions have reduced the carrying capacity of the land and have over-burdened the sensitive environment[62]. Currently, the many years of war have armed the general population, which puts all wildlife in danger of poaching for food and profit.

10. Democratic Republic of the Congo (Zaire):

Population. No current information. Estimated at 300 and could decline below 100 by 1980[62]. Small populations found in parts of Shaba, Kasai and Kwango Provinces in the southern and southeastern part of country[62]. Kundelungu National Park (7,600 km2) and Upemba National Park (10,000 km2) did contain a few cheetahs[62].

Principal Threats. Agricultural development, poaching and loss of habitat.

Taxonomy. There is no listing for the Northern Congo population.

11. Egypt:

Population. Cheetah tracks have been seen and at least 5 animals were seen around the Sitra water source in the Qattara Depression in the western and northwest parts of the country, and north of Qara Oasis. It is believed there is still a small population that remains there[24, 3, 78]. In 1994, tourism was banned in Marsa Matruh Province (where the Qattara depresion is situated) for five years to protect wildlife from poaching 71. A proposed cheetah-gazelle sanctuary in northwest Qattara has been prepared[78]. The cheetah is totally protected, although enforcement is likely to be inadequate.

Principal Threats. Restricted habitat, possible conflict with nomadic herdsmen, and insufficient numbers of cheetahs to sustain a population.

12. Ethiopia:

Population. In 1975 the population was estimated to be 1000 animals and it was believed that the populations could decline to 300 animals by 1980[62]. The cheetah was widely distributed from Addes to Djibouti in eastern Ethiopia. Also widely distributed through the southern parts of the country, between 200-1500m elevation, absent from the low lands of the Ogaden in the east, and no sightings in the north since 1937[94]. A small population was known to be in the Danakil Reserve[62]. In 1995, cheetahs were sited near Dolo[40]. Two cheetahs were seen in the dry desert scrub, 100km from Dolo, by American oil company employees. The cheetahs were seen on a rocky plateau. This area has a fairly large antelope prey population[40]. Other cheetah sightings have recently been in the Afder Zone, in and around the CherriHi/El Kere area, and in the Dolo region skins and live cheetahs are offered for sale[40]. One cheetah from the Dolo region is in captivity at the Royal Palace as of 1996[40]. Cheetahs are protected against hunting and capture although legislation is difficult to enforce.

Principal Threats. Civil war, habitat loss, extensive poaching, decline of prey, and fur trade.

13. Gambia:

Population. Reported that cheetahs may wander into Gambia from Senegal[6].

14. Iran:

Population. Estimates of 100-200[39] and less than 100[7]. Under the rein of the Shah of Iran the population was estimated at 400-450[28, 37, 7]. As of 1998 cheetahs are still to be found in very small groups in a variety of areas of this large country. A recent survey has been conducted by Hormoz Asadi showing 6 areas in the country where cheetahs still exist.

1. Evidence indicates definite dispersal of cheetahs from the Koshe-Yeilagh and Miandasht protected areas towards the southern Khorasan. The survey indicates that there are at least 15 to 20 cheetahs in southern Khorasan and groups of 5-8 cheetahs have been reported to be hunting wild sheep.
2. Cheetahs are surviving in the unprotected areas in Bafgh region of Yazd province. Much of this region consists of arid mountains and population estimates are still 10 to 15 animals including the Kalmand protected area.
3. A population is in the unprotected area of eastern Isfahan where the terrain consists of vast expanses of desert, unpopulated except for herdsmen grazing goats and camels. Here livestock numbers have increased and the past gazelle population has decreased, but this region may still support 5-10 cheetahs that are widely scattered.
4. A population is found in Kavir National Park and reports are frequent in this vast desert with arid mountains. The population corresponds with a gazelle population and there may still be 10 to 15 cheetahs here.
5. A population exists in the Garmsar, Damghan and Semnan unprotected areas in the northern part of

the plateau. Here, 5 to 10 cheetahs are in conflict with growing agriculture and human populations.

6. A population is found in the Khar Touran National Park and protected area, which may possess the highest cheetah density in Iran. Cheetah reports are frequent in this vast expanse of desert where there may be 15 to 20 cheetahs still alive[7].

Principal Threats. Loss of habitat, poaching, limited numbers of prey species. Direct persecution by humans, either shepherds or local hunters. They are easy targets for people in four-wheel drive vehicles and motorbike riders who chase cheetahs if they see them, causing them to die of exhaustion or leave the area.

15. Kenya:

Population. Estimation of 1,200 animals[30]. Species still occurs throughout the country, except in forests, montane moorland, swamps, and areas of dense human settlement and cultivation. Cheetahs are absent in western Kenya, the more densely populated parts of Central Province, and most parts of the coastal strip. Its distribution coincides with the distribution of Thompson's gazelle, Grant's gazelle, and gerenuk. Cheetahs occur throughout most of the arid northern and north eastern parts of Kenya. Although this area is vast and mostly unpatrolled and poaching is on the increase[30]. Populations of cheetahs are found in the following national parks and reserves; Nairobi National Park (114 km2), Tsavo National Park (20,821 km2), Amboseli National Park (329 km2), Meru National Park (870 km2), Samburu-Isiolo Reserve (504 km2), Kora Reserve (1500 km2), Masai Mara Reserve (1510 km2), Marsabit Reserve (2088 km2), Tana River Reserve (165 km2). All hunting of cheetahs is completely banned. Exports of live cheetahs stopped in the 1960's.

Principal Threats. Poaching, habitat loss, competition with agriculture and farming development.

16. Libya (Not a party to CITES):

Population. Cheetahs may still live around Fezzan oasis, SE of the country[71]. Little information is available. Formerly found across the south of the country, but last seen in 1980, possibly still exist in the south west corner where the country borders Algeria, in the Tassili National Park[19]. Until 1969 still found sparsely throughout the country except for the south and southeast[79].

Principal Threats. Unknown, lack of information, presumed lack of prey species and habitat loss.

17. Mali (Not a party to CITES):

Population. Estimated to be 200 to 500[62], believed to be much less than this currently[71]. Probably a small population still exists in the north west of the country bordering Mauritania and in the south part of Adghagh nrquote Ifoga chain, where cheetahs have been reported in late 1970's[71]. In 1990 skins were found for sale in Tibuta, north Mali[46]. There were a few cheetahs in Gurma National Park in the 1970's[71].

Principal Threats. Decline of prey, poaching, environmental desiccation and reduction of habitat due to drought conditions.

18. Malawi:

Population. Estimated at 50[62]. Absent in southern part of the country. A small population still exists in the western parks and a few individuals around Chiperi area south of Kasurgu Park. Animals seen to be coming and going from Zambia into parks with very few resident individuals in Malawi parks. There have been sightings of individual cheetah in Nyika National Park (3134 km2), Vwaza Marsh Game Reserve (986 km2), and Kasunga National Park (2316 km2)[27].

Principal Threats. Human population growth, loss of habitat and poaching.

19. Mauritania (not a party to CITES):

Population. Estimated at 100 to 500[62]. Possible small population and isolated individuals still exists in Aouker Plateau, Mauritania Adghagh, at the NE of Banc drquote Arguim National Park, in the northwest of the country (thought to be extinct due to the disappearance of their main prey, the Mhorr gazelle and decrease of dorcus gazelle) and Tidjika. No cheetahs exist in conservation areas[71].

Principal Threats. Decline of prey, poaching, environmental desiccation and reduction of habitat.

Taxonomy. Northern Mauritania are *A.j. venaticus* and in the south, *A.j. hecki*.

20. Mozambique:

Population. Estimated at 100[82]. Once widely distributed, now relic populations perhaps survive in parts of Gaza and Inhambane Provinces and south of the Zambezi River, and in the southern regions of Tete Province[93]. The Tete Region is believed to be absent of cheetahs now[82]. The Gorongoza National Park (3,770 km2) had a small population of cheetahs[93].

Principal Threats. Poaching due to civil war situation, lack of enforced protection.

21. Namibia:

Population. Estimated at 2,000-3,000 animals[61, 54]. Still widely spread throughout the country, although only small populations are found in the southern part of the country due to smallstock farming, jackal-proof fences and eradication of predators. Ninety-five percent of the population is on commercial farmlands to the north of the Tropic of Capricorn. Apart from farmlands, very small numbers of animals still occur in communal farming areas of Damaraland, Hereroland, Bushmanland, and Kaokaland. Individual animals are seen in Kavango and Caprivi. Only two conservation areas have populations of cheetahs Etosha and the Namib/Naukluft, but only 1.4 to 4% of the population lives in proclaimed conservation areas[61, 52, 82]. Possibly less than 100 animals live in the 2 conservation areas, Etosha National Park (22,270 km2) because high predator competition, and Namib/Naukluft National Park (49,768 km2), because of low prey density. Although protected game, cheetahs can be killed if livestock is threatened. In January 1992, at the CITES meeting a quota of 150 animals was given to Namibia for live export and trophy hunting[16].

Principal Threats. Live capture and shooting by livestock farmers and game farmers. Cheetahs are easily trapped, in large numbers, on farms that have "cheetah play trees". The trapping is indiscriminate. These animals are then shot as there is little export market for live animals. The majority of the current world's captive population of cheetahs has originated from Namibia[53].

22. Niger:

Population. Estimated at 50 to 406[2]. Still found in the Niger Sahel running from Mali to Chad with concentrations of 10 to 15 pairs in the L'Air Tenere Reserve in the northwest central park of the country. A few remain in the Termit Area. In Niger's Park W (the entire tri-country park is over 11,000 km2 of which Nigerrquote s protion is about 2,200 km2) in the extreme south west of the country bordering Benin and Burkina Faso there are still cheetahs[64, 26, 65, 25]. In a study between 1993 and 1995, 22 cheetahs were seen in this park in eight sightings with an estimation of at least nine cheetahs living in the park[86]. Small populations of cheetahs have been recorded in Reserve Naturelle Nationale de L'Air et du Tenere (20 or 30 animals) (77,360 Km2).

Principal Threats . Poaching, lack of prey species, conflict with livestock.

Taxonomy. A.j. venaticus in northern Niger and *A.j. hecki* in southern Niger.

23. Pakistan (Possibly Extinct):

Population. Information collected suggests that there are no more cheetahs in northern Baluchistan from Quetta westward. This was thought to be the last area claiming cheetahs in Pakistan[2]. Possibly some still exist in southwest Baluchistan on the Iranian border. It is very difficult for Pakistan officials to get information from these semi-autonomous areas. Specimens of hides were collected in the early 1970's[2, 58, 1, 8]. There is a current proposal to conduct a survey in Baluchistan and the Nushki desert region close to Iran for the potential occurrence of the cheetah[67].

Principal Threats. Loss of habitat, competition with livestock and poaching.

24. Senegal:

Population. No current information. Possibly still a few animals in Parc National Du Niokolo-Koba (8,000km2)[26].

Principal Threats. Lack of habitat.

25. Somalia:

Population. Only proof of existence is from cubs being sold by locals in the Kismajo area[33]. The situation for cheetahs in the country is at a critical point. They have been on the decline since the 1970's, in the north the records are old and not current and in the south of the country the civil war has caused an impact on the species[4]. Estimated at 300[62]. A traveler reported seeing eight animals in one days travel in the south of the country along the main road from Kenya, suggesting some numbers still occur in this region[10]. Formerly found throughout the entire country, reduced by half to two thirds as of 1975[62]. Previously found along the Ethiopian border in the north west and central areas of Somalia[94]. Live cheetahs and skins for sale in Djibouti market place and thought to come from Somalia[81].

Principal Threats. Civil war, agriculture expansion caused reduction of prey, and poaching for skins and live trade. Due to Shifta bandits and civil war, enforcement is inadequate.

26. South Africa:

Population. Estimated at 500-800[52, 27]. Individuals occur sporadically in the northern parts of the Cape Province. In the Kalahari Gemsbok National Park there is a small population of approximately 50 animals. A small population is found on the extensive commercial farmlands in the north western, northern and eastern Transvaal, to the southern border of the Kruger National Park and along the Zimbabwe and Botswana borders. They were exterminated in Natal by the 1930's. Since 1965, 64 animals from Namibia were reintroduced to Hluhluwe/Umflozi, 33 into Mkuzi Game Reserves, 18 into Eastern Shores, 13 into Itala, and 14 into Ndumu[79, 77] and over 10 into Phinda. Other reserves contain isolated groups too small to be considered as viable populations. The population in the Kruger National

Park is approximately 250 animals. Many cheetahs are imported to South Africa from Namibia for zoos, parks and private facilities, as well as for trophy hunting in small camps. South Africa does have several successful captive breeding facilities[51]. Only two parks hold large enough populations: Kruger National Park (19,485 km2) and the Kalahari Gemsbok National Park (9,591 km2). The cheetah was taken off the South African endangered species list in 1989. Permits are issued to control problem animals through shooting and live capture. Trophy hunting is allowed, but there is no legal export of the trophy.

Principal Threats. Livestock farming, small populations in unconnected conservation areas, and the believed success of captive breeding programmes in South Africa, which has eliminated the need to put much effort into the conservation of the remaining wild populations.

27. Sudan:

Population. Recent reports indicate that cheetahs are mainly distributed in southern Sudan[31]. Estimates of 1,200 animals, which could have declined by half by 1980[62]. Recent information in the north indicates that cheetah skins are used to make slippers and these are in great demand by rich Sudanese[76, 46]. Populations may still be present where adequate prey and livestock exist in semi-arid areas below the true desert in the central middle of the country[76]. Widely distributed throughout the south, as of 1982[35]. Recent information is lacking from the south of the country due to the long civil war. The population there could be greatly affected by the eight years of war. All wildlife has been severely affected by the availability of guns and ammunition[76]. Were very rare or non-existent in all parks and reserves[62]. Sightings of 10 animals in the southern reserve,*Southern National Park (23,000 km2), sightings also seen in *Boma National Park (22,800 km2), *Boro Game Reserve (1,500 km2), *Meshra Game Reserve (4,500 km2), *Badingile Game Reserve (8,400 km2), Ashana Game Reserve (900 km2), Chelkou Game Reserve (5,500 km2), Kidepo Game Reserve (1,400km2), Numatina Game Reserve (2,100 km2), and

Shambe Game Reserve (620 km2) (Hillman,1982). The cheetah has been a protected species since 1972. Effective 1 January 1989 Wildlife Conservation and National Park forces of Sudan issued a 3-year notice banning the hunting and capture of mammals, birds and reptiles in the Republic of Sudan.

Principal Threats. Poaching, loss of prey, indirect affects of the long civil war in the south of the country.

*Proposed not yet gazetted (1988).

28. Tanzania:

Population. Estimated at 1000, with a range of 500-1500[62]. Found in the grasslands of Masailand and a few localized areas of woodlands. Populations do exist in the Serengeti/ Ngorongoro Conservation Area (25,000 km2), possibly as many as 500[44, 14], however, the population suffers due to competition with lions and hyenas. There have been sightings in Mikumi National Park (3,230 km2), Tarangire National Park (2,600 km2), Katavi National Park (2,250 km2), and Ruaha National Park (10,200 km2)[15, 27].

Principal Threats. Poaching, predation and competition with other large predators.

29. Uganda:

Population. Estimated less than 200[62]. No current information available. Small numbers are thought to be found in the north east sector of the country and a few may still found in Kidepo National Park (1,400 km2)[93].

Principal Threats. Poaching and loss of habitat.

30. Western Sahara (Possibly Extinct) (Not a party to CITES):

Population. Presumed extinct. Last individual caught in 1976 and given to the zoo of Beni Abbes Scientific Research Center[71]. A possible population may still live in the upper lands of East Tiris (south east of the country), a region of abundant vegetation[71].

31. Zambia:

Population. Although cheetah records are very scant, the species distribution in the last three decades is encouraging[75]. The species is uncommon in many areas, however, as of 1969 cheetahs were still widely distributed in various parts of the country, but in low densities[5]. Populations were concentrated in the flood plains and along dry riverbeds. It was thought that the majority of the suitable habitats would disappear by the 1980's[62, 5]. Recently cheetahs occur in relatively low numbers in Kufe National Park (22,400 km2), South Luangwa National Park and Sioma Ngwezi National Park. In Lower Zambezi National Park, one or two have been sighted by tour operators at Jeki plain since 1990[75]. Experimental re-introduction of three male cheetahs into the Lower Zambezi took place in 1994[75].

Principal Threats. Poaching, loss of habitat, and expanding human population.

32. Zimbabwe:

Population. Estimated at 500-1000[91, 82, 52]. A 1991 Department of National Parks and Wildlife Management (DNPWLM) report estimated cheetah numbers using a computer model. This model predicted there were over 600 cheetahs within the Parks and Wildlife Estates, nearly 200 in communal lands, 400 on alienated land and nearly 200 on other state land, resulting in a total of 1,391 cheetahs throughout Zimbabwe. These estimates should however, be treated with caution as they are not based on actual data[95]. Farmers on private and commercial land in southern Zimbabwe have indicated an increase in the cheetah population and are concerned over the loss of valuable game and livestock to cheetahs. According to a 1997 report from the Ministry of Environment and Tourism DNPWLM, the amount of commercial ranchland with permanently resident cheetah populations has more than doubled in the last decade, with an estimate of 5,000 animals.

Cheetahs are largely absent from the northeast part of the country. Two main populations are found in the southern commercial farming areas and in the northwest conservation areas. These two areas account for about 400 animals. The remainder of about 100 animals is distributed over the middle

Zambezi Valley, the Midlands and Gonarezhou[91]. Over 50% of the population occur on privately owned farmland[95]. Less than 200 animals are thought to be in the conservation areas including Hwange National Park (14,650 km2), Matetsi Safari Area (2,920 km2), Kazuma National Park (313 km2) and Zambezi National Park (564 km2). Occasional sightings are reported in Matobo National Park (432 km2) and 10-20 animals are in the National Park and Safari area around Lake Kariba Valley. Small numbers occur in the Mana Pools National Park (2,196 km2) and the lower Zambezi area, unknown number in the Gonarezhou National Park (5,053 km2)[91]. Cheetahs are on the sixth schedule of the Parks and Wildlife Act and are also specially protected, which means that it is illegal to kill a cheetah under any circumstance without a Section 37 permit. This includes trophy hunting a cheetah, killing one as a problem animal or live capture. The Government opened trophy hunting on the cheetah in 1990, which is monitored by "hunting returns". Quota's set at the January 1992 CITES meeting allows for the export of 50 animals[16].

Principal Threats. Conflict with farmers and livestock and illegal killing of cheetahs.

CONCLUSION

During the past 25 years, the world’s cheetah population has declined by over 50%, from approximately 30,000 animals, to less than 15,000, whereas the human population has doubled during this time. The majority of the remaining cheetah populations are found outside protected reserves and are increasingly in conflict with humans. This is due to conflict experienced with lions and hyaenas, by cheetahs in game reserves. As human populations increase, the reduction of prey species available to cheetahs and the loss of habitat are the biggest threats facing the cheetah today. Another major problem facing the species is its lack of success in captivity, as the captive population is not self-sustaining but maintained by the wild population of cheetahs, which is under increasing pressure.

In order for the cheetah to survive into the 21st century, some simple and yet economically hard decisions will have to be made. The survival of the cheetah depends on the ability of range countries discussed in this paper to develop a Global Master Plan for the cheetah in its remaining ranges of Africa. A Global Master Plan will hopefully be developed with the assistance of the IUCN SSC's Conservation and Breeding Strategy Group (CBSG) during the next year.

Having been revered by humans for over 5,000 years, the cheetah is now facing extinction caused by human factors. In order to ensure this species' survival, we have to look critically at the political, social and economic issues facing wildlife conservation in Africa today. Countries like Namibia, Botswana and Zimbabwe, which have key remaining populations, urgently need to set the example with integrated conservation management programs to ensure the survival of the cheetah.

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APPENDIX II

2000/2001 INTERNATIONAL CHEETAH STUDBOOK SUMMARY

2000/2001
INTERNATIONAL CHEETAH STUDBOOK: SUMMARY

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THE STUDBOOK

The International Cheetah Studbook has the purpose of registering all cheetahs in the world held in both zoological and private facilities and providing information about existing animals by publishing the studbook contents thus creating the preconditions for selecting breeding animals.

The 2000 – 2001 studbook data includes all cheetahs known to be alive as of 31 December, 2001, and includes North American captive/born animals who died in 1970 or after and founding animals now dead who had live offspring in 1970 and after. The International Studbook has added captive animals around the world. It includes wild-caught and captive-born animals, which were alive in 1980 and after, as well as founders with live offspring form 1980. Each registered animal has a studbook card. In this edition of the International Studbook, historical records of cheetahs have been included.

The data on the following pages has been computerized using the International Species Inventory System's (ISIS) Sparks Studbook Program. The information was compiled from various sources: Bi-annual questionnaires sent to all facilities holding cheetahs; International Species Inventory System (ISIS); and importantly, personal communications. Excellent cooperation has been obtained from many facilities, and it is hoped that the data is accurate and complete. The Cheetah Studbook Keeper makes entries based on reported evidence and must assume that all information received from breeders is correct. Owners and holders of cheetahs are urged to check the studbook for accuracy and if there are any discrepancies, the studbook keeper would appreciate notification.

INTRODUCTION

The 2000 – 2001 International Cheetah Studbook is the eleventh edition of the world registry for captive cheetahs. This edition of the International Cheetah Studbook combines all information available for the period January 1, 2000 to December 31, 2001.

The captive population on December 31, 2000 was 1320 (675.645.0) animals in 264 facilities in 52 countries. On December 31, 2001 the total captive cheetah population was 1376 (710.666.0) animals in 264 facilities in 52 countries. The captive population of cheetahs live in eight geographical regions. Figure A2.1 shows the percentage of cheetahs living in these regions as of the end of 2001. Table A2.1 is a breakdown of the eight regions by country and includes the number of facilities and the number of cheetahs in each country for 2000 and 2001.

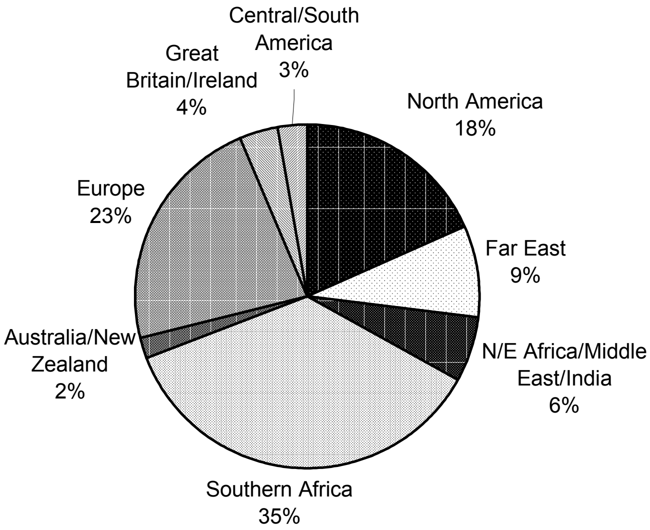

Figure A2.1 2001 Captive cheetah population by region, 1376 animals

This edition of the Studbook includes the major changes in the captive population from January 1, 2000 through December 31, 2000 (Section B) and January 1, 2001 through December 31, 2001 (see Section C). Section D is a summary of the captive population of cheetahs, by studbook number, at individual facilities as of December 31, 2001. The first column in Section D shows which of the bi-annual 2001 questionnaires had been returned by the facility concerned by April 2002 (either mid-year, end-of-year, both or none), to give an indication of how up-to-date the information used in the Studbook is. The last column shows the date of the last questionnaire returned by that facility, if information is available. Also included in this edition are all additions (section E), 2000 births (section F), 2001 births (section G), 2000 deaths (section H), 2001 deaths (section I) and 2000 – 2001 transfers (section J). Section K includes general comments and deaths notes by individual studbook number for 2000 – 2001 animals. Section L is a listing of Multiple Sires and Dams, which are listed in the Sire and Dam column of the Studbook as "Mult". Section M is a Studbook listing of all live animals as of December 31, 2001. Section N includes inbreeding coefficients for 2001 live animals. Animals that were formerly listed in SPARKS as T-Numbers (animals with a temporary Studbook number) and that did not influence the analysis of the 2000 – 2001 Studbook have now been given permanent Studbook numbers and are listed in Section O. Section P is a complete Studbook listing of animals. Animals that are still listed as T-numbers and that will be assigned permanent Studbook numbers for the 2002 Studbook are listed in Section Q. Section R includes articles submitted for publication in the International Cheetah Studbook.

Table A2.1 2000 - 2001 regional groupings of captive cheetahs

		2000					2001				
		Facilities	Total	M	F	U	Facilities	Total	M	F	U
Southern Africa	Botswana	1	2	2	0	0	1	2	2	0	0
	Namibia	29	168	94	74	0	27	163	90	73	0
	South Africa	15	283	136	147	0	18	313	151	162	0
	Zimbabwe	1	7	2	5	0	1	7	2	5	0
2000 – 4 countries, 46 facilities, 460 (234.226.0) animals							**2001 - 4 countries, 47 facilities, 485 (245.240.01) animals**				
North America	Canada	6	21	7	14	0	5	19	6	13	0
	United States	59	211	116	105	0	67	229	119	110	0
2000 – 2 countries, 62 facilities, 242 (123.1199.0) animals							**2001 - 2 countries, 62 facilities, 248 (125.123.0) animals**				
Europe	Austria	4	11	4	7	0	4	14	6	8	0
	Belgium	3	11	4	7	0	3	11	3	8	0
	Bulgaria	1	2	2	0	0	1	2	2	0	0
	Czech Republic	3	17	6	11	0	5	22	9	13	0
	Denmark	1	3	1	2	0	1	3	1	2	0
	France	13	59	28	31	0	13	60	31	29	0
	Germany	21	68	31	37	0	22	70	33	37	0
	Italy	2	5	2	3	0	2	5	2	3	0
	Netherlands	8	62	38	24	0	8	56	35	21	0
	Poland	3	11	7	4	0	3	12	9	3	0
	Portugal	3	7	3	4	0	3	6	3	3	0
	Russia	2	11	6	5	0	2	11	6	5	0
	Slovenia	1	1	1	0	0	0	0	0	0	0
	Spain	5	11	4	7	0	5	11	4	7	0
	Sweden	2	5	2	3	0	2	7	5	2	0
	Switzerland	4	12	7	5	0	4	12	7	5	0
	Uzbekistan	2	2	0	2	0	2	2	0	2	0
2000 - 17 countries, 78 facilities, 298 (146.152.0) animals							**2001 - 16 countries, 80 facilities, 304 (156.148.0) animals**				
Far East	Burma	1	2	1	1	0	1	2	1	1	0
	China	1	6	2	4	0	1	6	2	4	0
	Indonesia	2	9	6	3	0	2	9	6	3	0
	Japan	9	60	33	27	0	9	59	34	25	0
	Malaysia	1	2	0	2	0	1	2	0	2	0
	North Korea	1	1	1	0	0	1	1	1	0	0
	Singapore	1	1	1	0	0	1	7	4	3	0
	Sri Lanka	1	1	0	1	0	1	1	0	1	0
	Taiwan	1	1	0	1	0	1	1	0	1	0
	Thailand	3	26	12	14	0	3	28	12	16	0
2000 – 10 countries, 21 facilities, 109 (56.53.0) animals							**2001 - 10 countries, 21 facilities, 116 (60.56.0) animals**				
Britain/Ireland	England	10	30	16	14	0	11	33	18	15	0
	Ireland	2	16	8	8	0	2	11	5	6	0
	Northern Ireland	1	4	2	2	0	1	4	2	2	0
	Scotland	1	2	1	1	0	1	1	1	0	0
2000 – 4 countries, 14 facilities, 52 (27.25.0) animals							**2001 - 4 countries, 15 facilities, 49 (26.23.0) animals**				
N/E Africa/Middle East/India											
	Ethiopia	1	1	1	0	0	1	1	1	0	0
	India	1	3	2	1	0	1	3	2	1	0
	Israel	2	4	4	0	0	2	3	3	0	0
	Kenya	2	6	2	4	0	2	6	2	4	0
	Morocco/N Africa	1	2	1	1	0	1	2	1	1	0
	Qatar	2	4	2	2	0	2	4	2	2	0
	Saudi Arabia	1	4	2	2	0	1	5	3	2	0
	United Arab Emirates	4	50	26	24	0	3	58	31	27	0
	Dubai	1	2	2	0	0	2	2	2	0	0
2000 – 9 countries, 15 facilities, 76 (42.34.0) animals							**2001 - 9 countries, 14 facilities, 84 (47.37.0) animals**				
C/S America	Argentina	0	0	0	0	0	1	3	2	1	0
	Brazil	2	3	1	2	0	2	3	1	2	0
	Chile	1	2	1	1	0	1	2	1	1	0
	Cuba	1	3	2	1	0	1	3	2	1	0
	Mexico	4	25	10	15	0	4	25	10	15	0
2000 – 4 countries, 8 facilities, 33 (14.19.0) animals							**2001 - 5 countries, 9 facilities, 36 (16.20.0) animals**				
Australia/NZ	Australia	5	16	10	6	0	5	19	11	8	0
	New Zealand	2	9	6	3	0	2	10	7	3	0
	2000 - 2 countries, 7 facilities, 25 (16.9.0) animals						**2001 - 2 countries, 7 facilities, 29 (18.11.0) animals**				
Other	Unknown location	13	25	17	8	0	9	25	17	8	0
2000 Total – 52 countries, 264 facilities, 1320 (675.645.0) animals							**2001 Total - 52 countries, 264 facilities, 1376 (710.666.0) animals**				

From 1 January 2000 to 31 December 2001, 410 (204.190.16) new animals were registered. These additions include historical information on animals not previously registered, newly imported wild-caught animals, and births during this period. Historic information was received pertaining to 126 (65.51.10) animals, 57 (33.24) of which were wild-caught and 69 (32.27.10) were captive born. Forty-nine of these had a reported country of origin, and of those, 2 were caught in Botswana, 2 in Chad, 1 in Ethiopia, 1 in Iran, 8 in Namibia, 27 in Somalia, 2 in South Africa and 6 in Sudan.

Sixty-nine (32.27.4) 'historic' births were reported, of which 1 (0.1) occurred in 1993, 3 (2.0.1) occurred in 1994, 4 (2.1.1) occurred in 1995, 13 (4.7.2) occurred in 1996, 17 (8.7.2) occurred in 1997, 12 (5.5.2) occurred in 1998 and 19 (11.6.2) occurred in 1999. The newly reported 1993 birth was from Olmense Zoo, the 1994, 1995, 1997 and 1998 births were from Almaktoum and Fota Wildlife Park, the 1996 births were from Almaktoum, Fota and Huizen FD, and the new additions from 1999 were from Olmense, Almaktoum, Fota, SD-WAP and Fossil Rim.

An overview of the major changes during 2000 and 2001 is presented in Sections B and C. In the 2000 summary, the 1999 column includes corrections that were reported after the publication of the 1999 International Cheetah Studbook; therefore, it differs from the totals published in the 1999 International Cheetah Studbook.

2000 STUDBOOK INFORMATION

The captive cheetah population on December 31, 2000 was 1320 (675.645.0) animals in 264 facilities in 52 countries. Of the 1320 animals, 70% or 930 (482.448.0) are captive-born and 30% or 390 (193.197.0) are wild-born (see Figure A2.2). This figure shows a decrease by 21 in the number of captive-born animals in the population over 1999, and an increase in the number of wild-born animals since 1999 (345 in 1999 vs. 390 in 2000).

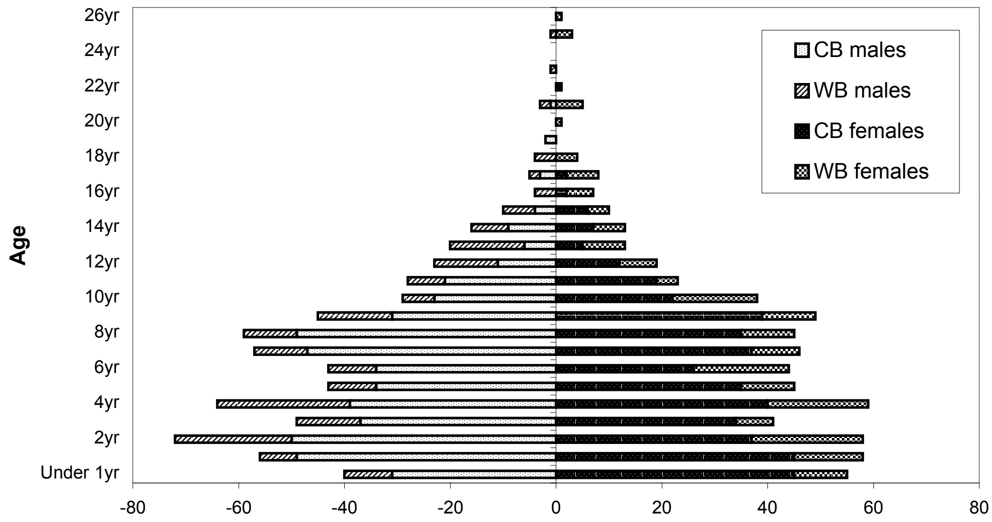

Figure A2.2 Age/sex structure of the 2000 captive cheetah population for wild-born (WB) and captive-born (CB) animals

Successful parentage was reported in 2000 with animals as young as 2 years old or as old as 12. The majority of successful breeding for both sexes occurs between 3 and 10 years of age. These data are relevant in assessing the age structure of the 2000 population. As shown in Figure A2.2, 55% or 721 animals (389.332) of the 2000 population are within the prime breeding age bracket (≥3-≤10 years of age). Of the animals in this age bracket, 26% or 191 (95.96) are wild-born. The percentage of sub-adult animals (0-<3 years of age) is 26% or 340 (169.171.0) animals, of which 24%, 82 (38.44) animals are wild-born. Seventeen percent or 221 (113.108) animals are older than the usual breeding age (>10) of which 51% or 112 (58.54) are wild-born.

From January 1 to December 31, 2000, 117 (49.67.1) new animals were registered. These new additions do not include the historical information gathered during this period, which is summarized in the introduction, but include newly imported wild-caught animals and births in 2000. Of these newly registered animals, 29 (13.16) were wild-caught, of which 22 (10.12) came from Namibia, 6 (3.3) came from South Africa and 1 (0.1) came from Somalia. These animals were imported to three private facilities in Namibia, two private research and breeding facilities in South Africa and one zoological facility in the United Arab Emirates. Five animals (3.2) were taken first into CCF and were then transferred to Cincinnati Zoo and White Oak Conservation Centre in 2001 as they were non-releasable but were valuable potential breeders.

During 2000, 88 (36.51.1) cubs were born in 27 litters at 15 facilities in 10 countries (see Section F). Table A2.2 lists these litters of cubs and facilities. These births represent a decrease in productivity over 1999, when 94 cubs were born. Of the 88 cubs born, 9 (2.6.1) died under 1 month of age, which represents a 10.2% infant mortality. 11 (8.3.0) cubs died between one month and six months of age. Total cub deaths fewer than six months of age were 20 (10.9.1), which represent 23.5% cub mortality, a much higher percentage than in 1999 (9.5%).

Table A2.2 2000 births by facility

Facility	No. Litters	No. Cubs	No. cub Deaths <1mo	No. breeding M/F
Columbus, USA	1	1 (0.1.0)	0 (0.0.0)	1.1
Dvurkralova, Czech Rep	1	5 (3.2.0)	1 (1.0.0)	1.1
Fossil Rim, USA	1	1 (0.1.0)	0 (0.0.0)	1.1
Fota, Ireland	1	5 (2.3.0)	2 (0.2.0)	1.1
La Palmyr, France	1	5 (2.3.0)	0 (0.0.0)	1.1
Maktoum, UAE	1	3 (2.1.0)	0 (0.0.0)	1.1
Nurnberg, Germany	1	4 (2.2.0)	0 (0.0.0)	1.1
Oakhill, USA	1	5 (2.3.0)	0 (0.0.0)	1.1
Oudtshoorn, SA	3	8 (5.3.0)	0 (0.0.0)	2.2
Peaugres, France	2	6 (2.4.0)	1 (0.1.0)	1.2
Phoenix, USA	1	4 (1.3.0)	0 (0.0.0)	1.1
Pret DW, SA	8	25 (9.15.1)	4 (1.2.1)	3.8
SD WAP, USA	2	8 (2.6.0)	0 (0.0.0)	2.2
Warsaw, Poland	2	4 (2.2.0)	1 (0.1.0)	2.1
Wass BRC, Netherlands	1	4 (2.2.0)	0 (0.0.0)	1.1
15 facilities	**27**	**88 (36.51.1)**	**9 (2.6.1)**	**20.25**

On a facility basis, 6% (15) of the 264 facilities that held cheetahs in 2000 had reproductive success. All of the facilities shown in Table A2.2 had previous reproductive success. There were 20 males and 25 females that were reproductively active during the year. The age distribution of successful breeders in 2000 is presented in Figure A2.3, and the age distribution of all breeding animals alive at the end of 2000 is presented in Figure A2.4. This data is relevant in assessing the age structure of the 2000 population presented in Figure A2.2. At the end of 2000 there were 157 (72.85) proven breeders alive in the captive population. During 2000, only 45 (20.25) animals, 3.4% of the captive population, successfully bred and 16% of these (7) were wild-caught animals.

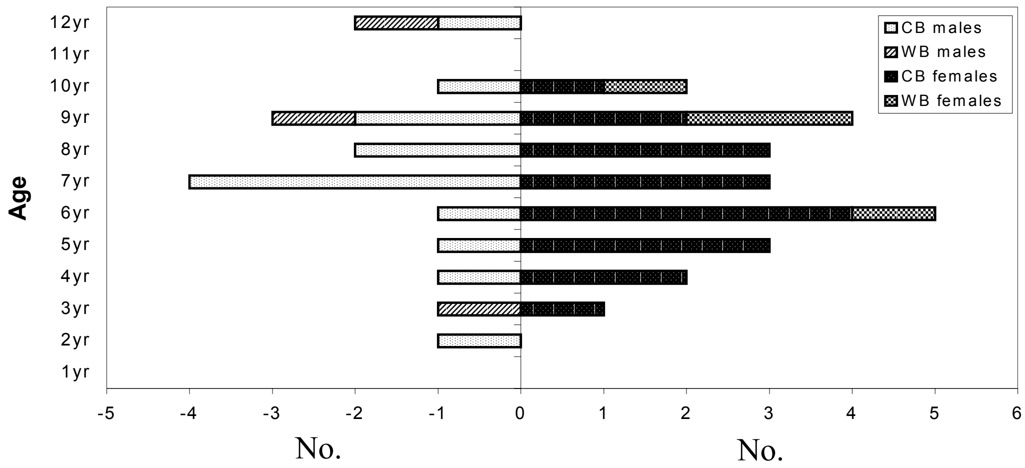

Figure A.2.3 Age distribution of animals that successfully reproduced in 2000.

Of the 1320 cheetahs alive in the 2000 population, 157 (72.85) animals are proven breeders or animals that have bred at least once. This number permits the computation of the effective breeding size (N_e) for the 2000 population using the formula:

$$N_e = \frac{4 \times M \times F}{M + F} = 155.9$$

where M is the number of breeding males and F is the number of breeding females. This value (N_e) is equivalent to 12% of the captive population.

Deaths reported in 2000 totalled 100 (50.49.1), including cub deaths. Figure A2.5 shows the age at death of captive-born and wild-caught cheetahs by sex in 2000. Of the animals that died, 39% or 39 (21.18) animals were within the prime breeding age group ($\geq$3-$\leq$10 years of age); 22% or 22 (11.10.1) animals were under 3 years of age, of which 55% or 12 (5.6.1) were under 1 year old; and 39% or 39 (18.21) were over 10 years of age.

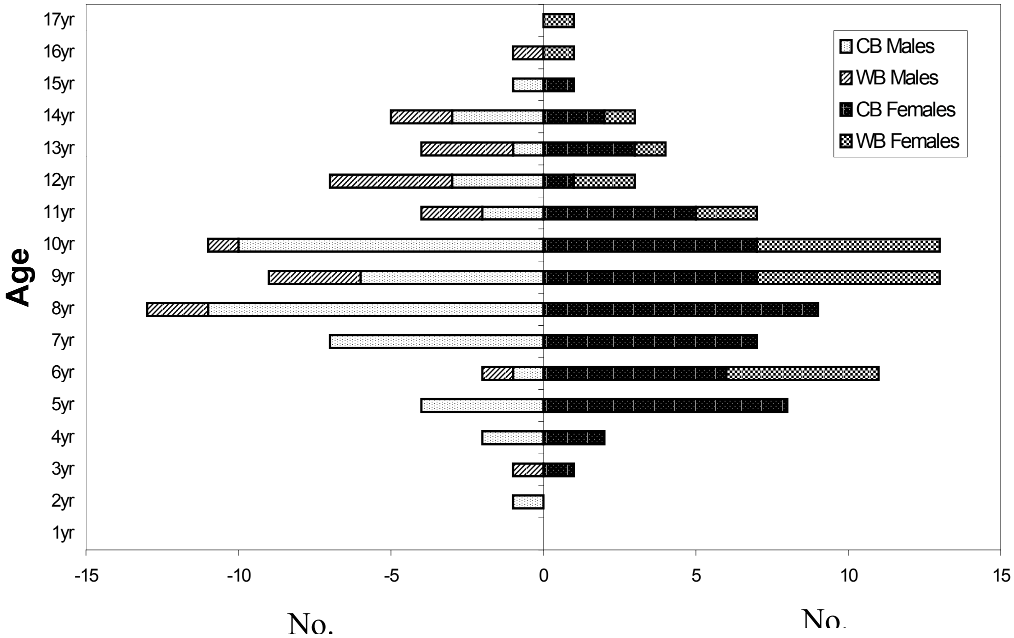

Figure A2.4 Age distribution of proven breeders alive as of 31 December 2000

During 2000, 75 known facilities transferred animals either into or out of their facilities. Forty-eight facilities transferred 109 (55.54) cheetahs to 54 facilities. There are 10 new facilities holding cheetahs, and 6 facilities that are no longer holding cheetahs. Since the end of 1999, there has been an increase of 21 animals in the world's captive cheetah population.

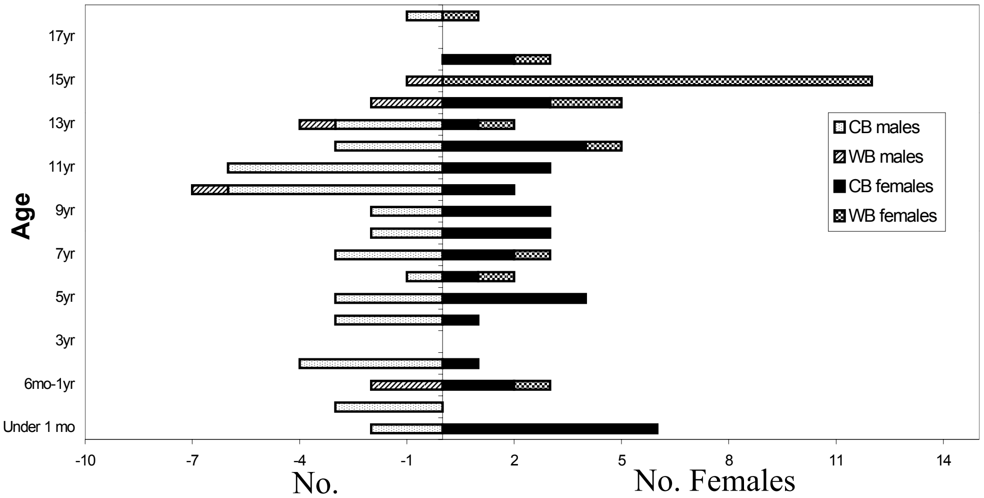

Figure A2.5 Age at death of captive-born (CB) and wild-born (WB) cheetahs, 2000.

2001 STUDBOOK INFORMATION

The captive cheetah population on December 31, 2001 was 1376 (710.666.0) animals in 264 facilities in 52 countries. Of the 1376 animals, 70% or 968 (507.461.0) are captive-born and 30% or 408 (203.205.0) are wild-born (see Figure A2.6). This figure shows an increase by 38 in the number of captive-born animals in the population over 2000, and an increase in the number of wild-born animals since 2000 (390 in 2000 vs. 408 in 2001).

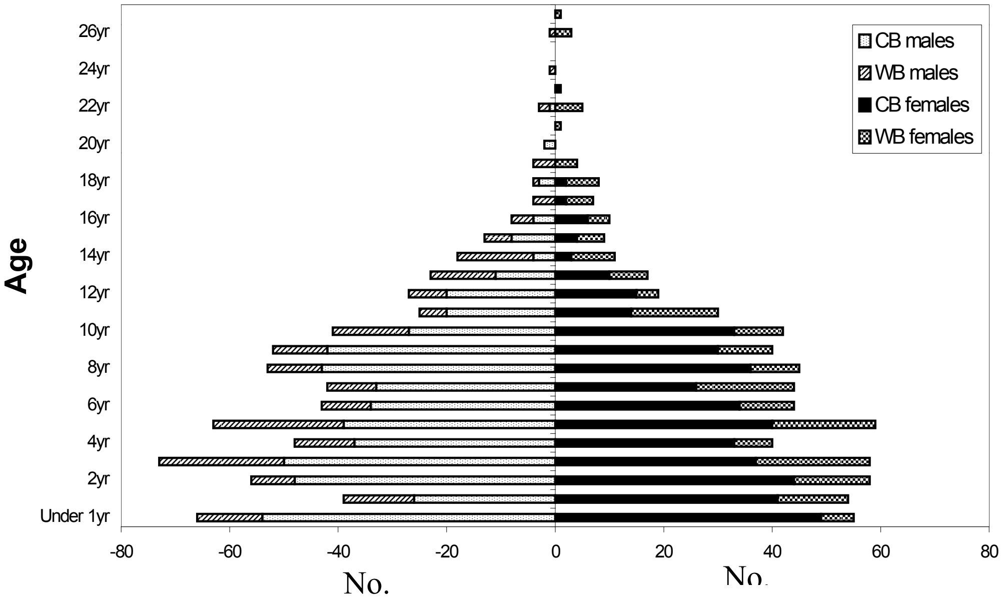

Figure A2.6 Age/sex structure of the 2001 captive cheetah population for wild-born (WB) and captive-born (CB) animals.

Successful parentage was reported in 2001 with animals as young as 2 years old or as old as 16. The majority of successful breeding for both sexes occurs between 3 and 10 years of age. These data are relevant in assessing the age structure of the 2001 population. As shown in Figure A2.6, 57% or 786 animals (415.371) of the 2001 population are within the prime breeding age bracket (≥3-≤10 years of age). Of the animals in this age bracket, 27% or 212 (110.102) are wild-born. The percentage of sub-adult animals (0-<3 years of age) is 24% or 329 (162.167.0) animals, of which 20%, 66 (33.33) animals are wild-born. Eighteen percent or 253 (129.124) animals are older than the usual breeding age (>10) of which 49% or 125 (58.67) are wild-born.

From January 1 to December 31, 2001, 164 (88.71.5) new animals were registered. These new additions do not include the historical information gathered during this period, which is summarized in the introduction, but include newly imported wild-caught animals and births in 2001. Of these newly registered animals, 27 (17.10) were wild-caught, of which 9 (4.5) came from Namibia, 13 (8.5) came from Botswana and 5

(5.0) came from Somalia. These animals were imported to two private facilities in Namibia and two private research and breeding facilities in South Africa and one in the United Arab Emirates. Two animals (1.1) were taken first into CCF and were then transferred to White Oak Conservation Centre as they were non-releasable but were valuable potential breeders.

During 2001, 137 (71.61.5) cubs were born in 43 litters at 20 facilities in 14 countries (see Section G). Table A2.3 lists these litters of cubs and facilities. These births represent an increase in productivity over 2000, when 85 cubs were born. Of the 137 cubs born, 26 (12.9.5) died under 1 month of age, which represents a 19% infant mortality. 9 (5.4.0) cubs died between one month and six months of age. Total cub deaths fewer than six months of age were 35 (17.13.5), which represents 25.5% cub mortality, a considerably higher percentage than 2000.

Table A2.3 2001 births by facility

Facility	No. Litters	No. Cubs	No. cub Deaths <1mo	No. breeding M/F
* Hannover, Germany	1	5 (2.3.0)	0 (0.0.0)	1.1
* Perth, Australia	1	1 (0.1.0)	0 (0.0.0)	1.1
Almaktoum, UAE	4	9 (4.5.0)	3 (2.1.0)	4.3
Belfast, Northern Ireland	1	3 (0.0.3)	3 (0.0.3)	1.1
Dvurkralova, Czech Rep	1	3 (1.2.0)	0 (0.0.0)	1.1
Fossil Rim, USA	1	4 (2.2.0)	0 (0.0.0)	1.1
Fota, Ireland	1	1 (0.1.0)	1 (0.1.0)	1.1
Hoedspruit, SA	7	16 (8.8.0)	0 (0.0.0)	7.7
Mito Cho, Japan	1	2 (2.0.0)	0 (0.0.0)	1.1
Oakhill, USA	1	3 (0.3.0)	0 (0.0.0)	1.1
Olmense, Belgium	1	4 (3.1.0)	0 (0.0.0)	1.1
Oudtshoorn, SA	2	7 (5.2.0.)	0 (0.0.0)	2.2
Peaugres, France	3	19 (12.7.0)	6 (5.1.0)	1.2
Pret DW, SA	8	24 (10.12.2)	5 (2.1.2)	3.7
Rockton, USA	2	9 (6.3.0)	2 (1.1.0)	1.2
San Diego Zoo, USA	1	3 (1.2.0)	1 (0.1.0)	1.1
SD WAP, USA	1	1 (0.1.0)	0 (0.0.0)	1.1
Vienna, Austria	1	4 (2.2.0)	1 (0.1.0)	1.1
Warsaw, Poland	1	6 (5.1.0)	1 (1.0.0)	1.1
Wass BRC, Netherlands	4	13 (8.5.0)	3 (1.2.0)	1.3
20 facilities	**43**	**137 (71.61.5)**	**22 (12.9.5)**	**32.39**

* indicates first-time reproductive success

On a facility basis, 8% (20) of the 264 facilities that held cheetahs in 2001 had reproductive success. As shown in Table A2.3, 90% (18) of those facilities had previous reproductive success, and 10% (2) of the facilities had success for the first time in 2001. There were 32 males and 39 females that were reproductively active during the year. The age distribution of successful breeders in 2001 is presented in Figure A2.7, and the age distribution of all breeding animals alive at the end of 2001 is presented in Figure A2.8. This data is relevant in assessing the age structure of the 2001 population presented in Figure A2.6. At the end of 2001 there were 160 (75.85) proven breeders alive in the captive population. During 2001, only 71 (32.39) animals, 5% of the captive population, successfully bred and 24% of these (16) were wild-caught animals.

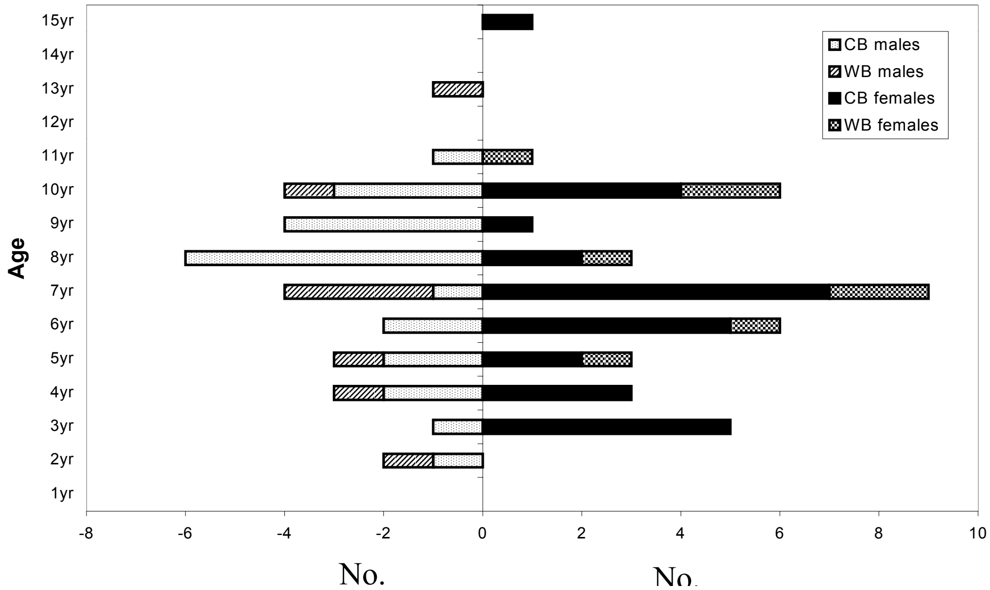

Figure A2.7 Age distribution of animals that successfully reproduced in 2001.

Of the 1376 cheetahs alive in the 2001 population, 160 (75.85) animals are proven breeders or animals that have bred at least once. This number permits the computation of the effective breeding size (N_e) for the 2001 population using the formula:

$$N_e = \frac{4 \times M \times F}{M + F} = 159.4$$

Where M is the number of breeding males and F is the number of breeding females. This value (N_e) is equivalent to 11.6% of the captive population.

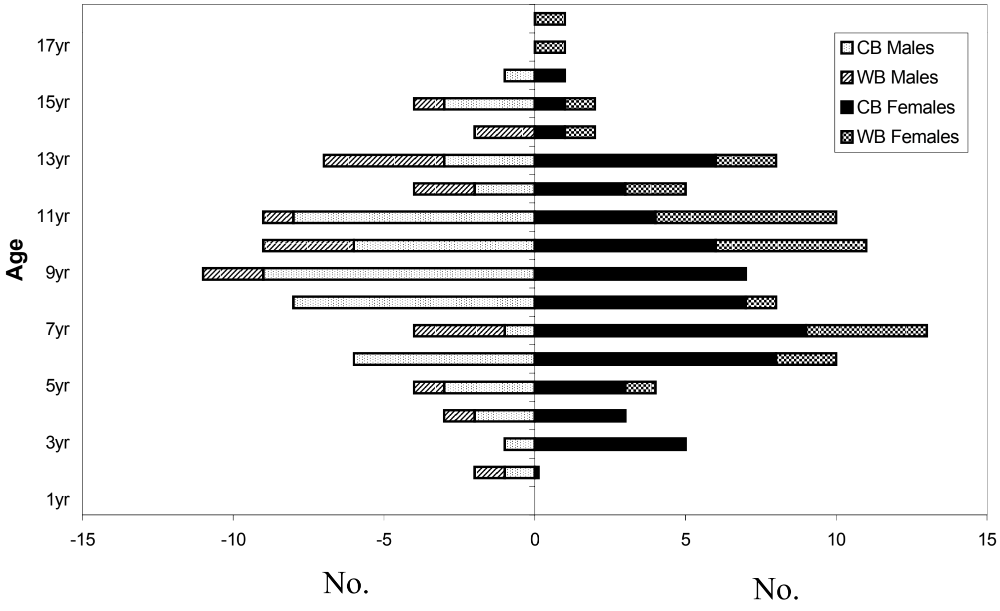

Figure A2.8 Age distribution of proven breeders alive as of 31 December 2001.

Deaths reported in 2001 totalled 112 (56.51.5), including cub deaths. Figure A2.9 shows the age at death of captive-born and wild-caught cheetahs by sex in 2001. Of the animals that died, 32% or 34 (19.15) animals were within the prime breeding age group (≥3-≤10 years of age); 41% or 46 (24.17.5) animals were under 3 years of age, of which 74% or 34 (17.12.5) were under 1 year old; and 29% or 32 (13.19) were over 10 years of age.

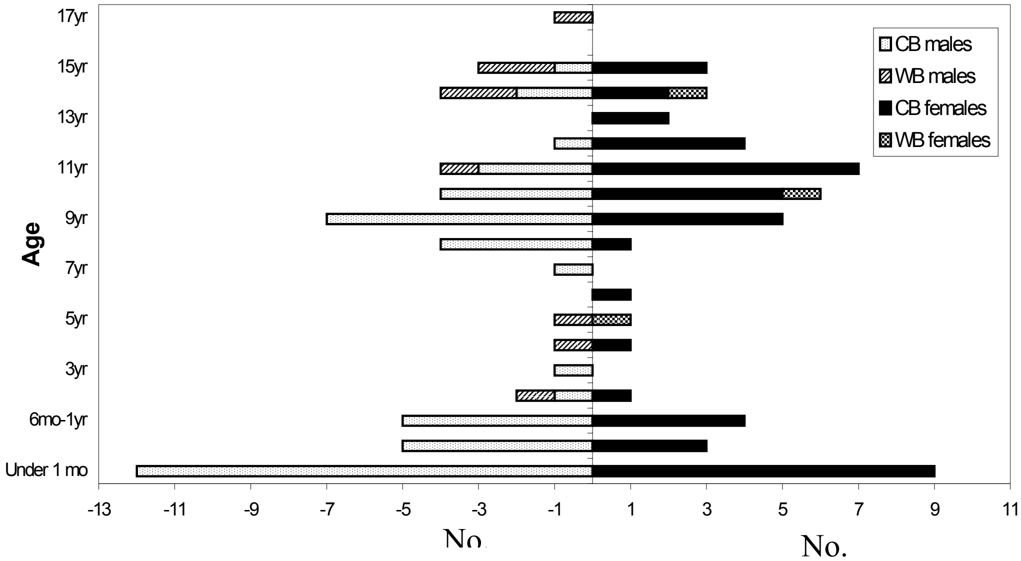

Figure A2.9 Age at death of captive-born (CB) and wild-born (WB) cheetahs, 2001.

During 2001, 75 known facilities transferred animals either into or out of their facilities. Forty-two facilities transferred 118 (64.54) cheetahs to 60 facilities. There are 9 new facilities holding cheetahs, and 7 facilities that are no longer holding cheetahs. Since the end of 2000, there has been an increase of 56 animals in the world's captive cheetah population.

CONCLUSION

The relative success of the world's captive cheetah population over the past few years indicates that an increased reproductive success throughout the world's cheetah facilities can be achieved through a cooperative management program. This will become even more important to work towards as the availability of importing wild cheetahs into captive facilities declines.

There will always be some wild-caught cheetahs that cannot be released back into the wild. It is the responsibility of the world's zoos to cooperate in maximising the breeding success of these important wild founders, as set out in the goals of the World

Zoo Strategy. The main goal of the world's zoos is to manage the captive cheetah population without the need for wild-caught animals.

In August 2001, a first Global Cheetah Master Planning meeting took place in South Africa supported by the AZA's Cheetah SSP and facilitated by the IUCN SSC's Conservation and Breeding Specialist Group (CBSG). This Global Master Plan began the process of international cooperation in *in-situ* and *ex-situ* cheetah management. The meeting was attended by 53 invited delegates from 10 countries, including the USA, Australia, Britain, The Netherlands, Kenya, Zimbabwe, the United Arab Emirates, South Africa, Tanzania and Namibia. Working groups dealt with issues ranging from the status and threats facing cheetahs in the wild outside of protected areas, cheetah/human conflict, genetic management, international collaboration, cooperation between captive breeding programs, education, veterinary and disease issues and public awareness, among others. The workshop will result in a series of actions and steps, including the establishment of a global Cheetah Interest Group, for enhanced collaboration and focused conservation efforts for the cheetah. A second meeting will be held in July 2002 to continue facilitating the development of a comprehensive conservation action plan for this species

During the Global Master Plan workshop, the status of the global captive cheetah population as estimated from the International Cheetah Studbook (1985-2000) was reviewed (Bingaman-Lackey et al., in Bartels et al. 2001). The total number of living animals listed in the International Studbook in Australia, Europe, Japan, North America, and Southern Africa is 1065 in 161 different facilities. These numbers do not represent all animals and institutions with living animals in the studbook, but is rather a subset of animals that are more likely to be in a managed program either now or in the near future. The various regional programs have different concerns, and the regional populations have different characteristics. Below is a brief description of the status of these populations as presented by Bingaman-Lackey et al. (2002), in Bartels et al. (2001).

Demography

Overall, using data from the past 15 years, the global captive population has not been self-sustaining (i.e., Life Table lambda [λ] less than 1.00). However, success in reproducing cheetahs varies greatly both among (Table A2.4) as well as within regions. In Table A2.4 the estimates of lambda are based on data from 01/01/1985-31/12/2000. The Census λ is the average annual growth rate of the population. It is based on the total number of living animals at the end of each year and does not take into account the source of those animals. The Life Table λ is an estimate of what the annual growth rate would be in the absence of importation/exportation, and is based on the age specific estimates of survival and fecundity. The difference between these two estimates of the annual growth rate is important. If the census λ is greater than 1 and the Life Table λ is less than 1 (as is the case in all regions outside of the species' range) it suggests that the population has grown more because of importation than captive breeding and that the populations, as managed during that time period, are unlikely to be self-sustaining. Based on Table A2.4, only the southern African region has produced sufficient offspring to be considered a self-sustaining population; however, there are also some significant differences among facilities within regions. For example, although the North American population as a whole has a Life Table λ of 0.96, the Life Table λ for this time period for three North American Facilities (Fossil Rim Wildlife Center, White Oak Conservation Center, and the San Diego Wild Animal Park) was 1.10. This large difference within a region may be an important indicator as to how cheetahs could be managed such that a population could become self-sustaining.

Genetics

Table A2.4 contains the number of Founder Genome Equivalents (FGE) in each regional population. FGE is a convenient method of expressing Gene Diversity (GD), and is equal to:

$$FGE = 1/(2*(1-GD))$$

Table A2.4 also contains the potential FGE (pFGE) for each regional population. The pFGE is the maximum possible FGEs for the region if all extant founder alleles in the region could be brought to the same frequency in the regional population. While this potential number is not actually attainable, the difference between the actual and potential FGEs in a population gives an indication as to whether importation of additional founder lines would be required to increase the amount of gene diversity in a regional population. As can be seen in Table A2.4, most regions may be able increase their amount of gene diversity by a considerable extent by preferentially breeding underrepresented founder lines.

Whereas the numbers of animals in Table A2.4 can be summed to determine the total number of animals, the same is not true of FGEs. The total FGE would only equal the sum of the Regional FGEs if there were no founder lines shared among regional populations. The sum of the Regional FGEs is 75, whereas total FGE is 42. This suggests that there is considerable sharing of founder lines among regions, and that in order to ensure that genetic material/animals imported into a region can help to increase the region’s FGE a careful analysis of the International Studbook is necessary.

Region	# Animals	# Facilities	Census λ	Life Table λ	FGE	pFGE
Australia/ New Zealand	27	8	1.08	0.88	9	13
Europe	357	72	1.02	0.97	20	71
Japan	62	9	0.99	0.91	8	25
North America	260	62	1.01	0.96	17	56
Southern Africa	359	10	1.05	1.05	21	214

Table A2.4 Status of regional populations (Bingaman-Lackey et al. 2002)

The development and collaboration of successful regional breeding programs is critical in order to contribute to the sustainability of the captive population worldwide. It is hoped that you, the captive managers of cheetahs, will continue to assist with the accurate record keeping for collectively managing this species in captivity. As the Studbook Keeper, the data presented to you in the International Studbook is only as accurate as that which is reported. Please check these records and report any discrepancies.

The development of a Global Master Plan will be a critical component for the long-term future of the species. As the free-ranging population of cheetahs continues to decline and a large amount of genetic diversity of the remaining populations is lost, the captive and wild populations should be managed in cooperation.

References

Bingaman-Lackey, L., Willis, K., Marker, L. 2002. Viability of the Captive Population Working group, In: Global Cheetah Conservation Action Plan, edited by Bartels et al. 2001, IUCN, SSC CBSG.

APPENDIX III

BUSH ENCROACHMENT AND UNGULATE DENSITY ON COMMERCIAL FARMLANDS IN NORTH-CENTRAL NAMIBIA

This Appendix has been submitted as the following paper:

Bush encroachment and ungulate density on commercial farmlands in north-central Namibia. N.D. Muroua, L. Marker, M. Nghikembua and R.M. Jeo. Submitted to the *African Journal of Ecology*.

BUSH ENCROACHMENT AND UNGULATE DENSITY ON COMMERCIAL FARMLANDS IN NORTH-CENTRAL NAMIBIA

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RUNNING HEAD: Bush Encroachment and Ungulate Density

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ABSTRACT

Bush encroachment is a major problem in southern Africa, yet little research has been done on its impacts on native ungulates. We examined population density and seasonal distribution of common ungulate species, including kudu (*Tragelaphus strepsiceros*, Pallas), oryx (*Oryx gazella*, L.), eland (*Taurotragus oryx*, Pallas), red hartebeest (*Alcelaphus bucelaphus*, Pallas), warthog (*Phacochoerus aethiopicus*, Pallas), steenbok (*Raphicerus campestris*, Thunberg), and common bush duiker (*Sylvicapra grimmia*, L.) over different vegetation zones by conducting driving strip counts from 1995 - 2000. The study area, located in north-central Namibian farmland, included habitat types classified according to bush density, and ungulate density was calculated seasonally for each habitat type. All species, except duiker, showed significant differences in population density across different habitats. Eland, oryx and red hartebeest showed higher population densities in less encroached areas; kudu were found in areas with higher bush density. Red hartebeest and warthog were found almost exclusively in open areas. Seasonal distribution varied significantly for oryx and eland, suggesting seasonal movement, while kudu and red hartebeest appeared to be resident. Thus, ungulate species such as oryx and eland probably require areas much larger than a single commercial farm. These data suggest that bush encroachment may be changing ungulate density and distribution in Namibian thornbush ecosystems, which may have profound impacts on the persistence of a globally significant population of cheetahs that prey upon these ungulate species.

INTRODUCTION

In Namibia, as in much of Africa, the majority of biodiversity is found outside of national parks (Pimentel et al., 1992; Barnard, 1998; Soule and Sanjayan, 1998) where livestock grazing has been the predominant land-use practice for several centuries. Consequently, much of the native wildlife in Namibia (and throughout much of sub-Saharan Africa) must coexist with livestock production (Mabutt, 1984; Kinahan, 1991; Archer, 1995; Meik et al., 2002). A large portion of non-protected area in Namibia is privately-owned commercial farmland, which comprises about 40% of the landbase and contains the majority of larger ungulate populations (about 70%, Richardson, 1998). Understanding the relationship between ungulate density and distribution and human-mediated impacts on commercial farmland is a prerequisite for designing efficient conservation strategies for these lands.

Recent human-mediated impacts include overgrazing, fire suppression, fragmentation of historical migration routes, establishment of permanent water sources and extirpation of the largest herbivores and top carnivores (for a review, see Barnard, 1998). A consequence of these ecological changes is the conversion of open savannahs to dense, acacia-dominated thickets with little grass cover, a process known as ‘bush encroachment’. This problem is especially prevalent on commercial farmlands in north-central Namibia, to the extent that bush encroachment has measurably reduced the economic productivity of the Namibian livestock industry (Quan, Barton and Conroy, 1994). These habitat changes and the resulting heterogeneity of the current vegetation structures (expressed in terms of density woody plants) both play potential roles in the determination of ungulate density and distribution.

Although considerable conservation efforts and government wildlife policies are focused on management of large mammalian species (reviewed by Griffin, 1998 and Richardson, 1998), relatively few studies have been conducted to determine the impacts of bush encroachment on large and medium-sized ungulates living in the commercial livestock farming area of north-central Namibia. This is unfortunate since a globally significant population of cheetahs (Joubert and Morsbach, 1982; Marker-Kraus et al., 1996) is found in this region and depends upon these large and medium sized ungulates for a prey base (Marker-Kraus et al., 1996).

Here we report results from a 4½ year study on the distribution of ungulates on commercial farmland in Namibia. The objective of this study was to examine the relative abundance of common ungulate species over habitats composed of different bush densities. We used a road strip count technique in order to document the seasonal density of kudu (*Tragelaphus strepsiceros*, Pallas 1766), oryx (*Oryx gazella*, L.1758), eland (*Tragelaphus oryx*, Pallas 1766), red hartebeest (*Alcelaphus bucelaphus* Pallas 1766), warthog (*Phacochoerus aethiopicus,* Pallas 1766), steenbok (*Raphicerus campestris,* Thunberg 1811*)*, and common bush duiker (*Sylvicapra grimmia,* L. 1758) in relation to different vegetation types. This study provides baseline data regarding the density and distribution of ungulates over the different vegetation density zones on commercial farmland in north-central Namibia.

MATERIALS AND METHODS

Study Area

The farm Elandsvreugde is situated 44km East of Otjiwarongo (16° 39' 0" E, 20° 28' 12" S) in the Otjozondjupa region of Namibia. The 7300 ha farm is owned by the Cheetah Conservation Fund (CCF) and is part of the Waterberg Conservancy. The Waterberg Plateau, a 4100km^2 sandstone uplift, lies on the southern periphery of the study area and is the dominant geological feature of the region. The study area is semi-arid and lies between the 400mm and 450mm annual rainfall isopleths. There is marked seasonality with most rainfall occurring between November and April. There are three major seasons influencing the area climate; a wet-hot season (January - April), a dry-cold season (May - August) and an intermediate season (September – December). The wet and intermediate seasons are characterized by extensive thundershowers and flooding, with considerable variation in the amount of precipitation between years (Barnard 1998). The topography of the farm is generally flat with only few undulations; consequently, rainfall run-off is slow and there are no permanent river systems on the farm. The farm also has a number of man-made semi-permanent water reservoirs (known as "dams" in Namibia).

The region is situated in the Thornbush Savannah vegetation zone defined by Geiss (1971). Vegetation is typical of xeromorphic thornbush savannah with dominant woody plant genera consisting of *Acacia*, *Dichrostachys*, *Grewia*, *Terminallia*, and *Boscia*. Understory vegetation is relatively sparse, although ephemeral forbs are present following rain. This region has been extensively modified over the last century through human-mediated causes compounded by natural climatic fluctuations (Louw and Seely, 1982; Prins and van der Jaeugd, 1993; Hoffmann, 1997; Pallet, 1997). Some native woody species such as *A. mellifera*, *A. tortillis*, and *D. cinerea* have proliferated, and perennial grasses have been reduced throughout this area (Bester, 1996; Rhode, 1997).

Although cattle farming is no longer practiced, some parts of the farm are heavily encroached by *A. mellifera, A. tortillis* and *D. cinerea* as a result of previous management practices. There is also large open field that was formerly used for maize production and some remnant patches of open savannah are present. The farm is bordered by a 5-strand barbless border fence that allows wild ungulate movement and all internal fencing has been removed. Thus, the farm provides an ideal location to examine habitat preference for ungulates.

Through the use of aerial photographs and ground observations, the study area was divided into six different vegetation zones, based on the percentage canopy cover (Table A3.1) as a measure of the vegetation density and habitat type. Open field and transition areas that were previously cleared for maize production were classified as separate habitat types.

Table A3.1 Description of vegetation class by canopy cover. Typical thornbush areas are differentiated from vegetation classes that have developed as a consequence of previous clearing for maize production. Strip counts were designed to sample each vegetation class

VEGETATION CLASS	CANOPY COVER	AREA (percentage)
Thornbush		
Savannah (SAV)	6% - 15%	394.2 ha (5.4%)
Common Bush 1 (CB1)	16% - 30%	1 299.4 ha (17.8%)
Common Bush 2 (CB2)	31% - 75%	2 737.5 ha (37.5%)
Thick Bush (TB)	76% - 100%	781.1 ha (10.7%)
Former Maize Field		
Open field (F)	0% - 5%	1 627.9 ha (22.3%)
Transition Area (TA)	**40% - 80%**	**459.9 ha (6.3%)**

Strip Counts

Driving strip counts were conducted along two permanently marked routes, travelling at a maximum speed of 30km/h with an observer standing in the back of an open vehicle. The routes were designed to sample different vegetation zones in approximate proportion to the area that each zone occupies on the farm. Strip count routes were marked with 50 short metal poles, which were placed at 350 - 1600 metre intervals. Markers were used record the location of sightings and to delineate different vegetation classes occurring along the strip. We sampled each of the two routes at least three times a month during three different times of the day (morning, evening and night) for minimum of six counts each month. The starting time for each count was determined by the time of sunrise and sunset. Morning counts commenced at about 15 minutes before sunrise, evening counts commenced at about 1.5 hour before sunset and night counts commenced at approximately 2100h. For night counts, the observer utilized a handheld spotlight. Each count was approximately 1.5 – 2 hours in duration. All mammals observed were recorded along with their location and when possible age class and sex was also recorded. The vehicle was permitted to stop briefly for data recording, counting and identification of large herds, especially when the animals were distant. Standard binoculars were used to count and to identify distant animals.

Relative Density Calculations and Estimating Strip Width

In order to calculate animal density, the perpendicular sighting distance from the road from where the animal was first seen was recorded for a subset of the counts, starting in September 1999. However, because the sighting distance data was relatively sparse, we combined and averaged sighting data for the larger ungulates (oryx, kudu, red hartebeest and eland) and the smaller ungulates (duiker, warthog and steenbok). We used data collected primarily by a single observer (author N.M.) to reduce inter-observer variability. Sighting distance estimates were calibrated periodically using objective measurements (i.e. estimating distance and checking with a tape measure or by pacing). Maximum and mean sighting distance for large and small ungulates by different habitat type is shown in Table A3.2. Sighting distance data was used to calculate an estimated strip width (ESW), based on fitting a probability detection model (half-cosine model) to a histogram of frequency of distance observations using the program DISTANCE (Thomas et al. 1998). ESW was then used in all ensuing density calculations.

Table A3.2 Comparison of different strip width estimators for large and small ungulates observed in the study area. Maximum and mean sighting distances were calculated for each habitat type. Estimated Strip Width (ESW) was calculated using the programme DISTANCE.

	Large Ungulate			Small Ungulate			Human
Habitat Type	**Max**	**Mean**	**ESW**	**Max**	**Mean**	**ESW**	
SAV	400	90.44	117.39	70	26.29	42.98	146.72
CB1	420	62.18	78.61	200	23.35	53.40	72.80
CB2	200	35.95	56.56	100	16.84	27.72	56.98
TB	200	39.50	56.94	100	18.39	29.22	57.42
FIELD	1400	202.65	312.72	600	83.99	97.53	>500
TA	300	91.55	132.18	50	22.50	41.08	186.50

Because our sighting distance data were limited, we also determined a separate and independent estimate of strip width by measuring visibility distance for human subjects. Human subjects walked into the bush, on a compass bearing perpendicular to the road, until human subjects were out of sight from the view of an observer in the back of an open vehicle (similar to the viewing conditions during strip counts). Perpendicular distance back to the road was measured by pacing, and 2-4 randomly determined points for each marker location were measured in this manner. We verified general correspondence between human and modelled estimators of strip width (Table A3.2).

Linear distance (strip length) for each vegetation zone was measured using GPS data. To determine the effective sample area per species in each vegetation zone, we simply multiplied the effective strip width for the vegetation zone by the linear strip length for each vegetation zone. Species density for each vegetation zone was estimated using sightings per square kilometre of sampled area.

Although our study design called for one count per mouth for each time and circuit (totalling 6 counts per month), replicate counts were often performed. Because replicate counts did not always represent equal sampling effort for each time and route, we averaged results from replicate counts for each route and time. Overall density each month was calculated as the mean of the six route and time combinations. In this way, the final density calculation weighted each circuit and time equally. Variance was calculated in a similar manner, as a weighted variance for all counts performed during each month. A two-way analysis of variance (ANOVA) was used to examine the statistical relationship between habitat type, season and population density.

Seasonal Density

Seasonal density for each of the three seasons described above was calculated as the weighted mean of all counts during these time periods (see above). A two-way analysis of variance (ANOVA) was used to examine the statistical relationship between habitat type, season and population density.

RESULTS

Sighting distances and effective strip width

Average sighting distances and ESW varied substantially according to vegetation zone (Table A3.2). ESW for Thick Bush habitats were very similar to Common Bush 2 areas, although the bush density and crown closure was greater for Thick Bush. This is probably because areas classified as Thick Bush typically have larger and taller shrubs which allows sighting of animals underneath the canopy. Not surprisingly, ESW was greater for larger ungulate species than for smaller ungulate species. Night counts had lower visibility and consequently smaller ESW, evening counts had the highest visibility. We calculated and applied a different ESW for each time of count.

Sighting distances for human subjects were very similar to the effective strip width for larger ungulates. This suggests that strip width can be estimated *ad hoc* and applied to strip counts where distance data was not collected, or where multiple observers are collecting data and reliable distance estimates are not feasible (for example, a game census conducted by local community members). This measure provides an independent measure of strip width and thus lends confidence to subjective distance estimates that are typically collected during strip counts.

Habitat preference

Animal density varied significantly by vegetation zone for all ungulate species except duiker (Table A3.3).

Table A3.3 Results from 2-way analysis of variance regarding the seasonal habitat preferences of ungulate species.

	Habitat			Season			Habitat x Season		
	df	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**
Oryx	5	95.26	< 0.001	2	4.01	< 0.01	10	1.21	0.286
Eland	5	160.00	< 0.001	2	1.04	0.04	10	1.05	< 0.001
Red hartebeest	5	4.42	< 0.001	2	1.28	0.353	10	1.39	0.404
Kudu	5	2.40	0.037	2	3.16	0.279	10	4.41	0.183
Duiker	5	1.25	0.284	2	4.16	0.016	10	0.04	0.941
Steenbok	5	37.90	< 0.001	2	4.06	0.007	10	1.87	0.879
Warthog	5	11.02	< 0.001	2	5.11	0.018	10	0.51	0.05

Oryx, eland and red hartebeest had an inverse relationship with bush density and were found primarily in the cleared field. For all thornbush habitats, these species were found in highest densities in savannah area (Figure A3.1). Kudu had the opposite relationship and were found in highest densities in thicker bush habitats. It has been suggested that greater kudu, a browser, are enhanced by bush encroachment (Barnard 1998). Our data are consistent with this assertion, and we observed the highest densities of kudu in thicker thornbush habitats.

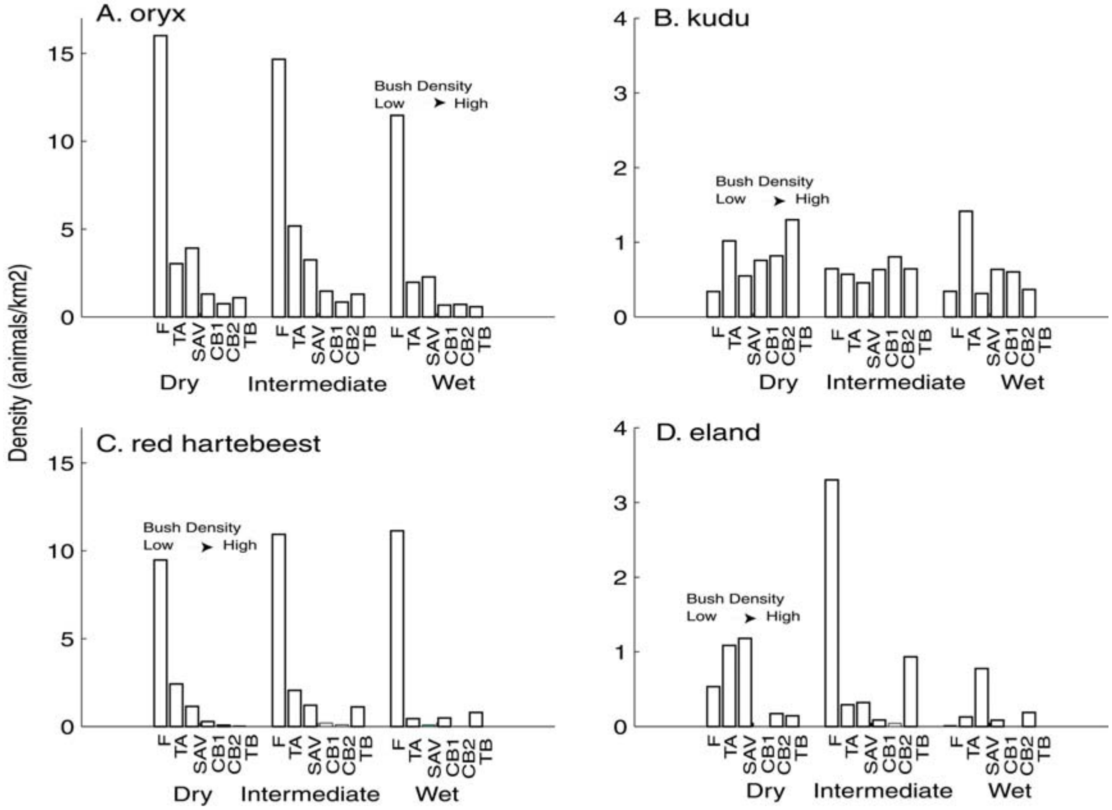

Figure A3.1 Relative density (animals per km^2) for large ungulate species according to bush density during the 3 seasons (dry, intermediate and wet) for Elandsvreugde (1995- 2000). Density was calculated by taking the average number of each species sighted, divided by the sampled area (strip width multiplied by the strip length) for each habitat type.

However, kudu were distributed throughout different habitat types and the relationship between population density and vegetation density was only marginally significant ($p = 0.03$, Table A3.3). We also observed the high densities of kudu in the transition areas that were previously cleared for maize production. Thus, although kudu were found in highest densities in Thick Bush areas, they utilize a wide variety of habitat types. Steenbok and warthogs were also found primarily in the cleared field (Figure A3.2).

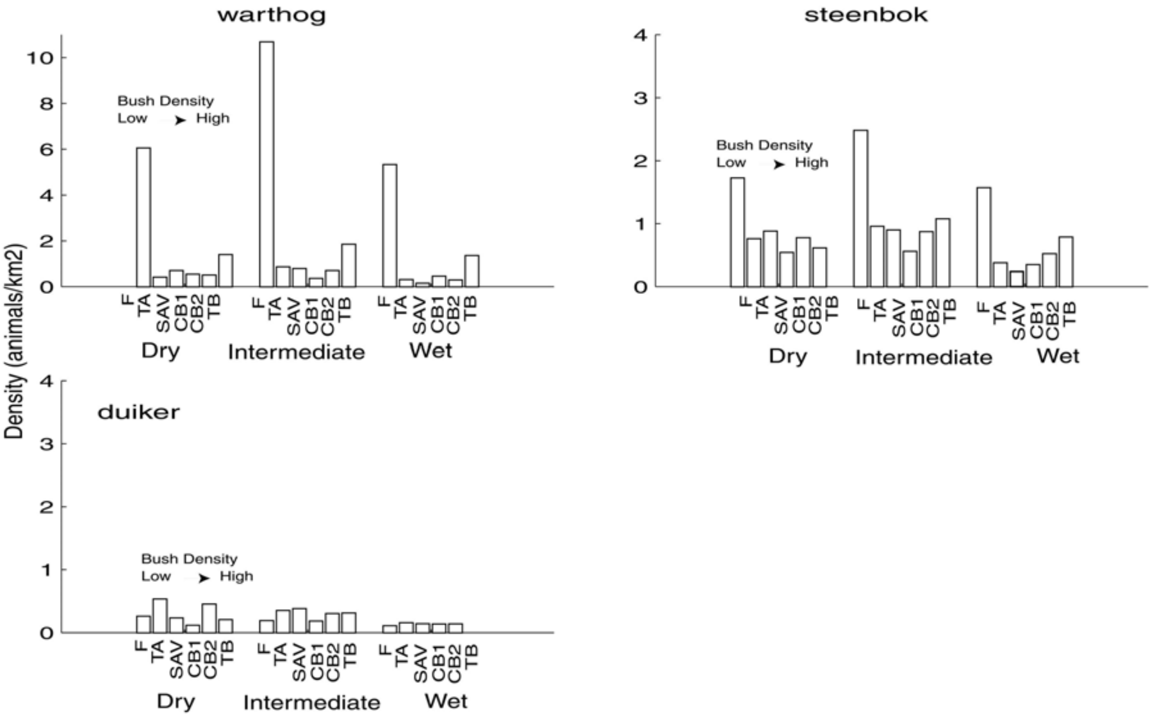

Figure A3.2 Relative density (animals per km^2) for small ungulate species according to bush density during the 3 seasons (dry, intermediate and wet) for Elandsvreugde (1995- 2000). Density was calculated by taking the average number of each species sighted, divided by the sampled area (strip width multiplied by the strip length) for each habitat type.

Seasonal trends and interactions

Red hartebeest and kudu did not exhibit seasonal differences in density, suggesting that these species are year-round residents of the study area. Oryx and eland, however, showed significant differences in seasonal abundance, suggesting that these species move in and out of the study area.

Warthog, steenbok and duiker also showed significant seasonal differences in density. It was unclear whether these animals actually moved in and out of the study area, or simply became more or less visible during different times of the year, although we did not observe differences in ESW according to season. This may be a sampling artefact, as sample sizes for sighting distances of smaller ungulates was fairly low.

There were surprisingly few significant interactions between habitat and seasonality. Only eland and warthog showed significant interactions (Table A3.3, Figures A3.1, A3.2). Eland tended to be found in the cleared field during the intermediate season, and in the transition area and savannah during the other seasons.

DISCUSSION

Ungulate Density and Habitat Preference

Statistical analysis suggests a strong relationship between observed species distribution and vegetation density. For grazers, such oryx and red hartebeest, population densities decline with an increase in woody vegetation density, and consequently bush encroachment probably has the greatest adverse impact on grazer density. This finding is consistent with (Skarpe, 1986), who found that the disappearance of palatable grasses and an increase in woody species reduces the quality of the habitat for grazers such as red hartebeest. According to (Bothma, 1989), the red hartebeest's diet consists almost entirely of grass (82% - 100%). Our findings suggest that the majority of red hartebeest are resident in cleared field habitats throughout the year and avoid heavily encroached areas.

Bush encroachment, on the other hand, may benefit browsers such as kudu (Barnard, 1998) and is probably neutral for duikers. The F-statistic of a standard 2-way ANOVA (Table A3.3) can be considered a measure of general habitat selectivity for our study. Kudu and duiker had the lowest F-statistic, and eland and oryx had the highest. These data suggest that kudu and duiker may be least sensitive to habitat impacts, which is consistent with the general observation that kudu and duiker are often the last ungulate species extirpated from impacted areas. The other ungulate species are probably more susceptible to habitat impacts including increasing bush encroachment and these species all showed significant differences in population density according to habitat. A caveat is that although kudu were found in highest densities in thick bush areas, they were also found in high densities in transition areas with young, even-aged stands of *Acacia* shrubs, suggesting that kudu may prefer and utilise a diverse mixture of habitat types and may utilize young patches of bush, possibly created and maintained by seasonal fires.

Seasonal Variation

This study revealed considerable seasonal variation in numbers of several species over different vegetation zones. Kudu and red hartebeest did not exhibit significant seasonal variation in density, suggesting that populations of these species are resident on the study area. Oryx and eland showed significant seasonal variation suggesting that they move in and out of the study area in different seasons. Successful management of these species probably requires areas much larger than a single commercial farm.

Higher animal densities were recorded for almost every species in the dry and intermediate seasons than in the wet season. At face value, these findings contradict with studies done by Jarman (1973) and Nagy and Knight (1994) that animals have a tendency to aggregate or to form larger groups during the rainy season and to split or disperse during the dry months. However, the seasonal variation of most species was considerably large, especially for eland and oryx, and aggregation may occur outside the study area. As such, the study area may be utilized as a dry season grazing area for species with significant seasonal differences in distribution. The seasonal aggregation of ungulates in the study area is probably influenced by large-scale spatial and temporal heterogeneity in abundance and quality of food as described by Bonifica (1992). The high ungulate immigration to the study area can also be related to the findings of Parris and Child in 1973 that hunting by people and overgrazing by livestock is a direct disturbance to wild ungulates, causing a shortage of preferred food and habitat which may occur outside of our study area, particularly during the drier months.

Observation done by one of the authors (N.M.) during the monthly game counts showed that the grass biomass in the study area was very high throughout the wet season, but drastically decreased from middle of the dry season when ungulate numbers increased in all vegetation zones. This drastic decrease in grass biomass was directly related to the high rate of ungulates movement into our study area. This finding also suggests that landscape-scale design of conservation areas should identify and incorporate sufficient grazing refugia during dry months.

We observed significant interactions between season and habitat for eland. Eland are thought to be predominantly browsers but have been reported to switch to grazing when the grass is green and high in protein (Bothma, 1989). However, we observed very low eland density during the wet seasons in our study area, even in cleared field areas where grass production is greatest and eland are reported in adjacent livestock farms during the wet seasons. The observed distribution pattern is more consistent with the findings of Frywell and Sinclair (1988) who suggest that migratory species move toward the habitats with lower food biomass during the wet season. This study's findings do not support the statement by Skinner and Smithers (1990) that eland occur only on short grass plain during transit, since eland were seen for long periods in this vegetation zone.

We suggest that this is due to differential biomass, where grazing in the cleared field probably provides greater biomass than browsing during the intermediate season, and a mix of browsing and grazing strategies are employed during the dry season, where we observed eland distributed in both cleared field and savannah areas.

CONCLUSIONS

This study provides baseline data on seasonal distribution of ungulates in different habitat types. We found that oryx, eland and red hartebeest may be the most sensitive to habitat changes associated with bush encroachment, while kudu may be facilitated by bush encroachment. These results suggest that bush encroachment may be substantially shifting ungulate density and distribution in Namibian thornbush ecosystems. These findings suggest that factors outside of the study area may severely impact migratory species, especially eland and oryx populations. Actions by single farmers could impact much larger areas, since eland and oryx are seasonally wide-ranging and utilize different areas seasonally. Although the farm is part of the Waterberg conservancy and hunting and poaching are strictly regulated, human impacts that occur outside of the conservancy could dramatically impact eland and oryx populations and consequently the large carnivores, including the Namibian cheetah, that depend on these species as a preybase. Additional information regarding home range size and larger-scale habitat utilization may facilitate systematic, science-based design of conservation areas that incorporate the ecological needs of native ungulate species.

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APPENDIX IV

MORPHOMETRIC PROTOCOLS USED WHILE MEASURING CHEETAHS

Appendix IV: Morphometric protocols used while measuring cheetahs

Both upper and lower canines were measured using the protocol shown, while the both front and hind feet were measured using the same foot protocol. We suggest that future authors could use these protocols in order to facilitate direct comparisons between cheetahs in different studies, or to state clearly where any deviations occurred.

Measurement	Protocol used
Body mass	Taken using a hanging scale, with cheetah on a stretcher, then adjusted for the stretcher mass
Total body length	Tip of the nose to the end of the last caudal (tail) vertebra
Head--body length	Tip of the nose to the base of the tail - measured to the notch on the sacrum
Tail length	Base of the tail (sacrum) to the end of the last caudal vertebra
Skull length	From the stop to the top of the occipital bone, which can be felt as a notch on the back of the skull
Skull width	Across the widest points of the zygomatic arches
Muzzle length	Tip of the nose to the stop
Muzzle girth	Circumference measured immediately below the stop with the mouth fully closed
Canine length	From the gum-line to the point of the tooth
Chest girth	The widest point of the ribcage
Abdomen girth	Just in front of the hindlegs, at the narrowest point
Total foreleg length	Highest point of the scapula to the base of the foot, measured to the back of the palmar pad.
Total hindleg length	Top of the ilium (the highest point of the hip) to the base of the foot
Foot width	The widest point of the foot
Foot length	The back of the palmar pad to the tip of the digital pad
Testicle width	The widest point of the testicle
Testicle length	From the base of the testicle, measured outwards

APPENDIX V

MORPHOMETRIC DATA FOR CHEETAHS PUBLISHED FROM VARIOUS STUDIES

Appendix V – Morphometric data for cheetahs published from various studies.

Four of the datasets refer to *Acinonyx jubatus jubatus* (this study; du Preez 1976; Labuschagne 1979; McLaughlin 1970a), while two refer to *A. j. raineyii* (Caro 1994; McLaughlin 1970b). All measurements are in centimeters (cm), apart from mass, which is in kilograms (kg). Statistical comparisons were made between datasets where possible, and significant variation ($P < 0.05$) is denoted using the following signs: ^{1} denotes significant variation from this study, ^{2} from du Preez (1976), ^{3} from Labuschagne (1979), ^{4} from McLaughlin (1970a), ^{5} from Caro (1994), and ^{6} from McLaughlin (1970b).

Body measurement	CCF mean (this study)	Etosha N.P. Namibia (du Preez 1976)			Kalahari Gemsbok N.P. South Africa (Labuschagne 1979)			South Africa (McLaughlin 1970a)			Serengeti N.P. (Caro 1994)			East Africa (McLaughlin 1970b)		
		Mean	*n*	Range	Mean	*n*	Range	Mean	*n*	Range	Mean	*n*	Range	Mean	*n*	Range
Male mass	45.6^{4,5,6}	44.1	8	38.6--57.6	53.9	7	39--59	55.0^{1,5,6}	4	50--62	41.4^{1,4,6}	23	28.5--51.0	61.0^{1,4,5}	4	58--65
Female mass	37.2^{4,6}	35.9	8	29.5--44.5	43.0	6	36--48	48.5^{1,5}	2	39--58	35.9^{4,6}	19	21.0--43	52.0^{1,5}	2	41--63
Male total length	202.2^{5,6}	202.4	10	194.4--222.3	206.0	7	191--221	201.3^{5,6}	14	179--222	190.6^{1,4,6}	24	172--209.5	209.4^{1,4,5}	5	198--224
Female total length	192.4^{6}	193.1	10	179.7--210.8	190.0	7	184--196	186.0	1	-	189.8^{6}	16	174--208	207.4^{1,5}	5	191--236
Male body length	125.5^{5}	130.8	10	126.4--141.0	-	-	-	-	-	-	122.5^{1,6}	24	113--136	127.0^{5}	2	124--130
Female body length	120.1^{5}	124.8	10	117.5--134.6	-	-	-	-	-	-	124.5^{1}	16	113--140	-	-	-
Male tail length	76.7^{5}	71.6	10	68.0 -81.3	71.5	7	65--76	72.8^{5}	6	60--79	68.1^{1,4}	24	63--74	66.0	1	-
Female tail length	72.5^{5}	68.3	10	62.2--76.2	66.7	6	63--69	-	-	-	65.5^{1}	19	59.5--73	73.0	1	-
Male chest girth	71.7^{5}	70.1	10	66.0 -78.7	-		-	-	-	-	69.2^{1}	21	62--77	-	-	-
Female chest girth	67.3^{4,6}	63.0	10	54.6--69.9	43.0	6	36--48	48.5^{1,5,6}	2	39--58	66.2 ^{4,6}	12	61--72	52.0^{1,4,5}	2	41--63
Male shoulder height	77.0^{4}	85.7	10	78.7--96.5	88.1	7	83--94	79.9^{1}	8	74--86	-	-	-	76.8	6	74--81
Female shoulder height	73.6	80.8	10	73.7--69.9	84.7	6	79--84	70.0	1	-	-	-	-	75.3	3	67--84

APPENDIX VI

SAMPLE POPULATION OF CHEETAHS USED FOR GENETIC ANALYSES

Appendix VI – Sample population of cheetahs used for genetic analyses

ID # (RC#)	Region	Family Analysis**		Sex
822*	1gob	sib 1		F
823*	1gob			F
824	1gob			M
825	1gob	sib1		M
826*	1gob	sib 2		M
827	1gob	sib 2		M
844*	1gob	sib 3		M
845	1gob	sib 3		F
846	1gob	sib 3		F
854*	1gob			F
855	1gob			F
871*	1gob	D1		F
877	1gob	off 1		M
878 (112)	1gob	off 1		F
889	1gob			M
907	1gob			F
908*	1gob			M
1065*	1gob			M
1079*	1gob	sib 4		M
1080	1gob	sib 4		M
1081	1gob	sib 4		M
1082*	1gob			M
1083*	1gob			F
1100 (802)	1gob			F
1101	1gob	D2		F
1102	1gob	off 2	sib 5	M
1103	1gob	off 2	sib 5	M
1136	1gob	off 2	sib 5	M
1149	1gob			M
1150	1gob			M
862	2gro	sib 6		M
863*	2gro	sib 6		M
864	2gro	sib 6		F
903*	2gro			M
919*	2gro			F
947*	2gro			M
954	2gro	sib 7		M
955	2gro	sib 7		M
958*	2gro	sib 7		F
961	2gro	sib 8		M
962	2gro	sib 8		M
963*	2gro	sib 8		F
964	2gro	sib 8		F
965*	2gro	sib 9		M
966	2gro	sib 9		M
992 (882)	2gro	D3		F
993*	2gro	off 3	sib 10	F
994	2gro	off 3	sib 10	M
995	2gro	off 3	sib 10	M
1060*	2gro	sib 11		M
1061 (559/893)	2gro	sib 11		M
1062*	2gro			M
1063 (959)	2gro	sib 12		M
1064*	2gro	sib 12		M
1122	2gro			M
1123	2gro			M
1125	2gro			F
1128	2gro			M
1142	2gro			M
1143	2gro			M
807	3oka	D 4		F
808	3oka	off 4	sib 14	M
809	3oka	off 4	sib 14	M
817	3oka	sib 15		M
818*	3oka	sib 15		M
819	3oka	sib 15		M
895	3oka	D 5		F
896*	3oka	off 5		F
897*	3oka			M
929	3oka	sib 16		M
930	3oka	sib 16		M
931*	3oka	sib 16		M
932*	3oka			M
933*	3oka			M
934	3oka			M
935	3oka			M
942	3oka			F
945*	3oka	sib 17		M

Appendix VI continued

ID # (RC#)	Region	Family Analysis**		Sex
946	3oka	sib 17		M
948 (233)	3oka	D 6		F
949	3oka	off 6	sib 18	F
950	3oka	off 6	sib 18	M
951	3oka	off 6	sib 18	M
953	3oka			M
968	3oka	off 7	sib 19	M
969	3oka	D 7		F
970*	3oka	off 7	sib 19	M
971	3oka	off 7	sib 19	F
972	3oka			F
973*	3oka			M
978 (400)	3oka			F
987	3oka			M
988	3oka	sib 20		M
989	3oka	sib 20		M
1004	3oka	off 8	sib 20	M
1006	3oka	D 8		F
1008	3oka	off 8	sib 20	M
1009	3oka			F
1012	3oka	off 8	sib 20	M
1016	3oka	sib 21		M
1017*	3oka	sib 21		M
1028*	3oka			F
1029	3oka	sib 22		M
1030*	3oka	sib 22		F
1043*	3oka			M
1044*	3oka			M
1055	3oka	sib 23		M
1056	3oka	sib 23		F
1057*	3oka	sib 23		F
1058*	3oka	sib 24		M
1059	3oka	sib 24		M
1074*	3oka			F
1075*	3oka	sib 25		M
1076	3oka	sib 25		M
1077	3oka	sib 25		M
1078	3oka	sib 25		F
1095	3oka			M

ID # (RC#)	Region	Family Analysis**		Sex
1096	3oka			M
1097	3oka			F
1112	3oka	sib 26		F
1113	3oka	sib 27 (26?)		F
1114	3oka	sib 28 (26?)		M
1115	3oka	sib 29 (26?)		F
1116	3oka	D 9		F
1117	3oka	off 9	sib 30	F
1118	3oka	off 9	sib 30	F
1119	3oka	off 9	sib 30	F
1129	3oka	sib 31		M
1130	3oka	sib 31		F
1131	3oka	sib 31		M
1132	3oka	sib 31		F
1151	3oka	sib 32		M
1152	3oka	sib 32		M
1153	3oka			F
1159	3oka	off 10	sib 33	F
1160	3oka	off 10	sib 33	F
1161	3oka	off 10	sib 33	M
1162	3oka	D 10		F
890	4oma	sib 34		M
892*	4oma	D 11		F
893	4oma	off 11	sib 35	M
894	4oma	off 11	sib 35	F
900	4oma	sib 34		M
901*	4oma	sib 34		M
904	4oma	sib 36		M
905*	4oma	sib 36		F
906	4oma	sib 36		F
913	4oma	sib 13		M
914*	4oma	sib 13		M
915	4oma			M
927*	4oma			M
943	4oma			M
944*	4oma			F
959	4oma			M
1021*	4oma			F
1031*	4oma	off 12	sib 37	F

Appendix VI continued

ID # (RC#)	Region	Family Analysis**		Sex
1032	4oma	off 12	sib 37	M
1033	4oma	off 12	sib 37	M
1034	4oma	D 12		F
1035	4oma	off 12	sib 37	M
1046	4oma	sib 38		F
1047*	4oma	sib 38		M
1048	4oma	sib 38		M
1049	4oma	sib 39		M
1050	4oma	sib 39		M
1051	4oma	sib 39		M
1052*	4oma			F
1053	4oma			M
1054*	4oma			F
1066*	4oma			F
1067*	4oma			F
1068*	4oma			M
1070*	4oma			M
1094	4oma			M
1108	4oma			M
1109	4oma			M
1111	4oma			M
1138	4oma	off 13	sib 40	M
1139	4oma	off 13	sib 40	M
1140	4oma	off 13	sib 40	M
1141	4oma	D 13		
804*	5otj	D 14		F
805	5otj	off 14	sib 41	M
806	5otj	off 14	sib 41	F
820	5otj			F
821 (052)*	5otj			M
830	5otj	D 15		F
831 (320)*	5otj	off 15	sib 42	M
832	5otj	off 15	sib 42	M
833	5otj	off 15	sib 42	M
834	5otj			M
835 (688)	5otj			M
836	5otj			M
837	5otj	sib 43		F
838*	5otj	sib 43		M
840	5otj			M

ID # (RC#)	Region	Family Analysis**		Sex
840 (442)	5otj			M
849	5otj			F
850	5otj	off 16	sib 44	F
851	5otj	off 16	sib 44	F
852	5otj	off 16	sib 44	M
853	5otj	D 16		F
860*	5otj			F
861	5otj			M
865 (174)	5otj	sib 45		M
866	5otj	sib 45		M
867 (190)	5otj			M
868 (293)*	5otj	sib 46		M
869 (082)	5otj	sib 46		M
870	5otj			M
881 (640)*	5otj			M
882*	5otj			M
883	5otj			M
886*	5otj			M
888*	5otj			M
891	5otj	sib 47		F
902*	5otj	sib 47		F
937	5otj			M
938 (143)	5otj			M
952 (711)	5otj			M
956	5otj			F
967 (353)	5otj			F
974 (540)*	5otj	sib 48		M
975	5otj	sib 48		M
976	5otj	sib 48		M
977 (490)*	5otj			M
979 (730)	5otj	sib 49		M
980	5otj	sib 49		M
984 (442)*	5otj			F
985 (987)	5otj	sib 50		M
986*	5otj	sib 50		F
990	5ojt			M
991	5otj			M
1002	5otj			F
1003	5otj	D 17		M
1014	5otj	off 17	sib 51	

* = cheetahs used in unrelated analysis, ** sib = sibling groups, D = Dam of offspring groups, off = offspring groups

Appendix VI continued

ID # (RC#)	Region	Family Analysis**		Sex
1015*	5otj	off 17	sib 51	F
1025*	5otj	off 17	sib 51	M
1026*	5otj			F
1042	5otj			F
1069*	5otj			F
1084*	5otj	D 18		F
1085	5otj	off 18	sib 52	M
1086	5otj	off 18	sib 52	M
1088	5otj	off 18	sib 52	M
1089	5otj	off 19	sib 53	M
1090*	5otj	off 19	sib 53	F
1091	5otj	off 19	sib 53	M
1092	5otj	D 19		F
1105 (742)	5otj			M
1107 (409)	5otj			F
1144 (143)	5otj	D 44		F
1145	5otj	off 20	sib 54	M
1146	5otj	off 20	sib 54	F
1147	5otj	off 20	sib 54	F
1148	5otj			M
1154 (720)	5otj	D 21		F
1155	5otj	off 21	sib 55	F
1156	5otj	off 21	sib 55	M
1157	5otj	off 21	sib 55	M
1158 (671)	5otj			M
1163 (572)	5otj	sib 56		M
1164 (791)	5otj	sib 56		M
1167 (559)	5otj			M
1168	5otj			F
1170	5otj			M
856	6out			M
857	6out			M
858	6out			M
859	6out			M
926*	6out			F
940*	6out			F
996*	6out			M
997	6out			M
998	6out			M

ID # (RC#)	Region	Family Analysis**	Sex
1018	6out	sib 57	M
1019*	6out	sib 57	F
1022*	6out		M
1023*	6out		M
1071	6out	sib 58	M
1072*	6out	sib 58	M
1133	6out		F
801	7win	sib 59	M
802	7win	sib 59	M
810	7win		F
811	7win		M
812	7win		M
813	7win		M
814	7win		M
815	7win		M
816*	7win		M
829	7win		F
847*	7win		M
898	7win		M
899	7win		M
916*	7win		M
917	7win		M
920	7win	sib 60	M
921*	7win	sib 60	M
999*	7win		M
1000	7win		M
1001*	7win		F
1002	7win		F
1036	7win	sib 61	F
1037	7win	sib 61	M
1038	7win	sib 61	M
1039	7win	sib 61	F
1040	7win		M
1073	7win		M
1135	7win		M
1137	unk		M
884	unk		M
885	unk		M

* = cheetahs used in unrelated analysis, ** sib = sibling groups, D = Dam of offspring groups, off = offspring groups

APPENDIX VII

ALLELE FREQUENCIES FOR ALL LOCI

AND SUBPOPULATIONS

Appendix VII: Allele frequencies for all loci and subpopulations.

Allele sizes are given in bp.

Locus	Allele	1gob	2gro	3oka	4oma	5otj	6out	7win	8ser
Fca 008	158	0.192	0.409	0.293	0.526	0.267	0.444	0.350	0.722
	160	0.346	0.227	0.517	0.237	0.400	0.444	0.250	0.111
	164	0.385	—	0.138	0.105	0.100	—	0.200	—
	168	—	0.136	0.034	—	0.050	—	—	0.111
	170	—	0.091	0.017	0.079	0.100	0.056	0.050	—
	172	0.077	0.136	—	0.053	0.083	0.056	0.150	0.056
Fca 026	137	0.077	—	—	—	0.017	0.167	—	
	141	0.077	—	—	0.029	0.033	0.056	0.077	
	143	0.000	—	0.020	—	0.017	—	—	
	145	0.154	0.300	0.180	0.147	0.233	0.111	0.423	
	147	0.462	0.550	0.640	0.588	0.550	0.389	0.346	
	149	0.038	—	0.020	0.029	0.100	—	—	
	151	0.192	0.150	0.140	0.206	0.050	0.278	0.154	
				—					
Fca 051	180	—	—	—	—	0.016	—	—	—
	182	0.125	—	0.036	0.050	0.016	0.188	0.115	0.111
	184	0.083	—	0.036	0.100	0.016	0.063	0.115	0.167
	186	—	—	0.036	—	—	—	0.038	—
	188	0.667	0.773	0.750	0.850	0.839	0.750	0.615	0.667
	190	0.125	0.227	0.143	—	0.113	—	0.115	0.056
Fca 085	126	—	—	0.017	—	—	—	—	—
	128	0.077	0.045	—	—	0.030	—	0.045	—
	130	0.462	0.364	0.759	0.553	0.652	0.389	0.636	0.571
	132	0.231	0.136	0.069	0.105	0.061	0.056	0.045	0.071
	134	—	0.091	—	0.053	0.045	0.167	0.045	—
	140	0.038	0.182	0.017	—	0.030	—	—	0.214
	142	0.038	—	0.052	0.079	0.076	—	0.045	0.143
	144	—	—	—	0.026	0.030	—	—	—
	150	0.154	0.182	0.086	0.184	0.076	0.389	0.182	—
Fca 096	196	—	—	—	—	0.018	—	—	
	198	0.045	0.045	0.022	0.156	0.018	—	0.077	
	202	0.227	0.227	0.348	0.031	0.089	0.188	0.346	
	204	0.136	0.091	0.087	0.125	0.089	0.313	0.115	
	206	0.045	—	—	—	—	—	0.038	
	208	0.273	0.182	0.217	0.188	0.286	—	0.154	
	210	—	0.091	0.174	0.094	0.214	0.063	0.038	
	212	0.045	—	0.022	—	—	—	—	
	214	0.227	0.364	0.130	0.406	0.286	0.375	0.231	
	218	—	—	—	—	—	0.063	—	

Appendix VII continued

Locus	Allele	1gob	2gro	3oka	4oma	5otj	6out	7win	8ser
Fca 097	127	0.250	—	0.028	—	—	—	—	
	131	—	—	0.028	—	—	—	—	
	133	0.083	—	—	—	—	—	—	
	135	0.250	0.375	0.500	0.333	0.478	0.125	0.273	
	137	—	0.125	—	—	—	0.250	—	
	139	0.167	0.125	0.278	0.444	0.261	0.375	0.318	
	141	—	0.250	0.083	0.056	0.087	0.000	0.136	
	143	—	—	—	0.056	—	—	0.045	
	147	0.250	0.125	0.083	0.056	0.174	0.250	0.227	
	149	—	—	—	0.056	—	—	—	
Fca 117	154	0.208	0.045	0.327	0.225	0.156	0.063	0.231	
	156	0.292	0.091	0.096	0.100	0.172	0.125	0.308	
	158	0.292	0.500	0.288	0.300	0.234	0.375	0.000	
	160	0.042	0.091	0.077	0.075	0.125	0.063	0.038	
	162	0.042	0.182	0.038	0.150	0.109	0.250	0.115	
	164	0.125	0.091	0.154	0.100	0.188	0.125	0.308	
	166	—	—	0.019	0.050	0.016	—	—	
Fca 126	122	—	—	0.037	0.056	0.030	—	—	—
	124	0.167	0.455	0.241	0.444	0.348	0.438	0.545	0.333
	126	0.500	0.227	0.574	0.194	0.455	0.125	0.318	0.389
	128	—	—	—	—	0.061	—	0.045	0.056
	132	0.042	—	0.019	—	—	—	—	—
	134	0.250	0.273	0.130	0.278	0.076	0.438	0.091	—
	136	0.042	0.045	—	0.028	0.030	—	—	0.167
	140	—	—	—	—	—	—	—	0.056
Fca 133	123	—	0.100	—	—	0.017	0.071	—	
	125	0.042	—	0.043	0.031	0.034	—	0.038	
	127	—	0.050	0.022	—	—	—	0.038	
	129	—	0.050	0.065	0.063	0.034	0.071	0.077	
	131	0.167	0.250	0.261	0.406	0.379	0.643	0.385	
	133	0.500	0.550	0.326	0.344	0.379	0.214	0.115	
	135	0.208	—	0.261	0.156	0.155	—	0.192	
	137	0.083	—	0.022	—	—	—	0.038	
	139	—	—	—	—	—	—	0.038	
	141	—	—	—	—	—	—	0.077	
Fca 169	107	0.375	0.500	0.125	0.333	0.227	—	0.429	
	109	0.250	—	0.500	0.667	0.318	—	0.286	
	111	—	—	0.125	—	0.318	—	0.071	
	113	0.375	0.500	0.250	—	0.136	—	0.214	

Appendix VII continued

Locus	Allele	1gob	2gro	3oka	4oma	5otj	6out	7win	8ser
Fca 187	132	0.115	0.500	0.196	0.400	0.265	0.250	0.182	
	134	—	—	0.018	—	—	—	—	
	138	0.731	0.364	0.643	0.425	0.618	0.625	0.727	
	140	0.154	0.136	0.143	0.175	0.118	0.125	0.091	
Fca 212	115	—	—	—	0.038	0.026	—	—	
	117	0.100	0.250	0.024	—	0.079	0.250	0.143	
	119	0.050	0.000	0.024	—	0.000	0.063	—	
	123	—	—	—	0.115	0.079	0.375	—	
	125	0.250	0.500	0.619	0.423	0.526	0.125	0.357	
	127	0.300	0.150	0.143	0.269	0.079	—	0.071	
	129	0.300	0.100	0.167	0.154	0.158	0.188	0.429	
	131	—	—	0.024	—	0.053	—	—	
Fca 214	161	—	—	—	—	—	—	0.038	
	163	0.038	0.056	—	—	0.016	0.063	0.077	
	165	—	—	0.018	0.111	—	—	—	
	169	0.231	0.444	0.250	0.139	0.422	0.750	0.115	
	171	0.346	—	0.232	0.389	0.063	—	0.308	
	173	0.038	0.056	0.107	—	0.047	—	0.115	
	175	0.269	0.333	0.179	0.139	0.266	0.188	0.308	
	177	0.077	0.111	0.161	0.194	0.172	—	0.038	
	179	—	—	0.054	0.028	0.016	—	—	
Fca 224	165	—	0.045	—	—	—	0.111	—	—
	167	0.042	0.182	0.074	0.111	0.129	—	—	—
	169	0.208	0.000	0.167	0.083	0.113	—	0.318	0.056
	171	0.458	0.409	0.296	0.389	0.306	0.278	0.273	0.167
	173	0.083	0.318	0.389	0.417	0.371	0.556	0.318	0.333
	175	—	—	—	—	0.016	—	—	0.444
	177	0.208	0.045	0.074	—	0.065	0.056	0.091	—
			—						
Fca 247	150	—	—	0.017	—	0.015	—	—	
	154	0.231	0.227	0.276	0.342	0.182	0.188	0.167	
	156	0.423	0.409	0.310	0.447	0.303	0.500	0.375	
	158	—	—	0.034	0.026	0.045	0.063	—	
	160	0.038	0.091	0.052	—	0.076	—	0.042	
	162	0.308	0.273	0.293	0.132	0.318	0.188	0.333	
	164	—	—	0.017	0.053	0.061	0.063	0.083	

Appendix VII continued

Locus	Allele	1gob	2gro	3oka	4oma	5otj	6out	7win	8ser
Fca 290	210	0.045	0.063	0.036	0.028	—	—	0.038	
	216	—	0.125	0.036	0.056	0.029	0.167	—	
	218	0.455	0.313	0.214	0.250	0.265	0.389	0.423	
	220	0.455	0.438	0.643	0.583	0.500	0.278	0.500	
	224	0.045	0.063	0.036	0.056	0.206	0.111	0.038	
	226	—	—	—	0.028	—	0.056	—	
	228	—	—	0.036	—	—	—	—	
Fca 298	217	—	—	—	—	0.015	—	—	—
	219	—	—	0.037	—	—	—	—	—
	221	0.846	0.682	0.593	0.553	0.647	0.929	0.654	0.667
	225	—	—	0.019	—	0.059	—	0.115	—
	227	0.154	0.318	0.352	0.447	0.279	0.071	0.231	0.333
Fca 310	116	—	0.045	—	—	—	—	—	—
	120	0.208	0.364	0.426	0.350	0.485	0.278	0.231	0.111
	122	0.208	0.227	0.056	0.200	0.103	0.111	0.231	0.111
	124	—	—	—	—	—	—	—	0.333
	126	0.417	0.227	0.407	0.350	0.353	0.444	0.231	0.389
	128	—	0.045	—	—	—	—	—	0.056
	130	0.167	0.091	0.111	0.100	0.059	0.167	0.308	—
Fca 344	119	—	—	0.017	—	—	—	—	—
	121	0.577	0.455	0.655	0.500	0.636	0.500	0.667	0.643
	123	0.423	0.545	0.328	0.500	0.364	0.500	0.333	0.357
Fca 014	152	0.045	0.091	0.045	0.125	0.146	0.188	0.063	0.625
	154	0.136	0.182	0.136	0.031	0.021	0.063	0.125	0.188
	156	0.136	—	0.136	0.031	0.042	—	0.188	—
	158	0.364	0.364	0.273	0.313	0.313	0.563	0.375	—
	160	—	0.045	—	—	—	—	—	0.125
	162	0.318	0.318	0.409	0.500	0.479	0.188	0.250	—
	168	—	—	—	—	—	—	—	0.063
Fca069	106	—	—	—	—	—	0.071	—	
	108	0.364	0.250	0.250	0.281	0.158	0.143	0.417	
	110	0.227	0.300	0.444	0.313	0.395	0.071	0.333	
	112	0.091	0.200	0.083	0.094	0.184	0.500	—	
	114	0.318	0.250	0.222	0.313	0.263	0.214	0.250	

Appendix VII continued

Locus	Allele	1gob	2gro	3oka	4oma	5otj	6out	7win	8ser
Fca 075	129	—	0.091	—	—	—	—	—	0.056
	131	0.500	0.364	0.528	0.281	0.500	0.214	0.333	0.389
	133	0.273	0.273	0.306	0.125	0.357	0.286	0.417	0.278
	139	—	0.045	—	0.094	0.024	0.429	—	0.167
	141	0.136	0.091	0.056	0.031	—	—	0.167	0.111
	143	0.045	0.045	—	0.156	0.024	—	0.083	—
	145	—	—	0.083	0.063	0.095	0.071	0.000	—
	147	0.045	—	0.028	0.250	—	—	—	—
Fca 078	192	—	—	—	—	—	—	0.083	
	194	0.136	0.150	0.059	0.385	0.176	0.300	0.083	
	200	—	—	0.029	0.077	0.118	—	—	
	202	0.182	—	—	—	0.029	—	—	
	204	0.364	0.450	0.618	0.269	0.412	0.500	0.500	
	206	0.136	0.150	0.088	0.192	0.118	0.200	0.250	
	208	0.045	—	—	0.038	0.059	—	0.083	
	210	0.136	0.150	0.147	0.038	0.088	—	—	
	212	—	0.100	0.059	—	—	—	—	
Fca 080	245	0.136	0.045	0.147	0.100	0.190	0.071	0.583	
	247	0.591	0.636	0.353	0.700	0.548	0.571	0.333	
	249	0.227	0.182	0.500	0.200	0.238	0.357	0.083	
	251	0.045	0.136	—	—	0.024	—	—	
Fca 088	107	0.227	0.045	0.273	0.125	0.180	0.071	0.143	0.111
	109	0.045	0.045	—	—	—	—	0.071	0.111
	111	0.227	0.273	0.386	0.438	0.500	0.500	0.357	0.500
	113	0.045	0.045	—	0.063	—	—	—	0.111
	115	0.455	0.500	0.318	0.313	0.300	0.357	0.357	—
	117	—	0.091	0.023	0.063	0.020	0.071	0.071	0.167
Fca 094	222	—	—	—	—	—	—	0.167	
	226	—	0.045	—	—	—	—	—	
	228	0.136	0.182	0.412	0.344	0.395	0.143	—	
	230	0.409	0.318	0.265	0.344	0.289	0.357	0.417	
	234	—	0.045	—	0.094	—	0.143	—	
	236	0.455	0.409	0.324	0.219	0.316	0.357	0.417	

Appendix VII continued

Locus	Allele	1gob	2gro	3oka	4oma	5otj	6out	7win	8ser
Fca 105	181	0.136	0.045	0.028	0.281	0.048	0.071	—	0.056
	183	—	—	—	—	—	—	—	0.389
	187	0.136	—	0.028	—	—	—	—	0.111
	189	0.409	0.318	0.333	0.188	0.452	0.500	0.417	—
	191	—	0.273	0.111	0.125	0.238	0.214	0.167	0.389
	193	0.318	0.227	0.472	0.375	0.238	0.214	0.333	0.056
	195	—	0.136	0.028	0.031	0.024	—	0.083	—
Fca 113	145	—	—	—	—	0.026	—	—	
	149	0.000	0.056	—	—	—	—	—	
	153	—	—	0.208	0.091	—	—	—	
	155	0.450	0.333	0.125	0.273	0.421	0.143	0.333	
	157	0.500	0.611	0.625	0.591	0.500	0.857	0.417	
	159	0.050	—	0.042	0.045	0.053	0.000	0.250	
Fca 161	173	0.318	0.500	0.471	0.531	0.556	0.357	0.500	
	177	0.182	0.182	0.206	0.063	0.056	0.143	—	
	179	0.182	0.182	0.118	0.219	0.111	0.000	0.167	
	181	0.273	0.136	0.206	0.156	0.250	0.429	0.333	
	183	0.045	—	—	0.031	0.028	0.071	0.000	
Fca 166	207	0.136	0.136	0.056	—	0.024	0.357	—	
	209	0.091	0.136	0.139	0.033	0.048	—	0.250	
	211	0.182	0.182	0.139	0.167	0.214	0.143	0.083	
	213	0.455	0.500	0.472	0.700	0.619	0.214	0.500	
	215	0.136	0.045	0.194	0.100	0.095	0.286	0.167	
Fca 171	106	0.045	—	—	0.033	—	—	—	
	108	0.045	—	0.029	0.000	—	—	—	
	110	0.182	0.091	0.118	0.167	0.053	0.000	0.083	
	112	0.182	0.227	0.235	0.167	0.316	0.714	0.167	
	114	0.318	0.091	0.441	0.133	0.211	0.214	0.333	
	116	0.045	0.273	0.118	0.333	0.237	0.000	0.167	
	118	0.091	0.318	0.059	0.167	0.184	0.071	0.250	
	120	0.091	—	—	—	—	—	—	
Fca 192	190	0.318	0.550	0.438	0.467	0.500	0.400	0.100	
	192	0.091	—	0.063	0.067	0.029	0.100	—	
	194	0.045	0.100	—	0.033	0.029	—	—	
	196	0.500	0.300	0.438	0.400	0.441	0.500	0.700	
	198	0.045	0.050	0.063	0.033	—	—	0.200	

Appendix VII continued

Locus	Allele	1gob	2gro	3oka	4oma	5otj	6out	7win	8ser
Fca 208	311	0.250	0.182	0.063	0.125	0.316	0.417	0.333	
	315	0.100	0.045	0.000	0.094	0.026	0.083	—	
	317	0.200	0.500	0.656	0.469	0.342	0.417	0.250	
	319	0.350	0.136	0.156	0.250	0.184	0.083	0.417	
	321	0.100	0.136	0.125	0.063	0.132	—	—	
Fca 225	231	0.409	0.227	0.389	0.286	0.450	0.143	0.417	
	233	0.318	0.500	0.361	0.321	0.400	0.143	0.250	
	237	0.091	—	0.028	0.036	—	—	0.167	
	239	0.091	0.273	0.139	0.357	0.125	0.714	0.167	
	245	0.091	—	0.083	—	0.025	—	—	
Fca 230	87	—	—	—	0.083	0.071	—	—	
	89	0.045	—	—	—	—	—	0.100	
	91	0.136	0.313	0.294	0.125	0.429	0.250	0.300	
	97	0.091	—	0.088	0.042	—	—	—	
	99	0.227	0.063	0.176	0.333	0.214	—	0.100	
	101	0.318	0.313	0.353	0.250	0.143	0.500	0.300	
	103	0.182	0.313	0.088	0.167	0.143	0.250	0.200	
Fca 327	189	0.136	0.455	0.200	0.286	0.421	0.500	0.250	
	191	—	—	—	0.036	0.026	—	—	
	193	0.591	0.318	0.367	0.321	0.263	0.417	0.417	
	195	0.227	0.136	0.267	0.143	0.158	0.083	0.250	
	197	0.045	0.091	0.167	0.214	0.132	—	0.083	
Fca 559	113	0.250	0.250	0.313	0.167	0.150	—	—	
	117	0.500	0.500	0.250	0.167	0.350	—	1.000	
	121	—	—	0.125	0.333	0.300	—	—	
	125	0.250	0.250	0.313	0.333	0.200	—	—	
Fca 042	208	—	—	—	—	0.125	—	0.250	
	212	0.250	—	0.083	—	—	—	—	
	220	0.250	0.250	—	—	—	—	—	
	224	0.250	0.250	0.583	0.500	0.875	—	0.500	
	228	0.250	—	0.083	0.250	—	—	0.250	
	232	—	—	0.083	—	—	—	—	
	236	—	0.500	0.167	0.250	—	—	—	

APPENDIX VIII

LOD SCORES FOR KNOWN DAMS AND OFFSPRING, SHOWING MISMATCHINGS AND PROBABILITY OF NON-EXCLUSION

Appendix VIII: LOD scores for known dams and offspring

Known Dam Aju ID#		Group	Offspring Aju#	0ffspring - Known Parent Loci Mismatching	LOD Dam to Offspring	Offspring Loci Typed	Known Parent Aju ID#	Known Parent Loci Typed	Offspring - Known Parent Loci Compared	Probability of Non-exclusion
1100	D2	Off 2 sib 5								
			1102	0	4.89E+00	12	1100	13	11	3.91E-04
			1103	0	3.88E+00	12	1100	13	10	5.52E-03
992	D3	off 3 sib 10								
			993	0	7.88E+00	31	992	21	17	4.48E-09
			994	0	5.36E+00	18	992	21	18	4.64E-05
			995	2		18	992	21	18	1.42E-07
807	D4	off 4								
			808	0		13	807	19	13	1.03E-03
			809	0	7.33E+00	16	807	19	15	2.62E-05
895	D5	off 5								
			896	0	6.76E+00	33	895	12	12	3.82E-07
948	D6	off 6 sib 18								
			949	0	8.56E+00	20	948	20	18	4.60E-06
			950	0	6.48E+00	22	948	20	20	4.41E-07
			951	0	1.07E+01	21	948	20	19	2.37E-06
969	D7	off 7 sib 19								
			968	1	5.56E+00	18	969	19	17	6.73E-06
			970	0	5.54E+00	34	969	19	17	4.32E-07
			971	0	6.77E+00	20	969	19	18	8.31E-06
1006	D8	off 8 sib 20								
			1004	0	6.63E+00	19	1006	17	15	2.13E-06
			1008	0	5.82E+00	16	1006	17	14	7.59E-04
			1012	0	4.74E+00	16	1006	17	15	1.09E-04
1116	D9	off 9 sib 30								
			1117	0	4.04E+00	8	1116	11	8	1.01E-02
			1118	0	4.55E+00	7	1116	11	7	3.73E-02
			1119	0	5.43E+00	12	1116	11	11	1.10E-02
1162	D10	off 10 sib 33								
			1159	0	5.14E+00	13	1162	17	13	1.72E-03
			1160	0	6.16E+00	16	1162	17	16	4.02E-05
			1161	0	5.75E+00	15	1162	17	15	6.38E-04
892	D11	off 11 sib 35								
			893	0	1.23E+01	19	892	35	18	1.73E-05
			894	0	5.58E+00	18	892	35	18	1.83E-05
1034	D12	off 12 sib 37								
			1031	1	7.30E+00	32	1034	17	15	9.18E-08
			1032	0	3.64E+00	17	1034	17	14	1.05E-07
			1033	0	6.48E+00	19	1034	17	17	5.62E-07
			1035	0	7.97E+00	18	1034	17	15	8.17E-07
1141	D13	off 13 sib 40								
			1138	0		15	1141	7	6	1.62E-04
			1139	0		16	1141	7	7	7.54E-05
			1140	0		15	1141	7	7	1.74E-03

Appendix VIII continued

Known Dam Aju ID#	Group	Offspring Aju#	0ffspring - Known Parent Loci Mismatching	LOD Dam to Offspring	Offspring Loci Typed	Known Parent Aju ID#	Known Parent Loci Typed	Offspring - Known Parent Loci Compared	Probability of Non-exclusion
804 D14	off 14								
		805	0	6.35E+00	21	804	33	17	6.48E-06
		806	0	2.72E+00	14	804	33	11	3.13E-07
830 D15	off 15								
		831	1	7.58E+00	35	830	24	22	5.94E-11
		832	0	6.95E+00	15	830	24	15	8.84E-05
		833	1	5.65E+00	15	830	24	15	4.03E-04
853 D16	off 16								
		850	5		19	853	18	16	8.40E-06
		851	5		17	853	18	16	5.68E-04
		852	2	2.44E+00	19	853	18	17	1.11E-06
		852	2		19	853	18	17	1.11E-06
1002 D17	off 17 sib 51								
		1014	0	5.47E+00	17	1002	19	17	8.12E-05
		1015	0	7.19E+00	32	1002	19	17	1.90E-06
1084 D18	off 18 sib 52								
		1085	0	3.78E+00	13	1084	24	12	1.43E-03
		1086	0	3.72E+00	12	1084	24	12	5.21E-04
		1088	0		12	1084	24	12	6.82E-06
1092 D19	off 19 sib 53								
		1089	0		16	1092	14	14	2.98E-06
		1090	0	5.96E+00	26	1092	14	14	1.67E-09
		1091	0	2.80E+00	14	1092	14	12	5.29E-07
1144 D20	off 20 sib 54								
		1145	0	5.75E+00	15	1144	15	15	2.17E-05
		1146	0	5.44E+00	15	1144	15	13	8.20E-05
		1147	0	6.53E+00	16	1144	15	14	3.18E-05
1154 D21	off 21 sib 55								
		1155	1	4.11E+00	15	1154	15	14	3.68E-04
		1156	1	5.46E+00	15	1154	15	15	1.16E-03
		1157	1	4.61E+00	15	1154	15	14	4.85E-04
1038 D 22	off 22 sib 61								
		1036	0		18	1038	13	12	1.72E-07
		1037	0		19	1038	13	13	5.96E-06
		1039	0		19	1038	13	13	2.46E-06
1052 D 23	off 23 sib 39								
		1049	1		15	1052	33	14	1.48E-06
		1050	0		14	1052	33	13	2.95E-07
		1051	0		15	1052	33	14	2.72E-07
847 win??	win								
		810	6		18	847	36	17	7.93E-04
		813	0		12	847	36	12	4.58E-02
		814	4		17	847	36	16	1.26E-03
		811	4		18	847	36	17	1.65E-06

APPENDIX IX (a & b)

QUESTIONNAIRES USED TO INTERVIEW FARMERS

Appendix 9a. Full survey questionnaire

1. Farmer's name, farm name and farm number
2. How many total hectares is your farm?
3. No. hectares fenced for livestock (no. wires in fence)?
4. No. hectares game fenced (no. wires in fence)?
5. Numbers of Livestock: no. cattle, no. sheep, no. goats?
6. Do you have a calving season (yes/no)? If yes, what months?
7. Do you have a herder with your small stock (yes/no)?
8. Do you have a dog with your small stock (yes/no)?
9. Do you have free-ranging wildlife living with your cattle? (yes/no) If yes, give numbers and species of animals.
10. Species of game and total numbers you can find in game-fenced area:
11. Do you lose livestock to predators (yes/no)? If yes, please list the number, age and type livestock killed and by what predators?
12. What farm management practices do you use to protect calves and small stock from predators? Describe.
13. Number and species of game species killed by predators. Please list what you know have seen and which predators:
14. What predators do you have problems with?
    a. Cheetahs (yes/no), why/why not?
    b. Leopards (yes/no), why/why not?
    c. Jackals (yes/no) why/why not?
    d. Other (list), describe.
15. Do you use poison to control any of these predators (yes/no)? Did in the past (yes/no)? Do now (yes/no)?
16. Do you have a cheetah problem (yes/no)? How long (no. years)?
17. Is your cheetah problem seasonal or all year? If seasonal what months?
18. How often do you see cheetah or cheetah tracks on your farm? Weekly, Monthly, Other.
19. How many cheetahs have you removed from your farm each year?
    Please include date, total numbers, ages and sexes of animals, numbers of animals caught or killed together, other.
20. What was your method of removing the cats? Live –capture? Shot?
21. What prey species are cheetahs catching on your farm?
22. What is the largest group of cheetahs you have seen? Describe the age and group structure and where you saw them i.e. at water point, on a kill, in veld?
23. How many cubs do you see in a litter? Size of cubs at sightings?
24. Do you have a playtree? If yes how many?
25. Do you see any solutions for the survival of the cheetah on the Namibian farmlands and game farms?
26. Draw a map of your farm, and mark the following :
    a. Water points, dams and cattle water troughs mark with a D or WT
    b. Mark vegetation-type areas of your farm, thick bush, medium bush, savannah
    c. Mark with a **V** where cheetahs have been visually seen, **T** where cheetahs have been trapped, **K** where cheetahs have been killed.
    d. Please include dates (months and year if possible), number of animals, sex and idea of ages of animals i.e. adult, sub-adult, cubs.
    e. Mark with arrows, lines and/or circles areas where cheetahs travel through your farm and write cheetah area.

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1. Farmers name, farm name, farm number
2. Type of farm, livestock farm, game farm, both?
3. How many stock losses have you had in the past year due to cheetahs? # calves, # goats, # sheep
4. How many stock losses have you had in the past year due to leopards? # calves, # goats, # sheep
5. How many stock losses have you had in the past year due to other predators (list others)? # calves, # goats, # sheep.
6. During the past year has the number of cheetah on your farm increased or decreased from the previous year (I/D/same)?
7. What makes you think this? Increase or decrease of stock loss? More or less sightings or spoor? Other reasons?
8. During the past year would you consider your cheetah problem to be: Greater, Less, No Problem
9. Do you have a cheetah problem? (yes/ no) Why?
10. During the past year has the number of leopard on your farm increased or decreased from the previous year? (I/D/same)
11. What makes you think this? More or less stock losses? More or less sightings or spoor? Other reasons?
12. During the past year would you consider your leopard problem to be: Greater, Less, No Problem?
13. Do you have a leopard problem? (yes, no) Why?
14. List problems you have had with other predators the past year.
15. During the past year, how many cheetah or leopard (age and sex) did you remove?
    a. no. cheetah trapped? no. shot?
    b. no. leopard trapped? no. shot?

Appendix 9b: Condensed questionnaire (1993-1999)

1. Farmers name, farm name, farm number
2. Type of farm, livestock farm, game farm, both?
3. How many stock losses have you had in the past year due to cheetahs? # calves, # goats, # sheep
4. How many stock losses have you had in the past year due to leopards? # calves, # goats, # sheep
5. How many stock losses have you had in the past year due to other predators (list others)? # calves, # goats, # sheep.
6. During the past year has the number of cheetah on your farm increased or decreased from the previous year (I/D/same)?
7. What makes you think this? Increase or decrease of stock loss? More or less sightings or spoor? Other reasons?
8. During the past year would you consider your cheetah problem to be: Greater, Less, No Problem
9. Do you have a cheetah problem? (yes/ no) Why?
10. During the past year has the number of leopard on your farm increased or decreased from the previous year? (I/D/same)
11. What makes you think this? More or less stock losses? More or less sightings or spoor? Other reasons?
12. During the past year would you consider your leopard problem to be: Greater, Less, No Problem?
13. Do you have a leopard problem? (yes, no) Why?
14. List problems you have had with other predators the past year.
15. During the past year, how many cheetah or leopard (age and sex) did you remove?
    a. no. cheetah trapped? no. shot?
    b. no. leopard trapped? no. shot?

APPENDIX X

QUESTIONNAIRE USED TO EVALUATE PERFORMANCE OF LIVESTOCK GUARDING DOGS

Appendix X: Questionnaire used to evaluate the performance of Livestock Guarding Dogs

Date of questionnaire

Farmer information

1. Name of farmer
2. Farm size
3. Farm type
4. Level of involvement with Livestock Guarding Dog:

   Regularly/ often/ sometimes/ never/ only herder

Basic information regarding the Livestock Guarding Dog

5. Studbook number of dog
6. Sex
7. Date of birth
8. Sire studbook number
9. Dam studbook number
10. Litter number
11. Puppy Aptitude Test performed? If so, give score
12. Date of placement
13. Age at placement
14. Stock guarded
15. Time with farmer
16. Has dog moved owners? If so, give details and reason for transfer

Herder

17. Do you have a herder now?
18. Have you ever had a herder? If yes, have you employed the same herder since placement of the Livestock Guarding Dog, or have you changed herders?
19. Do you share information regarding the Livestock Guarding Dog with the herder?
20. Does the dog work well with the herder?

Interactions with other dogs

21. Do you have other dogs, apart from the Livestock Guarding Dog, with the herd? If so, how many? Describe other dogs with the herd
22. Does the Livestock Guarding Dog interact with other dogs? Describe how
23. Have you acquired any new dogs since getting the Livestock Guarding Dog?

Guidance from CCF

24. How much information regarding the Livestock Guarding Dog do you think that CCF has provided you with? Not enough/enough/too much
25. Do you feel you need more guidance regarding the Livestock Guarding Dog?

Attentiveness

26. Does the dog stay with the stock 24 hours a day?
27. Does the dog appear to be part of the stock?
28. Has the dog bonded with the stock?
29. Is the dog attentive to the herd?
30. How would you rate the dog’s attentiveness? Poor/ unsatisfactory/ good/ excellent
31. Has the dog been accepted by the stock?
32. Does the dog exhibit investigative behaviour?

Trustworthiness and behavioural problems

33. Is the dog submissive to the stock?
34. Is the dog trustworthy?
35. Has the dog ever exhibited behavioural problems?
36. If yes, did you report them to CCF?
37. Did you report the problems immediately or later?
38. Did you try to correct the problem? Describe how
39. Was the correction effective?
40. Do you have problems with the dog now? If so, describe problems

Protectiveness

41. Has the Livestock Guarding Dog effectively guarded the stock? If so, describe
42. How does the Livestock Guarding dog protect the stock?
43. How would you rate its protectiveness? Poor/ unsatisfactory/ good/ excellent
44. Level of stockloss before acquiring a Livestock Guarding Dog: 1 = none, 2 = slight (1-4 losses/yr), 3 = medium (5–9 losses/yr), 4 = high (10+ losses/yr)
45. Cause of stockloss before acquiring a Livestock Guarding Dog
46. Level of stockloss since acquiring a Livestock Guarding Dog: 1 = none, 2 = slight (1-4 losses/yr), 3 = medium (5–9 losses/yr), 4 = high (10+ losses/yr)
47. Cause of stockloss since acquiring a Livestock Guarding Dog

Care given to dog

48. Condition score of dog: poor/ unsatisfactory/ good/ excellent
49. What is the dog fed?
50. Quality of diet: poor/ unsatisfactory/ fair/ good/ excellent.

51. How often is the dog fed?
52. Are the dog's vaccinations up to date?
53. Does the dog have water freely available?

Farmer satisfaction

54. Overall, how would you rate how well the dog works? Very poor/ poor/ fair/ good/ excellent
55. Is it doing what you expected?
56. Has there been an economic benefit to having the dog? Would you recommend the programme to other farmers?
57. Are you confident with the dog?

Removals and mortality

58. Is dog still in the programme? If no, give date of removal
59. Reason for removal
60. If dog died – give date of death, and cause of death
61. Did dog die while still actively working in the Livestock Guarding Dog programme?

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