Ecological, endocrinological and ethological investigations of female mate choice in free-ranging white rhinoceros (*Ceratotherium simum simum*).

INAUGURALDISSERTATION

zur

Erlangung des akademischen Grades

doctor rerum naturalium (Dr. rer. nat)

an der Mathematisch-Naturwissenschaftlichen Fakultät

der

Ernst-Moritz-Arndt-Universität Greifswald

vorgelegt von
Petra Kretzschmar
geboren am 21. Januar 1969
in Berlin

Greifswald, 18. Dezember 2002

Dekan: Prof. Dr. rer. nat. Hildebrandt

1. Gutachter: Prof. Alberti

2. Gutachter: Priv.–Doz. Gansloßer

Tag der Promotion: 3. April 2003

TABLE OF CONTENTS:

SUMMARY:

It is an established fact that white rhinos do not breed very well in captivity. In this thesis the reasons for the low breeding success were established and solutions suggested. The thesis also aims to identify the main characteristics of males which breed successfully (which should help to improve the management of free living populations). To ensure effective species management, basic data about the breeding behaviour of the species was collected, using a multidisciplinary approach. In particular, the present study aims to establish whether female white rhinoceros choose their mates and, if so, which factors influence their choice. It also seeks to establish whether there is any relationship between androgens, environmental factors and mating activity. Genetic analysis of fatherhood was carried out using a novel method which, for the first time, made it possible to combine long-term behaviour observations with genetic analysis of fatherhood. In addition, the body and horn size of five males was measured, the concentration of testosterone in their faeces determined, and the characteristics of their territories investigated. All of these factors were then set in relation to their reproductive success. Foraging preferences of males and females were established and the nutritional composition of the food intake was analysed. The following criteria were used to measure the quality of male territories: vegetation structure, tree and grass species composition, the availability of frequently foraged or selected grass species as well as the nutritional composition of the forage. In addition, a non-invasive endocrine monitoring technique was developed to assess the androgen concentrations of free-ranging adult male rhinos. The study was carried out between March 1997 and May 1999 on a private game farm in Northern Transvaal, South Africa, where conditions were similar to those enjoyed by free-ranging populations.

Chapter 1:

Genetic analysis of fatherhood revealed that the females conceived more often from those males which possessed a territory where females spent 70 % of their time. This indicates that males having a high concentration of females in their territory also have a high level of mating success. In the present study, the females were not distributed equally over male territories, suggesting that differences in mating success did exist. Based on these results, the different distribution patterns were used to establish the influence of the male and territorial characteristics on reproductive success. It emerged that testosterone metabolite concentrations did not differ between adult males and cannot, therefore, influence the female's choice of mate among the territorial males. It also emerged that the territory sizes identified in the study (61 km^2 – 116 km^2) were much larger than any territories hitherto described for white rhinos, which is probably due to the low population density at the study site. Males with large body and horn size were found to have the largest territories. The male with the highest reproductive success – i.e. with the highest frequency of females in his territory - turned out to have both the largest body size and the largest territory. The next most successful male had the longest first horn, but only a small territory. It is therefore unclear to what extent reproductive success is influenced by territory size. However, it is not unlikely that male rhinos adopt two different

strategies to increase their mating success: 1. They try to increase the size of their territory and/or 2. They defend a small but attractive area.

Another area analysed was the quality of the territories, with a special focus on the availability both of the main food resource and of preferred grasses, as well as on the concentration of crude protein in the forage. The first step was to establish whether there were any differences between the sexes in respect of the most frequently consumed food and of the favourite food. It emerged that there were no major differences between males and females as regards feeding habits. Both selected individual grass species rather than grassland types. Both preferred highly palatable grass species and avoided grass species of low palatability. However, females showed a slight tendency to select high protein plants for foraging. The results of this analysis were used to compare territory quality. Since this comparison revealed only minimal differences, territory quality alone cannot explain the variation in distribution patterns. Other factors such as vegetation structure, tree species composition and territory size and body and horn size are more likely to have an impact on female distribution, but further data will be required to confirm this.

Chapter 2:

The faecal samples of adult, sub-adult and male calves were collected and analysed with an enzyme-immunoassay using an antibody directed against 17α-OH-testosterone-HS-BSA. Three lines of investigation demonstrated that metabolite measurements clearly reflect gonadal activity: 1. Following the injection of an adult male with synthetic GnRH, a 154 % increase in testosterone metabolite concentrations in the faeces was registered one day after treatment. 2. The testosterone metabolites of several males were measured, revealing that – as expected – there were marked between different age groups. 3. Both blood and faeces samples were collected from several males, revealing a clear correlation between the concentrations of testosterone.

All adult males exhibited seasonal trends in faecal testosterone excretion with higher concentrations between September and December compared to the rest of the year. The increase in androgen concentrations coincided with the beginning of the rainy season. This seasonal trend is confirmed by several behavioural observations: 1. The maximum number of fertile mating coincided with peak androgen concentrations. 2. Most intra-sexual conflicts occurred at the beginning of the mating season during a phase of low testosterone metabolite concentration, while inter-sex conflicts peaked during periods of high concentration. 3. A high testosterone concentration coincided with an increase in the area which males covered within their territories, probably related to their search for mating partners. Testosterone metabolite concentrations of individual males were also found to be correlated both with fighting activity and with courting activity. The possible implications of these findings for the management of captive and free-living populations are discussed in detail in the study.

ZUSAMMENFASSUNG:

Die Zuchterfolge in Zoos zeigen deutlich, dass sich Breitmaulnashörner in Gefangenschaft nur sehr schlecht vermehren. Ziel der Studie war es, mögliche Ursachen für die schlechte Reproduktionsrate zu untersuchen und Lösungen vorzuschlagen. Es wurde analysiert, ob es einen Zusammenhang zwischen Androgenen, Umweltfaktoren und Paarungsaktivität gibt. Ein weiteres Ziel war es, das Management von frei lebenden Populationen zu verbessern. Hierzu wurde untersucht, ob Weibchen eine Präferenz für bestimmte territoriale Männchen zeigen und anhand welcher Faktoren sie diese auswählen. Für die Studie wurde ein multidisziplinärer Ansatz gewählt, bestehend aus endokrinologischen, genetischen, ökologischen, verhaltensbiologischen und ernährungsbiologischen Untersuchungen. In der Studie wurde eine neuartige Methode verwendet, die erstmals ein genetische Vaterschaftsanalysen bei Breitmaulnashörnern ermöglichte. Es wurden verschiedene Körper- und Hornabmaße der Männchen, der Testosterongehalt im ihrem Kot und die Größe und Qualität ihrer Territorien etabliert und mit ihrem Paarungserfolg verglichen. Zur Beurteilung der Qualität der Territorien wurden die Struktur der Vegetation, die Verteilung von Baum- und Grasarten und die Qualität der Nahrung bestimmt. Die Qualität der Nahrung wurde anhand der Nahrungswahl von Männchen und Weibchen und anhand der Nährstoffzusammensetzung ihres Futters untersucht. Des Weiteren wurde erstmals eine Methode validiert, die mittels eines Enzym-Immunoassays den Hormongehalt im Kot von männlichen Breitmaulnashörnern erfasst. Die Studie wurde auf einer privaten „Wildtierfarm“, in der Limpopo Region in Südafrika, in der Zeit von März 1997 bis Mai 1999 durchgeführt, unter Bedingungen ähnlich denen von frei lebenden Nashörnern.

1. Kapitel :

Die genetischen Vaterschaftsanalysen haben gezeigt, dass Weibchen hauptsächlich von denjenigen Männchen Nachwuchs bekommen, in deren Territorium sie sich zu 70 % ihrer Zeit aufhalten. Das Ergebnis deutet darauf hin, dass Männchen mit einer hohen Anzahl an Weibchen in ihrem Territorium auch einen hohen Paarungserfolg haben. Die Weibchen waren nicht gleichmäßig über das Studiengebiet verteilt. Einige Männchen hatten eine höhere Konzentration an Weibchen in ihren Territorien als andere. Dies deutet auf Unterschiede im Paarungserfolg hin. Die Konzentration der Testosteronmetaboliten im Kot aller fünf Männchen war ähnlich und hatte vermutlich die Auswahl der Weibchen nicht beeinflußt.
In der Studie wurden die bisher größten für Breitmaulnashörner je beschriebenen Territorien, mit 61 km^2 – 116 km^2, gemessen. Ein Vergleich mit anderen Studien ergab, dass die Größe der Territorien mit der geringen Dichte der Population im Untersuchungsgebiet im Zusammenhang stand. Männchen mit großer Körper- und Horngröße hatten die größten Territorien. Das Männchen mit dem größten Territorium und der größten Körper- und Horngröße wies auch die höchste Anzahl an Weibchen in seinem Territorium auf und hatte sehr wahrscheinlich den größten Reproduktionserfolg. Das Männchen mit dem längsten Horn wies eine hohe Anzahl an Weibchen in seinem Gebiet auf, hatte jedoch nur ein kleines Territorium. Es ist daher nicht eindeutig, welche Rolle die Territoriumsgröße auf die Anzahl der Weibchen und somit auf den Reproduktionserfolg hat.

Es ist möglich, dass Männchen zwei verschiedene Strategien verfolgen um ihren Paarungserfolg zu erhöhen: 1. Sie vergrößern ihr Territorium 2. Sie verteidigen ein kleines, jedoch für Weibchen attraktives Territorium. Zur Bestimmung der Qualität der Territorien wurde die Qualität der Nahrung in den Territorien ermittelt. Hierzu wurden Untersuchungen zur Nahrungswahl von Männchen und Weibchen durchgeführt und die Nährstoffzusammensetzung ihres Futters analysiert. Männchen und Weibchen zeigten eine sehr hohe Übereinstimmung in der Wahl ihrer Nahrungspflanzen, wobei die von den Weibchen aufgenommene Nahrung einen leicht höheren Proteingehalt aufwies. Beide Geschlechter selektierten einzelne Grasarten innerhalb eines Fraßortes und zeigten somit ein sehr spezifisches Auswahlverhalten. Sie wählten proteinreiche, gut verdauliche Gräser und vermieden die Aufnahme von proteinarmen, schlecht verdaulichen Gräsern. Ein Vergleich der Territorien in Bezug auf die am häufigsten gefressenen Grasarten und bevorzugten Grasarten ergaben nur geringe Unterschiede und kann somit nicht die unterschiedliche Verteilung der Weibchen erklären. Andere Faktoren wie die Vegetationsstruktur, die Anwesenheit bestimmter Baumarten, die als Indikator für nährstoffreiche Böden gelten, die Territoriumsgröße und die Körper- und Horngröße hatte eher einen Einfluß auf die Verteilung der Weibchen und den Reproduktionserfolg der Männchen. Weitere Daten sind notwendig, um dies zu bestätigen.

2. Kapitel:

Die Kotproben von adulten und subadulten Männchen sowie männlichen Kälbern wurden mittels eines Immunoassays analysiert, bei dem ein Antikörper benutzt wurde, der gegen 17α-OH-Testosteron-HS-BSA gebildet wurde. Die Ergebnisse weisen daraufhin, dass die neu etablierte Methode die Konzentration von im Körper zirkulierendem Testosteron zuverlässig widerspiegelt. 1. Die Injektion von synthetischem GnRH führte einen Tag nach der Behandlung zu einem Anstieg um 154 % der im Kot gemessenen Konzentration von Metaboliten des Testosterons. 2. Die Konzentration der Testosteronmetaboliten von Männchen verschiedener Altersklassen zeigte gemäß den Erwartungen einen deutlich Unterschied in der Konzentration. 3. Es bestand eine eindeutige Korrelation zwischen dem Gehalt von Testosteron im Kot und im Blutplasma. Es konnte weiterhin ein jahreszeitlicher Verlauf der Konzentration von Testosteron im Kot von fünf adulten Männchen gemessen werden. In der Zeit von September bis Dezember wurde ein höherer Gehalt an Testosteronmetaboliten gemessen als im Rest des Jahres. Der Anstieg der Werte stand vermutlich im Zusammenhang mit der Regenzeit. Verhaltensbeobachtungen haben den saisonalen Trend bestätigt. Erfolgreiche Verpaarungen traten am häufigsten zum Zeitpunkt der höchsten Testosteronkonzentration auf. Territoriale Kämpfe zwischen Männchen wurden am häufigsten während niedrigen Testosteronkonzentrationen beobachtet, während Konflikte zwischen Männchen und Weibchen bei hohen Konzentrationen auftraten. Des Weiteren zeigte sich, dass Männchen in der Zeit hoher Testosteronkonzentrationen größere Gebiete durchstreiften, eventuell auf der Suche nach Paarungspartnern. Es konnte auch nachgewiesen werden, dass Männchen, die seltener in Konflikte verwickelt waren oder die häufiger mit empfängnisbereiten Weibchen zusammen beobachtet wurden, höhere Konzentrationen in den Testosteronmetaboliten aufwiesen als andere. Die Bedeutung der Ergebnisse für das Management von im Zoo lebenden und frei lebenden Populationen wird detailliert in der Studie diskutiert.

ACKNOWLEDGEMENTS:

- I am deeply grateful to Prof. Dr. G. Alberti for supervising the study.
- Many thanks are due to PD Dr. U. Gansloßer of the University Erlangen-Nürnberg who supported me throughout the study with fruitful ideas, literature and with enthusiastic students.
- The study would not have been possible without financial support which was kindly provided by the DAAD („Stipendium zur wissenschaftlichen Aus- und Fortbildung im Ausland“) and the Fazit-Stiftung Gemeinnützige Verlagsgesellschaft mbH („Promotionsabschlußstipendium“).
- I am deeply grateful to Tilman L. whose interest in the rhinos made it possible for me to conduct the study at the study site. I am very sorry that he has no chance anymore to read the final version of my work as he died.
- Special thanks also to the other owners of the farm, who gave me permission to drive and work on their area and who got used to the sighting of a red car standing in front of their rhinos.
- I especially want to thank Twing L. who allowed me to stay in her house.
- Throughout my stay in South Africa I got logistic help from G. Whyat-John. He gave me friendship, and a home for me and my assistants in Johannesburg and he always helped me repairing my car.
- Lots of thanks to the staff of the farm who assisted me with the challenges that evolved from such a complex project. Special thanks go to Ilze and Andre for wonderful evening dinners.
- Special thanks to William, who gave me insight in tracking of white rhinos. Without his experience the work would have never been possible.
- I wish to express my thanks to all the assistants who helped me in the field and who provided me with emotional support: Maaike Bausch, Eva Roth, Alexandra Aberham, Matt Taylor, Britta Kiefer and Elke Kraus.
- I convey my gratitude to Dr. Dehnhard and his laboratory assistant for hormone analysis and for fruitful comments on the manuscript.
- Special thanks also to Britta Kiefer who conducted the nutritional analysis of the forage and who shares her knowledge on nutrition of rhinoceros with me.
- I also want to thank K. Kellner for genetic analysis of skin samples for parentage tests.
- The nutritional analysis of faecal samples were kindly conducted by M. Lechner-Doll and his team.
- Lots of thanks to A. Gumbert who was involved in planning the project and who always helped my with statistical problems.
- I am deeply greatful to my parents, who made it possible for me to undertake the project through financial and emotional support.
- Warm thanks also to B. Lüders for his friendship during this difficult time of writing
- I am deeply grateful to Steffie Duch. The long hours she spent with me improving my english are gratefully acknowledged.
- I also want to thank Prof. Dr. C. Groves, Tom Frazier, Adrian Schrader, Gabi Glück and Anne Grohman for comments on the manuscript.
- So many other people helped me during the project. As I can not mention all I wish to thank them herewith

INTRODUCTION:

The southern white rhinoceros (*Ceratotherium simum simum*) was on the brink of extinction by the end of the 19th century. Intensive protection and extensive translocations of individual animals into small nature reserves and privately owned land led to a rapid recovery of the population (Pienaar 1970, Emslie & Brooks 1999, Rookmaaker 2000). From a single population of barely 20 animals in 1885, there are now more than 11640 in wild populations, with an additional 770 animals in captive breeding institutions worldwide (International Rhino Foundation 2002). Ninety percent of all white rhinos in Africa live in South Africa (Emslie & Brooks 1999). The concentration of the whole population in one country is risky as political instability could easily lead to the decimation of the population again. Captive populations could act as a safety net in times of war and civil unrest, but white rhinos do not reproduce very well in captivity (Gunn et al. 1998, Rieches 1998, Schwarzenberger 1999) and the reasons for the low reproductive rates are still not fully understood. Lindemann (1982) found out that the main requirement for successful breeding is the presence of more than one male. Male-male competition seems necessary for male sexual behaviour to be stimulated while females need to exert some selection among potential mates for oestrous cycling to be initiated (Owen-Smith 1988). Other factors, however also have influences on the breeding behaviour of rhinos, as even large mixed groups kept in captivity often fail to reproduce (Gunn et al. 1998, Rieches 1998, Schwarzenberger 1999). Stress resulting from abnormal social relationships in captivity, nutritional deficiencies or a lack of seasonal variation in food supply can influence the hormone balance and are likely to cause infertility in male and female rhinos (Gunn et al. 1998). So far there is no long-term study that has been able to monitor hormone profiles of free living white rhinoceros and to determine the influence of social and environmental factors on hormone profiles. A detailed study of the reproductive behaviour of rhinos in wild populations is required to improve breeding in captive white rhinoceros. This may also help to improve breeding of the highly endangered northern subspecies of the white rhinoceros (*Ceratotherium simum cottoni*); only 25 animals are known to exist in a single population in Africa today (International Rhino Foundation 2002). The study of reproductive biology of the white rhino has therefore been proposed as a research priority by the AZA Rhino Advisory Group, the International Rhino Foundation, and SOS Rhino.

Study of the reproductive behaviour of the white rhinoceros is also important for the conservation of free living populations. The reduction in numbers at the end of the 19th century may have led to a reduction in the genetic variability of the species, but this has not been investigated yet. Today, free living white rhinos exist only in small discrete populations - over 8440 individuals live in 247 wild populations (Emslie & Brooks 1999) - which are prone to inbreeding. This could lead to a further reduction in its genetic variability resulting in reduced fertility and viability (Baur et al. 1995), and reduced adaptability of the species to changes in the environment (Foose 1991). Knowledge of the reproductive behaviour of the rhinos could help in assessing the number of breeding animals in these populations, and to assess the problem of inbreeding (Schreiber et al. 1995; Parker & White 1997). Competition over mates and strict female mate choice increase the degree of inbreeding in a population as only a small number of all possible breeding animals (= effective population size) in a population actually reproduce. To conserve genetic diversity small populations or

populations with strict female choice need to be managed. The success and effectiveness of management programs could be improved if one could identify reproductively successful males and exchange them between populations (Schreiber et al. 1995; Parker & White 1997).

Female mate choice occurs in species were females invest more time and energy into their offspring than males (Trivers 1972). A high level of investment in one offspring reduces the potential of a female to produce another (Partridge & Halliday 1984). This is a conflict for the female, as according to evolutionary theory, individuals aim to increase the number of direct descendants (Darwinian fitness) or of genes passed on to their offspring (Inclusive fitness, Hamilton 1964 cited in Clutton-Brock & Harvey 1978). Females may have developed a certain strategy in order to solve this conflict. One strategy is to select the best possible mate according to traits that signal either direct material benefits or indirect genetic benefits (review: Andersson 1994, Møller & Jennions 2001). The female can gain direct benefits if the male possesses a high quality breeding territory, if he shows anti-predator behaviour, or if he protects her from harassment by other males, or just by the absence of directly transmitted diseases (Brandt 1989, Byers et al. 1994, Nefdt 1995, Klein et al 1999, Møller & Jennions 2001). Indirect benefit occurs when the selected male carries genes that contribute to the survival and reproductive ability of the female's offspring (Fisher 1958 cited in Andersson 1994, Patridge 1983).
The high investment of female white rhinos into their offspring and the low investment by the males suggest that female mate choice exists in the species. After 16 months of gestation female white rhinos give birth to a juvenile of approximately 40 kg in weight which they suckle for up to a year (Player & Feely 1960, Owen-Smith 1973, Dittrich 1972). In contrast to females, males take no care of the young. They join up with the female about two weeks before mating and leave her a few days afterwards (Owen-Smith 1973, 1975). Studies on free living white rhinos already indicate that mate choice occurs in the species. Females were observed to mate more often with territorial α- bulls than with non-territorial β-bulls (Owen-Smith 1973, 1975, Rachlow 1998). Alpha bulls are usually older and have higher androgen levels than β-bulls (Rachlow 1998). They successfully defend a territory while β-bulls adopt a subdominant status until they acquire their own territory (Owen-Smith 1973, 1975, Rachlow 1998). It is not yet known, however, whether females further select among the territorial males. Female white rhinos can move freely between up to seven territories but spend most of the time in one or two adjacent territories (Owen-Smith 1973, 1975). It is likely that their preference for certain territories is also reflected in their mating behaviour.

The aim of the study was to assess whether female mate choice goes beyond the selection of territorial males in white rhinoceros and to determine factors influencing pairing success of territorial males (chapter one). In addition, a non-invasive technique was developed to measure testosterone metabolites in the faeces. The hormone levels of free ranging male white rhinoceros were monitored over a period of two years and the influence of social and environmental factors on androgen concentrations was established (chapter two). The study was conducted on a population of white rhinoceros classified as wild according to the definition of the African Rhino Specialist Group (Emslie & Brooks 1999).

GENERAL METHODS:

Study site and study animals:

Data were collected between March 1997 and May 1999 from a population of individually known white rhinoceros living on a private game farm in the Limpopo Region, South Africa (Fig. 1). Poaching is a major threat to a rhino population in this area. To protect the population, the name and location of the farm as well as the size of the population are not given by request of the farm owners. The area was 300 km^2 in size, situated within the historical range of the population and surrounded by a fence of two meters in height. It housed a population of several dozen rhinos. The population was founded in 1990 from individuals coming from different areas in South Africa: Sabi Sand, Umfolozi and Kruger National Park.

Figure 1: Map of the Republic of South Africa showing the area in which the study site was situated (grey oval). A more detailed location of the site is not given due to the risk of poaching.

Since its foundation, the population has grown successfully with a rate of increase of 15 % per year (Kretzschmar 2002). The animals have been left to themselves except for a few occasions. Three male rhinos were shot between 1991 and 1994 by professional hunters. In 1998 almost all subadult males between four and six years of age were removed from the area in order to prevent fighting between adolescents and territorial males. Hunting of adult males and removal of subadult males certainly had an influence on the

social system of the population but it is unlikely that this had an influence on the territory system and mating activity of the rhinos described in the study. The study commenced three years after removal of the last adult male. Adult males probably built up new territories by then as they were observed to take over a territory immediately after the previous owner had left (see chapter 1). The removal of subadult males between four and six years of age almost certainly had no influence on the territory system and mating activity of the rhinos as they were too young. Males usually start to defend a territory or take part in mating activity when they are ten years of age (Owen-Smith 1973). The removal of individual animals is not one of the criteria of the African Rhino Specialist Group (AfRSG, Emslie & Brooks 1999) which distinguish between wild, semi–wild and captive populations. The study population departs in respect from the definition of a wild population in that that they are given food supplementation during winter. But the classification of "semi-wild", which assumes that: "individuals live in an area of less then 10 km^2 in size, in a compressed density and spacing and with a high degree of management", differs considerably from the present situation. It appears thus justified to classify the population as wild.

Vegetation:

The study site was originally a cattle farm which was transformed into a game farm in 1990. A vegetation assessment carried out at the study site described the vegetation as a typical savannah in a certain stage of degradation (EEC 1998). Trees, shrubs and to a much lesser extent dwarf shrubs dominated the grass layer, resulting in a low grass cover. Most of the vegetation was rather homogeneous. Variation was found to occur dependening on soil texture (clay/sand content) and soil depth. The geological formations occurring on the study site were gneiss, granite and granite gneiss, and alluvium. Three different vegetation types were identified within the survey, which correspond to the "veld types" described by Acocks (1988): mixed bushveld dominated by broad leafed woody species, sweet veld with a high sclerophyllous element, and a vegetation type which forms a transition between scleophyllous and broad leafed mixed veld. The sweet veld is a type of grassland which can be utilised throughout the year, as important grazing plants maintain their palatability and nutritional value throughout their life cycle. In contrast to the sweet veld, the mixed bushveld is suitable for grazing during only six to ten months of the year as important grazing plants of this area lose their palatability and nutritional value at maturity (Van Rooyen et al. 1996). The grass and tree species composition of the study site is further described in chapter 1.

Climate of the study area:

Daily temperature at the study site was measured using a maximum/minimum thermometer. Mean maximum and minimum day temperature during the observation period were between 31.7° C and 19.6° C in the summer and between 28.7° C and 16.8° C in the winter (Figure 2).

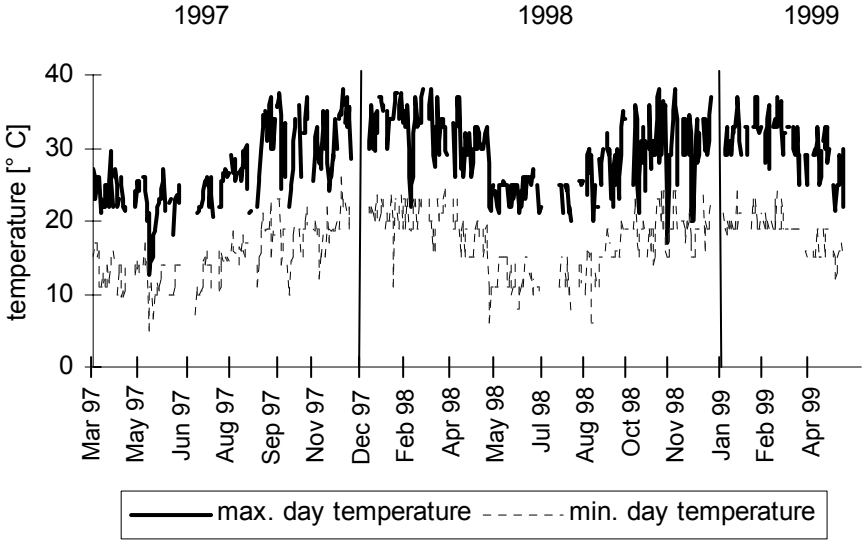


Figure 2: Maximum and minimum day temperatures measured at the study site between 15.3.1997 and 7.5.1999. The lines indicate the beginning of a new year.

Between 1996 and 1999 monthly rainfall was measured daily by farm personnel at 21 different weather stations distributed evenly over the study site. Single measurements per station were added and the monthly average rainfall was calculated.

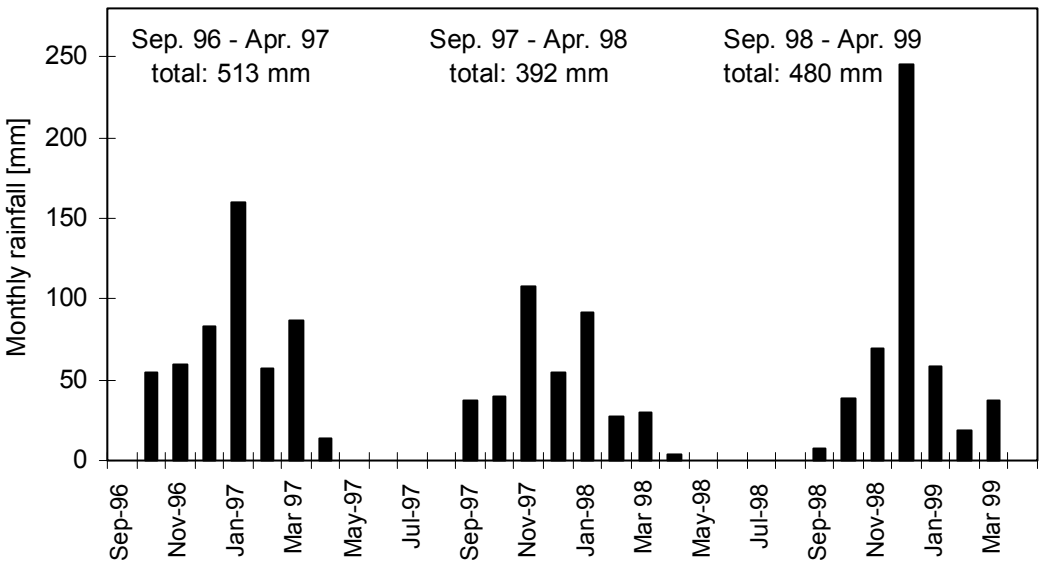


Figure 3: Monthly rainfall (in mm) measured between 1996 and 1999 on 21 different weather stations distributed all over the study site.

In all three years, rainfall began in September or October and ended in March or April (Figure 3). Most rainfall was measured in 1996/97 with a total of 513 mm and least in the following season (1997/1998) with 392 mm.

Identification of animals:

During the first year of study a catalogue was established for each individual including pictures of the animals taken from different points of view as well as a description of individual morphological features. All adult white rhinos and many subadults could be identified individually by variations in horn size and shape as well as in body size, hairiness of ears and tails, folds along the body and other characteristics. In June 1998 all animals were immobilised for management purposes (see below) and individually marked with a number code in the ear; notches were placed at prescribed positions of the ear representing different numbers (Fig. 4). The shape and positions of the notches differed between the animals, allowing identification of sexes and individual animals even from large distances or in thick bushes without seeing the whole animal.

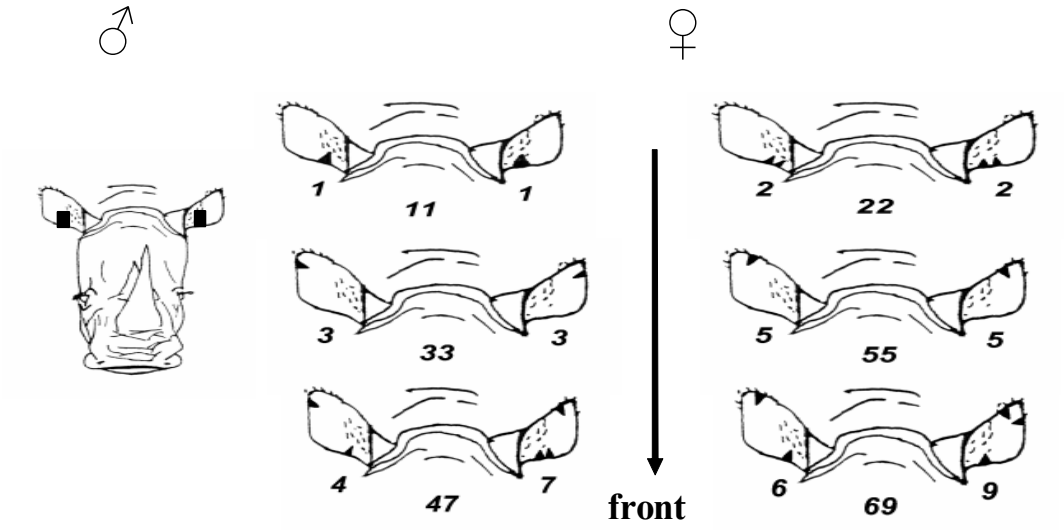


Figure 4: Number code used at the study site to identify individual rhinos. Sexes were differentiated by the shape of the notch: square for males, angles for females; the position of the notch represented a number: the right ear (seen from the front) gave the second digit number, the left ear the first digit number. (Picture from Aberham 2001)

Age of the animals:

In the course of the study, individuals were photographed repeatedly in order to record their development over the study period. Pictures of calves born during the study period were compared with pictures of calves of unknown age, born before the study began. This allowed the age of young animals to be established up to four years of age. The age of older animals was established by comparing their body and horn size with those of adult females described by Hillman-Smith et al. (1986) and Hillman-Smith (1997). It was not possible,

however, to establish the age of animals older than 6 years of age, as from this age on differences in horn and body size were too small for further differentiation. The animals were grouped into three different age categories: calves (0 – 2 years of age), subadults (females of 2 - 6 years of age) and adults (> 6 years), using a simplified version of the age classification of Owen-Smith (1973). All adult males on the farm were probably 10 years of age or older.

Locating males:

Five adult males were monitored continuously over a period of two years. The males were located by following their footprints (tracks) with the help of a professional game tracker. Tracks of territorial males were distinguishable from tracks of non-territorial males, adult females and others by means of the characteristic scratch marks (Fig. 5) or scattered dung which territorial males usually place at regular intervals along the tracks to demarcate their territories (Owen-Smith 1973). The tracks of individual males were identified with the help of an experienced game tracker, by the size of their foot and the individual pattern of lines on its sole. The impressions made by the feet often revealed clear outlines of the outside edge of each hoof, and also the outline of the hind part of the digital cushion. Cracks which are present on the surface of the plantar cushion could be seen as raised ridges on fresh tracks (Fig. 5). These indentations are unique to each animal and together with the foot size provide information about the identity of an individual, as in black rhinos (Jewell et al. 2001). Fresh faecal samples of individual males could thus be identified, by collecting them along the tracks, without observing the actual process of decaecation. Additionally, scratch marks, dung heaps, feeding, resting and fighting places could be reliably assigned to individuals and their position established using global positioning system (GPS). Tracks of a particular male were located by driving within his territory along management roads. A track dating from the previous night or from the early morning was followed in the morning until the animal was sighted around midday. The length of a single track continuously followed was up to 15 km. Due to the large distance the males used to walk, and the large area which needed to be patrolled, occasionally a track was left or followed by car and a fresher track was picked up and followed until the animal was sighted. Locations of footprints and other signs established before the track was left were used for analyses only when identity was clear.

Locations of males were also established during daily routine patrol throughout the area (see locating females). With these methods five adult males were located every third day (median, interquartil range (IQR) = 5) over a period of two years and a total of 301 faecal samples of individual males were collected (median = 61 samples/male, IQR = 9).

Locating females

Locations of adult females were not determined by tracking because of the high number of females. Their positions were established by random sightings during daily routine patrol throughout the area (see above). The survey was done during the early morning and late afternoon, which is the main activity period of the rhinos (Owen-Smith 1973).

In July 1998, five adult females were immobilised and equipped with radio transmitters. Special ear transmitters were developed together with the 'Gesellschaft für Telemetriesysteme mbH' (Germany) for tracking the rhinos. They do not last as long as horn implants (pers. comment D. Pienaar), but the idea of using horn implanted radio transmitters was dropped by request of the farm owners. Radio-collars are often used for monitoring other species, but they are not optimal for rhinos as they often fall off because of the shape of the animal's neck and head (Alibhai & Jewell 2001). Previously tested ear tags (P2RL) developed by AVM showed a low transmission power (power output –10dBm, battery 3.5 V and 750 mA). I therefore aimed to achieve a higher transmission range using the smallest possible size. A transmitter of 50 g in weight and 60 mm x 30 mm x 15 mm in size (excluding silicon needed to fit transmitter to ear tag), with a power output of 3 dBM, a pulse duration of 25 ms, a repetition period of 1.5 seconds and a 3.5 V battery and 1900 mA/h, was selected. The transmitters stayed on the animals for up to two months before they fell off. During that time five females were located once a day and their position was recorded using GPS.

Immobilisation of rhinos:

In July 1998 all rhinos of the study site were caught by the manager of the farm. They were anaesthetised with a projectile dart containing etorphine hydrochloride (M99) and azaperone (Stresnil) in varying amounts depending on the size of the animal (recommended dosages for different age classes can be found in Du Toit 1998). The rhinos were kept tranquillised for approximately 15 – 30 minutes and revived with diprenorphine (M5050). The aim was to individually mark the animals with a number code in the ear and with passive transponders (S. trovan ®), which were placed into their hump and in their horns. During that time five adult females were equipped with radio transmitters, and faecal and blood samples of the whole study population, as well as data on body, horn and foot size, were collected. A more detailed description of body measurements taken can be found in chapter 1. Methods on faecal and blood collection are given in chapter 2.

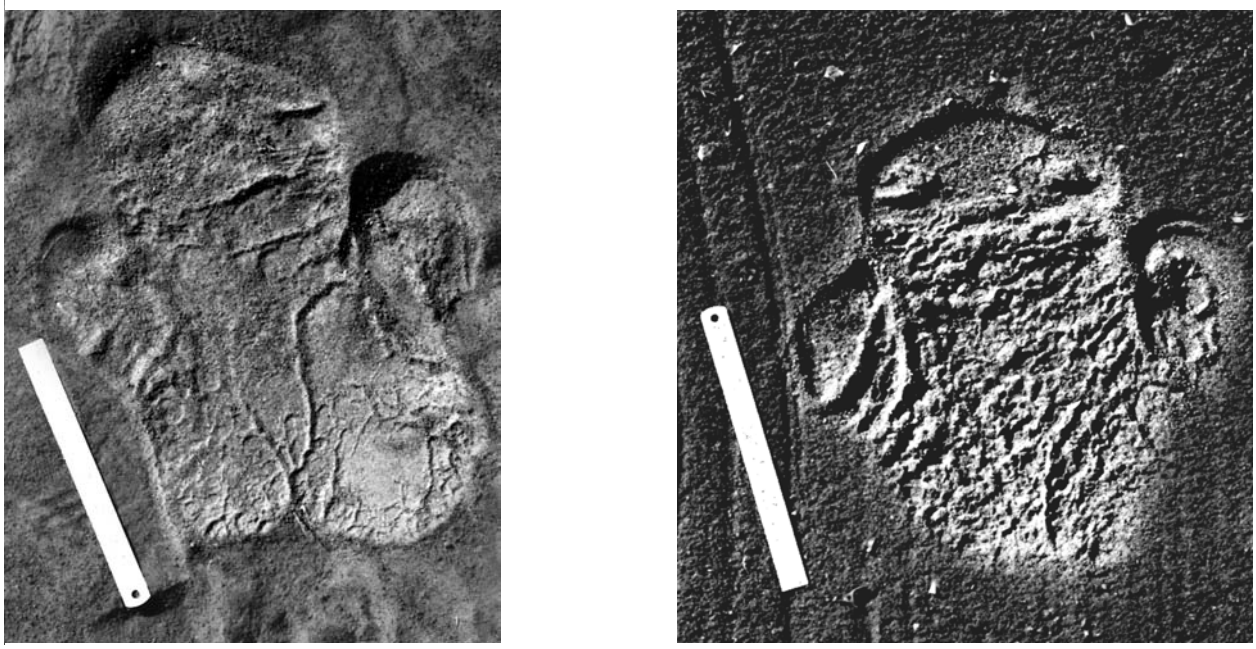


Figure 5: Impression of hindfoot of two different animals left in the soil. The impression of the three toes can be seen, as well as the cracks which are present on the surface of the plantar cushion.The object on the left hand side is 17 cm long.

Figure 6: Scratch marks of territorial males. Two different scratch marks can be seen (indicated by the arrows), which were placed on top of each other.

CHAPTER 1: IS MATING SUCCESS INFLUENCED BY MALE AND TERRITORY QUALITY?

INTRODUCTION:

The aim of this study was to assess whether female mate choice goes beyond the selection of territorial males in white rhinoceros and to determine factors influencing mating success of territorial males.

Mating systems of mammalian species are strongly influenced by the distribution of females which is often related to resources necessary for breeding (Emlen & Oring 1977, Andersson 1994). The large nutritional requirements for pregnancy and lactation require maximum nutrient intake by females (Gosling 1986, Rachlow & Bowyer 1998) which therefore often prefer areas containing large quantities or high qualities of resources (Emlen & Oring 1977). Males defending these high quality areas will have a higher number of females in their territories. They may also achieve greater reproductive success compared to other males (resource defence strategy, Emlen & Oring 1977, Halliday 1978) as the mating success of males is often dependent on the distribution of females (Emlen & Oring 1977). Thus in situations where resources are unevenly distributed or spatially clumped a situation may arise where differences in mating success between territorial males occur.
Males controlling those high quality territories are likely to be characterised by a large body, a large horn size or/and a high androgen level as these traits are usually associated with fighting abilities (Clutton-Brock et al. 1982, Jarman 1983, Gosling 1986, Nelson 1995). Thus females, when settling in an area, may choose a territory, but they also select the fitter males, since male competition for the best territory is an indirect measure of their quality (Searcy & Yasukawa 1983). In fact females, mating with a male in whose territory they reside, gain the direct benefits of the resources, and the indirect genetic benefits of fit males who were able to compete successfully for the resources (Andersson 1994). Nevertheless a female could select solely those characteristics that confer some advantage for her offspring (Halliday 1983), and could therefore choose male characteristics independently from territory traits. Males could thus attract females directly through certain characteristics such as body or horn size, or indirectly through the territory they hold, or through a combination of both (Bart & Earnst 1999).

Competition among males for territories or mates selects for strength, often achieved by large body size and for weapons such as antlers and horns (Jarman 1983). This leads to a marked sexual dimorphism in species with a high degree of polygyny (Andersson 1994). Adult male white rhinos are up to 30 % larger than females and have larger and heavier horns (Owen-Smith 1988, Pienaar et al. 1991). The differences in body and horn size are most likely an indication of the competition between males over territories or mates. Males occupy territories from 1.6 square kilometres (Umfolozi-Hluhluwe Complex, Republic of South Africa, Owen-Smith 1973) up to 50.4 square kilometres in size (Matobo National Park, Zimbabwe, Rachlow 1999) depending on the study site. Cows have overlapping home ranges and can move freely between male territories (Owen-Smith 1973). The size of the territories may vary between individual males by as much as

36 square kilometres, from 14.6 square kilometres to 50.4 square kilometres in Matobo National Park, Zimbabwe (Rachlow 1999). The differences in territory size suggest that competition for large territories or territories situated in high quality areas occurs in white rhinoceros, and that males defending those territories are characterised by a large body and/or horn size. The main food of rhinos, however, does not appear to be a resource which is worth defending. White rhinos are grazers (Owen-Smith 1973) and grass is widely distributed and of relatively uniform quality (Owen-Smith 1977). Nevertheless variation in, features such as soil type or slope can lead to different mineral and nutrient concentrations in the grass species (Rooyen & Theron 1996a), thereby creating a mosaic of male territories of different quality. Tropical forage is often chronically deficient in mineral elements (McDowell 1985 cited in McNaughton 1988) and these deficits could affect growth, puberty and adult reproductive performance (Bronson 1989). It is thus likely that female white rhinos show a preference for certain territories characterised by a high nutrient or mineral content as is the case in other grazing species (hartebeest Gosling 1974 cited in Gosling 1986, red deer Carranza et al. 1996), and that these preferences influence male mating success, as in pronghorn antelopes (Kitchen 1974) and Grévy's zebras (Ginsberg 1989).

The specific ecological resources which determine female distribution are difficult to assess as the availability of resources is not generally uniform, and preferences may change with changing availability (Manley et al. 1993). Therefore a variety of different methods were used in the study to describe the quality of the territory adequately. 1) The availability of grasses was established and their quality as food for grazers was assessed using plant characteristics described by van Oudtshoorn (1992) and others (Trollope et al. 1989, Dörgeloh 1999). This method is not based on the feeding preferences of rhinos at the study site. Therefore 2) the feeding preferences of male and female white rhinoceroses were established and the availability of frequently foraged or selected grass species were compared between male territories. Minor variations in the soil quality such as different levels of nitrogen, phosphate and calcium underneath a tree as compared to the open spaces (Van Rooyen et al. 1996), can affect the quality of a grass species. 3) To establish the mineral and nutrient concentration of the food in each territory the protein content, digestible energy, minerals, and fibre characteristics of the territorial males' intake were established. Since it is difficult and time consuming to collect ingested food samples (Zimmerman 1979), forage samples were collected for few animals and for a limited time only. 4) To account for seasonal changes in forage quality, the foods consumed were examined indirectly by analysing faecal samples collected over a time span of 16 months. Faeces provide a useful measure to determine the diet quality in both ruminants (various species: Grant 1995, white tailed deer: Howery & Pfister 1990, cattle: Zimmerman 1979, Wofford et al. 1985) and non-ruminants (horse: Mésochina et al. 1998, elephant: Greyling 2001) and are much easier to obtain than forage samples.

The quality of a territory can-not be determined by the composition of grass species alone, since various factors, such as weather, topography, geological formations and soil types can influence the quality of vegetation (Schwartz & Rennecker 1998). In order to describe localised conditions within each territory, the composition of tree species was established. The composition of trees reflects mean annual rainfall and the nature of the soil (van Wyk & van Wyk 1997) and, thus, provides an additional indirect measure for the quality of the vegetation (van Rooyen & Theron 1996a). The structure of the woody vegetation also plays an

important role in the rhinos' selection of suitable habitats. They favour an open to moderate low-shrub stratum and a moderate tree stratum and avoid a dense shrub area with sparse grass layers (Pienaar et al. 1993a, b, Pienaar 1994). To incorporate these preferences in the analysis, the vegetation structure of the territories was established.

The aim of the study was therefore to establish whether differences in distribution of rhinos do exist and whether these differences were correlated with differences in mating success; whether the quality of male territories described by means of food quality, vegetation structure and vegetation composition had an influence on the distribution of rhinos; and whether male morphological characteristics or androgen concentrations were correlated with their mating success.

METHODS:

Morphological characteristics:

A total of 18 different morphological characteristics were collected from immobilised male and female white rhinoceros (n = 56) of different age. Standard body and head measurements described by Hillman-Smith et al. (1986) and Rachlow et al. (1998) were used. These were complemented by measurements established in co-operation with D. Pienaar (senior scientist, Krüger National Park, Table 1, Fig. 10). Data were collected with a flexible tape measure and grouped into six different age and sex classes (adult and subadult females, female calves, adult and subadult males and male calves). Age classes were categorised as calves (0 – 2 years of age), subadults (2 – 6 years of age) and adults (> 6 years, see general methods). Data of adult females and males as well as adult and subadult males were compared to establish which of the morphological characteristics correlated best with the age and the sex of the rhinos. A Mann-Whitney test was used and p-values were adjusted with a sequential Bonferroni correction as data were used for multiple comparison. Morphological characteristics which correlated best with the age and the sex of the rhinos were chosen to compare body and horn measurements of the five adult males. Therefore the median value of each morphological characteristic was determined out of the five values obtained from each adult male, and the deviation of individual dimensions from the median value was calculated and compared between males.

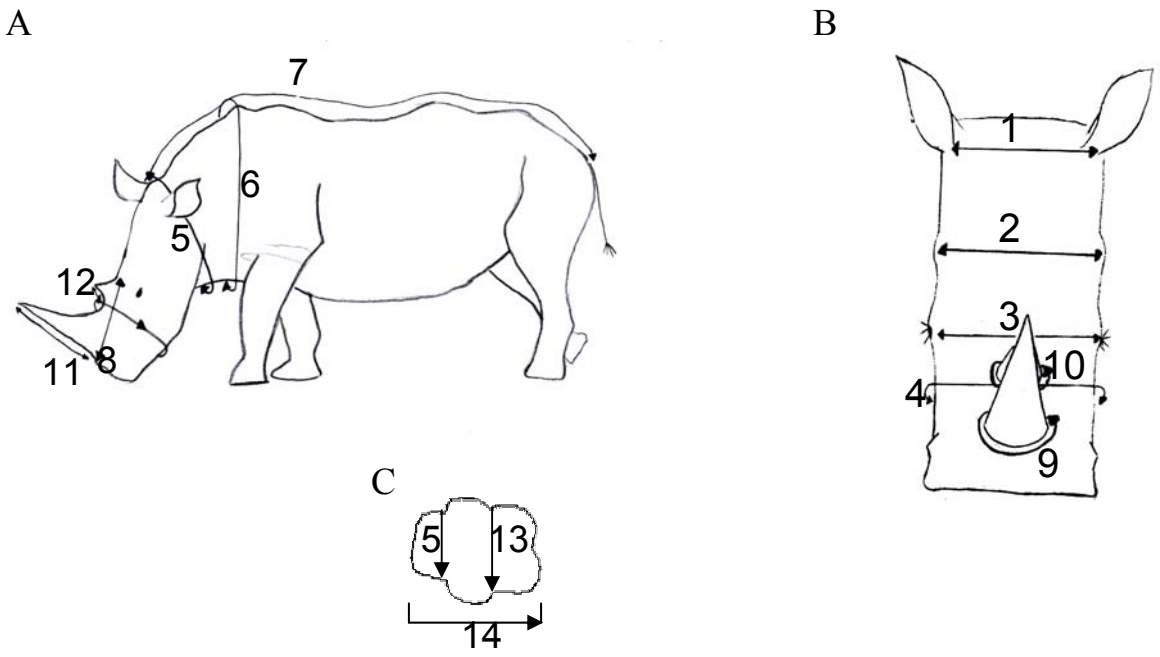


Figure 10: Sketches of body (**A**), head (**B**) and foot (**C**) indicating measurements taken from immobilised white rhinoceros. Measurements of hind foot (16, 17, 18) are equal to positions of the front foot (13, 14, 15).

Table 1: Measurements of head, body and foot dimensions taken from 56 immobilised white rhinos

measurements	Description
body measurements:	
1. distance between the ears:	length between the front base of the ear
2. distance between the temples:	distance between the temporal bulges
3. distance between the eyes:	distance between nearest points of eyes
4. head circumference*:	circumference between the horns
5. neck girth**:	measured around the neck, just behind the ears at the smallest circumference
6. hump girth:	measured around the neck at the widest circumference
7. body length*:	distance from the back of the tail to the back of the skull
horn measurements:	
8. total length horn base:	widest distance between base of anterior and posterior horn
9. anterior horn circumference*:	measured around the base of the anterior horn
10. posterior horn circumference:	measured around the base of the posterior horn
11. anterior horn length*:	length along the anterior curve of the anterior horn
12. posterior horn length*:	length along the anterior curve of the posterior horn
foot measurements:	
13. front foot, width lateral toes:	distance between lowest points of lateral toes of front foot
14. front foot length:	length between highest point of front toe and lowest point of heel
15. front foot, width front toe:	distance between most lateral points of front toe
16. hind foot, width lateral toes:	distance between lowest points of lateral toes of hind foot
17. hind foot length:	length between highest point of front toe and lowest point of heel
18. hind foot, width front toe:	distance between most lateral points of front toe

*according to Hillman-Smith et al. 1986, ** according to Rachlow et al. 1998

Territory size:

To establish the territory size of adult males, GPS locations of direct sightings or the location of footprints and other signs (scratch marks, dung heap etc.) of males collected during tracking and during daily routine patrol were used (see locating males general methods). However, signs of the animal were used only, when the pattern of lines on the underside of their feet allowed clear identification of the individual.

Territory size was established with the minimum convex polygon (MCP) method described by Mohr (1947), using the home range program Wildtrack for Macintosh, version 1.12 (Todd 1993). In the analysis, one GPS location per day was used. If several positions were gathered during tracking, the last location per tracking, usually the position of the animal when sighted, was chosen. For one of the five males, the minimum number of locations was too low to obtain asymptotic range estimates (Wildtrack, version 1.12 by Todd, 1993). Therefore for this male two locations per day were used for analyses, providing that at least 7 hours were in-between consecutive locations. Seven hours were assumed to be sufficient, to guarantee independence of consecutive locations, because males were observed to walk an average of 0.8 km per hour (n = 13). The median sampling interval between locations, the number of locations per animal, and the minimum number of locations required to describe asymptotic range estimates is given in the Results.

MCP´s are potentially problematic in describing range size as they are severely affected by a single outlying position (Baker et al. 2000). This method, however, is the only repeatable measure (Hundertmark 1998) enabling one to compare the size of the area used between different study sites; it was therefore favoured above others to estimate territory size. The areas established with minimum convex polygon methods included areas which were not used by rhinos, such as areas outside the fence or areas which were beyond the boundaries demarcated by faecal and urine markings. For a more realistic description of the areas used, the outer positions of each animal were connected on a map using Map Info Professional, version 5.0.1, Crystal Reports. Outlying positions (consisting of a single day excursion of the male mostly without demarcation of the area with faecal or urine marks) and physical borders such as fences were not included. The borders thereby established were used to describe territory quality (see below). For one male, who lost his territory in 1997, the size of the core area to which he always returned was established, instead of the territory size, by excluding the locations of trips lasting one to several days within the territories of the other males. To describe seasonal variations of the range used, all locations of an individual male collected within a three month period were grouped, and the area used within that time period was described using 100 % MCP methods. Starting with May 1997, eight different polygons were obtained for each individual. The Minimum Convex Polygon method was used for representing the area only, as more than one location collected within a day was included in the analysis. The area of overlap of individual territories was established by dividing the area of overlap by the total area of each individual. Therefore range estimates established with MCP 100 and Map Info were used. During tracking the length of a scrape mark was established by counting the number of steps (one step = 0.7 m length) and its average length was calculated.

Distribution of rhinos:

The distribution of rhinos was measured by counting their tracks found within a day along the waterholes of the study site. During monthly patrols all waterholes at the study site were visited within a day and checked for tracks belonging to different rhinos. Tracks of rhinos visiting the waterhole during the night and morning were included in the analysis. It was possible to differentiate between tracks of territorial bulls and others, but impossible to differentiate between the tracks of females and other males. It can therefore not be ruled out that individual animals might have been included more than once in the analysis, except for territorial males, although it is believed that the number of times animals were counted more than once is minimal, as rhinos usually drink only once per day, or more seldom (Owen-Smith 1973, Pienaar 1994). Territorial males were observed to visit several waterholes during a day, in order to check for females and other males. When their tracks were found on several occasions, they were only counted once in the analysis. It is likely that some animals were not included in the count, especially during the wet season, despite the fact that all waterholes on the study site were visited. The frequency of rhinos in each territory should thus be independent from the total number of animals analysed.

The analysis was started in February 1998 and was conducted monthly until April 1999, except for September 1998 and December 1998. A total of 41 waterholes was included in the analysis: 36 of them were filled with water during the dry season (permanent waterholes), and five were temporary waterholes, which dried up during the dry season. All waterholes enclosed within the border of a male's territory (established with Map Info, see Results) were included in the analysis. The number of waterholes enclosed by individual territories is given in the Results. Numbers of rhinos established monthly for each territory was added up to give the total numbers of rhinos found during the given time period.

Positions of females with juveniles of known fathers

Positions of females with juveniles of known fathers were determined using GPS locations of females collected during daily routine patrol (see general methods). Fatherhood was determined by genetic analysis, (see below). Two locations per day were used for analyses, provided that there was an interval of at least 7 hours between consecutive locations. Sightings of females were plotted on a map using Map Info Professional. Numbers of sightings within the territories of known sires were established by counting positions situated within the territory borders of males which were proven breeders of offspring. For one male borders were established using positions collected before he lost his territory (April – May 1997). The frequency of sightings of a female in the territory of the father of her offspring was determined from the number of sightings in the territory and the total number of sightings separately for each female.

Transect measurements:

Measurements on transect points located within male territories (established with Map Info Professional, see Results) were used to characterise the habitat of this territory. Transect points were placed at a distance of 0.8 minutes longitude and 0.8 minutes latitude to each other over the study area. This is equivalent to 1.48 km between each point from North to South and 5.35 km from East to West. The points were located using a GPS, giving a ± 100 m deviation in distance between points. At each transect point the vegetation structure and composition was measured. Two transect measurements were conducted; one at the beginning of the rainy season in October 1998 and the other at the end of the rainy season in April 1999. Even though the rains started in September 1998, only a few fresh shoots were observed, as rainfall was low (6.9 mm in September), so the conditions described in October are expected to reflect conditions during the dry season. Each survey took up to three weeks, during which no fresh growth was observed. Due to the smallness of the core area established for one male, the number of transect points was too low for habitat characterisation and he was left out in these analysis. The number of transect points for the males is given in the Results section.

Vegetation structure:

At each transect point the vegetation structure was measured. The structure was based on an assessment of the density of all bushes and trees of height of at least 1.70 m. This height was chosen, as it is expected to provide sufficient cover for adult rhinos which are approximately 1.70 m and more in height. The structure was categorised as follows: open, medium open, medium open to thick, and thick (see Fig. 11 - 14).
The number of transect points where this category occurred was divided by the total number of transect points of the study area/territory to establish the frequency of each category. For comparison of frequencies between the territories a new category was created, as the conditions for contingency tables were not met. The category was named "moderate open", combining the frequency of the categories „open", „medium open" and „m. open – thick ". To describe the densities, the number of trees within 100 m x 100 m squares of different densities was counted. The category "open" included up to 67 trees per 100 m^2, the category "medium open" comprised 68 - 115 trees per 100 m^2 and the category "medium open to thick" 116 - 500 trees per 100 m^2. The category "thick" included more than 500 trees per 100 m^2. In order to describe the degree of openness of a territory, each category was given a rank of increasing value, starting from "open" = 1 rising up to "thick" = 4. This value was multiplied by the frequency of each category in the territory of each male, separately for each season. The results of both seasons were then added in order to assess the degree of openness over the whole period.

Fig.11: Area at the study site classified as “open”.

Fig.12: Area at the study site classified as “medium open”

Fig.13: Area classified as “medium open to thick”

Fig.14: The category “thick” in the study area.

Tree species composition:

At each transect point the composition of tree and grass species was measured. The tree species composition was established at the end of the wet season, by determining the tree species occurring within a distance of approximately 50m around each transect point. The frequency of each tree species was obtained by counting the number of transect points where the species occurred, divided by the total number of transect points of the study area/territory. The height of trees was estimated by comparing its height with the height of a person standing next to the tree and subsequently averaged. To distinguish trees from shrubs, a tree was defined as a perennial woody plant growing to a height of at least 1.70 m.

Grass species composition:

The grass species composition was established within four 1m x 1m plots placed at right angles to each other, 10 meters away from the main transect point. Four single plots rather than one large plot were used for data collection, as the vegetation was heterogeneous at a small scale and it was assumed that several single plots would increase the chances of including single plant species, which was desirable for the study.
At the beginning of the wet season, only a few grass species could be identified, due to the lack of inflorescence, with only stubble remaining. The grasses were assigned to categories according to the similarity in appearance of the remaining parts: i.e. growth, width and strength of the leaves (Table 2). Species names included in the categories are given in the result section. More species may have been present but remained unrecognised.

Table 2: Description of the grass categories which were used at the beginning of the wet season.

Category	description
thin grass:	grass loosely tufted, leaves usually rolled in, up to 3 mm wide, leaves mainly emerging from the base of the plant
Enneapogon spec.:	grass densely tufted, leaves 3 - 5 mm wide, usually rolled in
broad grass:	grass loosely tufted, leaves between 10 - 20 mm wide
Eragrostis spec.:	grass loosely tufted, leaves between 2.8 - 4 mm wide, leaves mainly emerging from the stem and not from the base
tough grass:	loosely tufted grass, leaves 4 - 8 mm wide, hard, glabrous or sticky
tuff grass:	grass densely tufted, leaves 6 - 8 mm wide, usually flat
turpentine grasses:	dry leaves, rusty red, usually rolled in, 4 - 6 mm wide
short grass:	loosely tufted grass, leaves 5 - 12 mm wide, margin with sparse hairs, height 0.30 - 0.6 m
creeper:	widely branched grass, leaves 4 - 6 mm wide, usually flat

In each plot, the percentage cover of each grass species was estimated as well as its average height. The percentage of cover was established following Greig-Smith (1957), by estimating the proportion of the

ground area covered by the horizontal projections of the grass species. The average height of a grass species was determined by measuring the height of the average state of growth of individual grasses with a measuring tape. The average state of growth was assessed visually. Height and cover were then multiplied to establish the volume of each grass species at each plot. An average volume was established for each transect point and all single volumes of each grass species were added, giving the total volume per area per species. Afterwards the proportional volume of each species was calculated from the total volume of all species per area. The presence of a species on all four plots was combined per transect point giving a single count. The frequency of grass species was calculated from the number of transect points where it was present in relation to the total number of plots (n = 556 at the end of the wet season and n = 564 at the beginning of the wet season).

Food quality assessed by plant characteristics:

Three different plant characteristics (perenniality, palatability and grazing value, Table 3) were assigned to grass species identified at transect points during transect measurements. These characteristics describe the value of a grass species for grazing by animals (Trollope et al. 1989, van Oudtshoorn 1992, Dörgeloh 1999). Plant characteristics could only be assigned to grasses established at the end of the wet season, and not to categories established at its beginning, as they combined grass species of varied values.
The characteristics perenniality and palatability are two independent characteristics, while the grazing value is a combination of both. Their gradation is constant for most grasses; nevertheless, there are a few grass species whose values vary to a greater or lesser extent, especially in species with a wide geographical distribution (van Oudtshoorn 1992).

Table 3: Description of plant characteristics (van Oudtshoorn 1992) used within the study.

plant characteristic	description of plant characteristics
perenniality:	Describes the ability of a plant to produce a high amount of leaf material. An annual grass is channelling most of its resources to produce seeds for its own survival, while more leaf material is produced by perennial grasses.
palatability:	Describes the attractiveness of grass for animals by specific factors of forage: nutritive value, fibre content, unpalatable chemical substances and the moisture content. Four different categories were distinguished in the study following Euclea Ecological Consultants (1998): VU = very unpalatable, U = unpalatable, P = palatable, VP = very palatable.
grazing value:	Is a non-seasonal value which describes the value of a plant species for a grazing animal under normal, natural growing conditions (van Oudtshoorn 1992). The grazing value is based on a subjective assessment of various factors, such as leaf production ability, palatability, nutritive value, growth vigour, digestibility and perenniality. Five different categories were discriminated during the study: vh = very high, h = high, m = medium, l = low and vl = very low grazing value.

The frequency of grass species within a certain area (territory/study area) that have equivalent plant characteristics was calculated in relation to the total number of grass species, while the volumes of grass species with equivalent plant characteristics were added up, and related to the total volume to describe the proportional volume of grass characteristics within an area.

Food quality assessed by foraging analysis:

Food quality was assessed from the frequencies of how often males and females were foraging or selecting grass species. The foraging behaviour of male and female white rhinos was analysed by following the track of an individual animal while it was feeding. Every 100 m the vegetation was measured within a single 1 m x 1 m square (termed "patch") placed on the path of the animal. The percentage of the cover and the average height of each grass species within the square were determined the same way as described in the grass species composition. It was observed whether the animal was feeding at this particular point, and each grass species on which the animal was eating was recorded. Freshly eaten grass can be identified by the leaf tip, which turns brown with the passage of time after feeding. The height of the grass species before the animal was foraging was established by measuring the height of the plant of the same species in the surrounding area. The difference in height was calculated and multiplied by the cover of the grass species within the patch to establish the volume eaten by the rhino. The estimated volume does not correspond precisely to the quantitative intake in the diet, as cover and height of grass species before and after feeding were merely estimates. When the animal did not eat for a long time, a single feeding event was recorded, independent of the distance, while two feeding events in a distance of less than 100 m were not measured. Data collection was terminated if no feeding occurred within a distance of 1 km. Data were collected from adult animals only (males = 5, females = 6) and care was taken to collect a similar amount of data from different animals. The total of feeding and non-feeding patches for females and males was recorded, and the total number of patches for individual males is given in the Results section. The tracking sessions were situated in different areas. The number of feeding and non-feeding patches within one tracking session was therefore kept as equal as possible, in order to reduce the influence of the area on the grass species composition of the patches. The number of times a species was eaten relative to the total number of feeding patches gave its frequency. The grass species which were eaten less than six times in total were not included in the data analysis. The influence of a grass species on the selection of the feeding patches (patch selection) or on the decision to eat a plant (grass selection) were analysed in a hierarchical order (proposed by Johnson 1980, selection of the feeding patch within the territory represents a higher hierarchical level than the selection of particular food items within a feeding patch). Patch selection was determined by comparing the number of times a grass species was found on a feeding patch and a non-feeding patch with the total number of feeding and non–feeding patches using a G-test with Williams's correction or a Fisher exact test (see statistics). To establish the grass selection, the number of times a species was eaten was compared with the average number of times species were eaten. The average preference was established separately for males and females out of the average number of species eaten on a feeding patch divided by the average number of species found on a feeding patch.

Food quality described by the nutrient content in forage samples and faeces:

The nutrient content of the forage eaten by male rhinos was analysed from grass samples collected along the feeding trails of three territorial males. Feeding patches were determined as described in foraging analysis. The amount and grass species the animal eat, was identified and collected from a neighbouring patch. Grass was cut from 14 ± 8 (mean ± SD) feeding sites per male between morning and midday. Sample collection was finished, when an amount of approximately 2000 g of forage was collected. The samples were stored in a plastic bag in order to reduce evaporation and weighed at the end of the sample collection. Foraging samples were collected twice for each of the three males. The samples were dried in the open air until constant weight and stored in plastic bags in a cold, dark room until further preparation in the laboratory.

The food consumed was also indirectly examined by analysing faecal samples. Individually assignable faecal samples of males and females were either collected during tracking, or by random sightings of animals defecating. During tracking only samples from the preceding afternoon or night were collected, so that the exposure to the sun, heat and rain was low. The samples were taken from different parts of the dung heap, dried in the open air and stored in a freezer until further processing in the laboratory. The number of samples collected between November 1997 and March 1999 of adult females and males as well as the number of samples of individual males is given in the result section.

Chemical analysis of forage samples were performed by Britta Kiefer at the Ludwig-Maximilian-University Munich as part of her degree of veterinary medicine on white rhino nutrition (Kiefer 2002). The faecal samples were analysed in the laboratory of Dr. Lechner-Doll, Institute for Zoo and Wildlife Research, Berlin. The cell wall components: hemicellulose, cellulose and lignin were all determined with the same method by Goering & Van Soest (1970, see below), while the nitrogen content of forage and faecal samples was analysed by different methods used in the laboratories. Faecal nitrogen content was established using the method of Dumas (Association of Official Analytical Chemists (AOAC) 1968 cited in Wörner & Sieper 1997 see below), forage nitrogen content was established by the Kjeldahl method (Association of Official Agricultural Chemists 1965).

In forage samples, phosphorus levels were determined by a colorimetric method, potassium, calcium and sodium by flame photometry, chlorine by using an electronic Eppendorf Chloridmeter and magnesium, copper, zinc and iron by atomic absorption spectrophotometry. For a more detailed description of the methods used see Kiefer (2002).

Hemicellulose and cellulose content:

Samples were oven dried at 105 C over night and ground to a grain size of 0.2 mm (Retsch SM1, Haan, Germany). The weight of a filter bag was established and 0.5 g of the sample were weighed into the bag and then sealed. All samples were determined in duplicates and the average concentration was established. Samples were treated with amylase to ensure that starch does not influence the filtering of the sample, which could likely falsify NDF values (McQueen & Nicolson 1979 cited in Kiefer 2002). In the following the procedures to establish ADF, ADL and NDF are described. They give the concentration of cellulose and hemicellulose as follows: cellulose = ADF – ADL, hemicellulose = NDF – ADF.

Acid detergent fibre (ADF):

The samples were boiled for 60 minutes in an acid detergent solution (100 ml/bag) consisting of cetyltrimethylammonium bromide (20 g) in 1 N H_2SO_4 (1000 ml) using the equipment from Ankom Technology. After one hour 2000 ml hot water was added to rinse the samples. The filter bags were agitated in the water until the water was at neutral pH. Afterwards, they were placed into a beaker and covered with acetone. Bags were allowed to soak for 3 minutes. Afterwards, the filter bags were placed in an oven at 105 °C for 2 – 3 hours. After cooling down the bags were weighed again and ADF was calculated as follows:

$$\frac{(W_3 - (W_1 \times C_1)) \times 100}{W_2}$$

$\mathbf{W_1}$ = Bag tare weight, $\mathbf{W_2}$ = Sample weight, $\mathbf{W_3}$ = Weight after extraction process, $\mathbf{C_1}$ = Blank bag correction (final oven-dried weight/original blank bag weight)

Acid detergent lignin (ADL_{OM}):

After performing ADF 72 % H_2SO_4 was added to the bags to dissolve cellulose. The bags were agitated at 30 minute intervals for three hours and rinsed afterwards with hot H_2O until pH was neutral. The bags were washed with acetone to remove water. The filter bags were dried in an oven at 105°C for four hours. Afterwards the weight of the bags was established, the bag was then ashed in a pre-weighed beaker at 500 °C for 3.5 hours and weighed again in order to determine the lignin fraction including cutin.
ADL_{OM} was calculated as follows:

$$ADL_{OM}\ (\text{Dry matter basis}) = \frac{(W_4 - (W_1 \times C_2)) \times 100}{W_2 \times DM}$$

$\mathbf{W_4}$ = Weight of organic matter (OM) (loss of weight on ignition of bag and fibre residue), $\mathbf{C_2}$ = Ash corrected blank bag (loss of weight on ignition of bag/original blank bag)

Neutral detergent fibre (NDF):

The cell soluble material is extracted by boiling the samples in filter bags with a neutral solution (100 ml/bag) containing a mixture of sodium lauryl sulfate (30 g), ethylenediaminetetraacetic disodium salt, dihydrate (18.61 g), sodium tetraborate decahydrate (6.81 g), sodium phosphate dibasic (4.56 g) and triethylene glycol (10 ml) in 1000 ml distilled H_2O. Additionally, 20 g of sodium sulphite were added to the solution along with 4 ml of heat stable bacterial alpha-amylase (activity 17.400 Liquefon Units/ml). The samples were boiled and agitated for 75 minutes using the equipment from Ankom Technology. The filter bags were rinsed with 2000 ml of boiling H_2O and 4 ml of alpha-amylase afterwards. The bags were then oven dried at 105 °C for 2 – 3 hours and afterwards the weight of the bags was established.

$$NDF = \frac{(W_3 - W_1 \times C_1)) \times 100}{W_2}$$

Protein content:

The total nitrogen content of the faeces was determined using the method of Dumas (AOAC 1968 cited in Wörner & Sieper 1997). The sample under test was weighed into a metal container and placed into the reactor chamber of the autosampler (Heraeus, Macros N), where excess oxygen was introduced before. At about 990 °C the material was "mineralised". Formation of carbonmonoxide was probable at this temperature even under conditions of excess oxygen. The complete oxidation was reached in a CuO chamber with a platinum catalyst which was passed by the gaseous reaction products. The resulting gas mixture consisted of CO_2, H_2O and NO_x, and some excess O_2, which passed the catalyst. The gas mixture flowed through a silica tube packed with copper granules. In this zone, held at about 500 °C, remaining oxygen was bound and nitric/nitrous oxides were reduced. The leaving gas stream included the analytically important components CO_2, H_2O and N_2. Biproducts such as SO_2 or hydrohalogenides were absorbed at appropriate traps. For N-determination CO_2 was used as a carrier gas. Finally the gas mixture was brought to a defined pressure/volume/temperature state and was passed to a gas chromatographic system. Separation of the species was done by so called zone chromatography. In this technique a staircase type signal was registered. Step height was proportional to the substance amount in the mixture.

Blank values were taken from empty tin capsules. Calibration was done by elemental analysis of standard substances (Asparagin acid N = 10.52 %) supplied by the instrument's manufacturer. According to the supplier, the instrument's uncertainty stays below 0.3 w-% in the medium range. Although the detection limit for nitrogen at sample amounts of 2 to 3 mg was found to be at about 0.05 w-% (500 ppm). Fluorine is mineralised to form HF which reacts at the wall of the silica tubes. The gaseous products (SiF4 and relatives) can cause systematic errors which rarely become significant with respect to the 0.3 w-% tolerance. Crude protein was established by multiplication of nitrogen concentrations with the factor 6.25.

Genetic analysis of fatherhood:

Gene sequence information can not be used to determine paternity in the rhino because to few adequate genetic markers have yet been developed (van Coeverden de Groot et al. 2001). Therefore, a DNA fingerprinting method termed "Amplified Fragment Length Polymorphism (AFLP) " was used to determine paternity which does not rely on sequence data but rather on differences in the lengths of DNA-fragments after treatment with restriction enzymes. The AFLP method allows high-resolution genotyping of fingerprinting quality (Vos et al. 1995, Mueller & Wolfenbarger 1999). This method was established by Kellner (2000) for the white rhinoceros. The parentage test of the samples collected at the study site was performed at the Institute of Animal Breeding of the Ludwig-Maximilian-University as part of her D.V.M. thesis. Parentage could only be determined with the AFLP method when one parent was known. Therefore analysis of fatherhood was only carried out for young calves (age: median 1 year, IQR = 0) which were still accompanied by their mothers.

Blood samples were collected in July 1998 from immobilised animals. The blood samples were gathered in EDTA vacutainer, kept in a cooler box until the evening and frozen at – 12 °C until transportation to Germany. During transportation, samples were kept in dry ice and frozen again at – 12 °C until further analysis. At the Institute for Animal Breeding genomic DNA was isolated. The DNA was digested with 2

restriction enzymes, EcoRI and TaqI, resulting in a subset of restriction fragments. Adaptors with known sequences were ligated to each end of the fragments. These restriction fragments were selectively amplified in a PCR reaction and analysed on a polyacrylamide gel on a LICOR DNA Sequencer. An external standard was used to determine the size of the fragments in basepairs (bp). Polymorphisms were detected as the presence or absence of an amplified restriction fragment. A set of 64 AFLP primer combinations was tested and 12 primer combinations were selected for further investigation. They produced an average of 60 - 80 bands per PCR reaction and animal in a range of 50 to 510/800 basepairs (Kellner 2000). For parentage testing the combined exclusion rate (Jamieson & Taylor 1997) was used. More detailed information about the method can be found in Kellner (2000) and Kellner et al. (2001).

Statistics:

For data analysis, nonparametric statistics based on two-tailed tests were used. The calculation of the statistical tests was carried out using the statistic programs SPSS 8.0 for windows (© SPSS Inc.) and SsS 1.0 (Rubisoft Software GmbH). For descriptive statistics the median and interquartile ranges (IQR) were calculated, giving 25 % and 75 % of the data range. A G-test with Williams's correction was applied for contingency table data, when 20 % of the expected frequencies were above 5 % and no expected frequency were below 1.0. Otherwise a Fisher exact test was used when comparing two samples (Zar 1996). Feeding preferences of individuals could not be established due to the low sampling size. However, a similar amount of data from different animals was obtained to reduce errors obtained from pooling (Leger and Didrichsons 1994). Feeding preferences of individuals of the same sex were assumed to be similar, due to their similarity in body size and data was pooled. The Kruskall Wallis test (H) was used to test for differences between more than two data sets (Zar 1996). If the outcome of the test suggests a significant result, a Mann-Whitney U-test was applied for individual comparison between two samples. When data was used for multiple comparisons a sequential Bonferroni was applied to adjust p – values (Hochberg 1988). If there were tied ranks, a correction factor was computed (SsS 1.0, Rubisoft Software GmbH).

RESULTS:

Territorial behaviour:

The tracks of five adult males were followed over a distance of 1086 km (mean = 217 ± 76 km). During tracking a total of 3051 scrape and faecal marks were recorded. Scrape marks resulted from scraping the rear legs on the ground or over vegetation, often followed by spray urination. The average length of a scrape mark was 1.70 m (min. = 0.35 m, max. = 11.2 m). This behaviour was recorded in 2653 instances (mean = 531 ± 191 times/male). Faecal marks consisting of dung kicked with the hind legs after defecating. These marks were less often recorded (n = 398, mean = 80 ± 14 times/male).

Table 4: Number of scrape marks and faecal marks recorded for each adult male while following its track. For Schrägman the number of territorial markings before and after he lost his territory are reported.

study animals	distance followed [km]	number of scrape marks	number of faecal marks
Amsterdam	170	331	65
George	248	837	101
Kent	184	341	64
Rambo	336	640	77
Schrägman:			
before territorial loss	21	113	10
afterwards	127	391	81
Σ	1086	2653	398

Each of the five studied males showed scrape and faecal marking behaviour (Table 4). The male named "Schrägman", who lost his territory in June 1997, occasionally urinated in a stream like females (n = 11) and did not scatter the dung (n = 13) after defecating. However he still showed a high number of scrape (n = 391) and faecal marking (n = 81) behaviours. As these are characteristics for territorial males all males were classified in the following as territorial males.

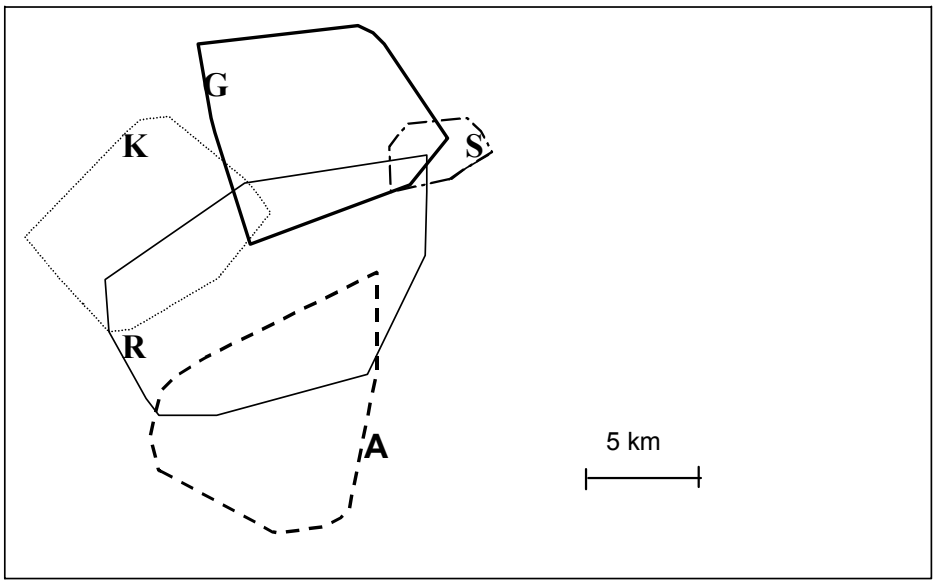
Table 5: Territory size of adult males calculated with two different methods: the 100 % minimum convex polygon (MCP) method and by connecting the outer positions of each animal** on a map using Map Info Professional. The total number of fixes and the minimum number of fixes which is required to describe asymptotic range estimates is given

territorial males	territory size [km^2]		number of fixes	
	MCP 100 %	Map Info	total	minimum number
Amsterdam	76.4	73.4	138	84
George	72.5	54.4	129	70
Kent	60.6	67.6	127	100
Rambo	116.0	74.5	173	162
Schrägman*	10.5	12.0	98	80

* Size of the core area which he used after territorial loss. Trips lasting one to several days into the territories of the other males were not included in the analysis.
** excluding positions consisting out of single day excursions mostly without demarcation of the area with faecal or urine marks or physical barriers e.g. a fence.

The size of the territories ranged between 60.6 km^2 and 116 km^2 (MCP 100 %, excluding the size of the core area established for Schrägman, Table 5, Figure 15). Rambo had the largest territory followed by Amsterdam and George. Kent had the smallest territory. For Schrägman no definite territory could be described. After territorial loss, he settled in a new area and made short trips lasting one to several days into the territories of the other males. However, he always returned into a small area, referred to as core area, which was 10.5 km^2 in size (Table 5).

A



B

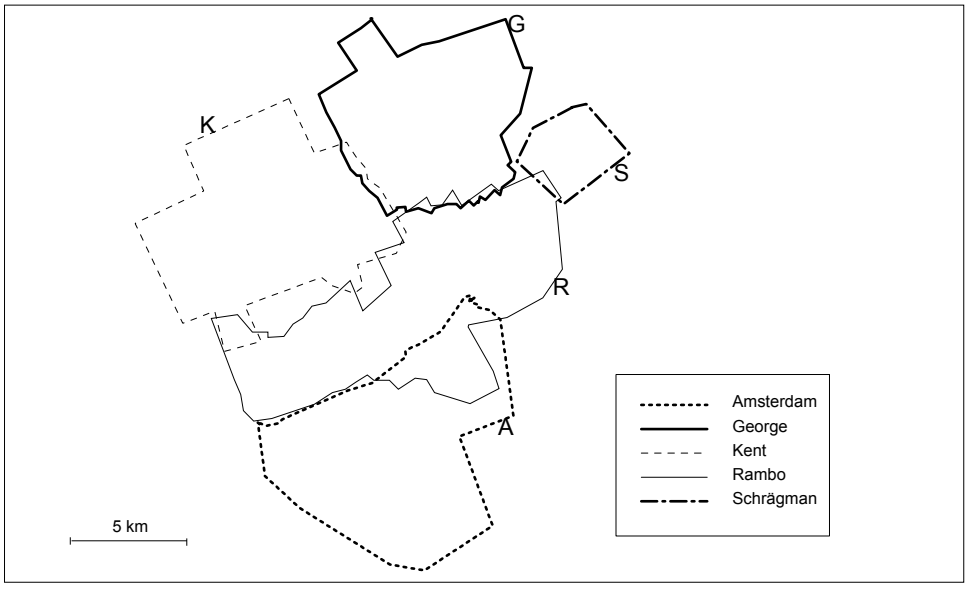


Figure 15: Territories of males expressing scent-marking behaviour in the study area between March 1997 and May 1999. For Schrägman (S), the size of the core area (excluding single excursions) which he used after territorial loss is given.The letters within the graph symbolise the name of the males.
Graph **A** indicates the range estimated using 100 % minimum convex polygon method. One sighting per day was included in the analyses. **B** indicates the range established by connecting the outer positions of each animal using Map Info Professional. Outliers consisting of single trips of males without demarcation of the area with fecal or urine marks and physical borders (fence around the study site) were not included.

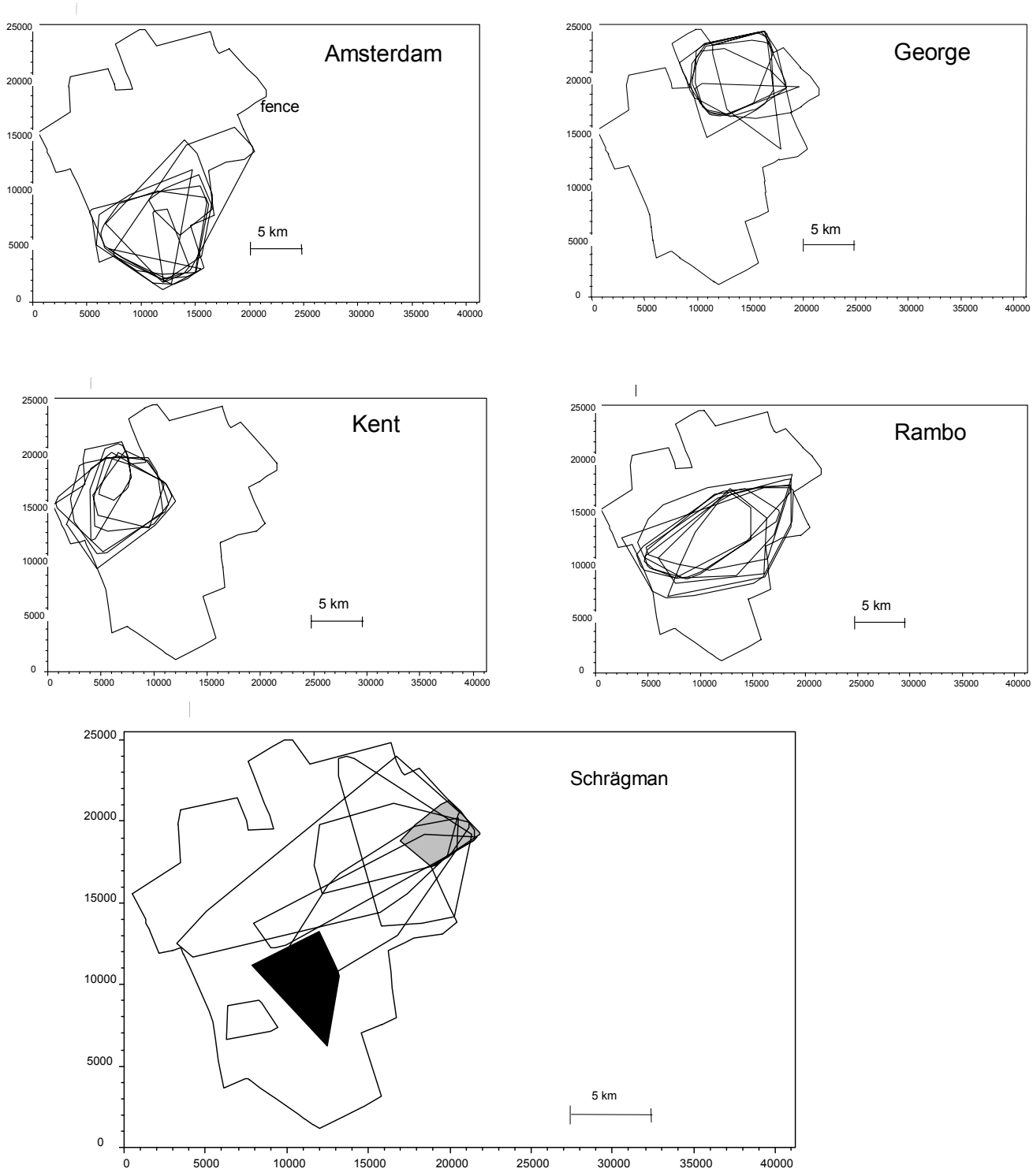


Figure 16: Range used by five territorial males within three months periods during a two year study period. Minimum convex polygons (100 %) were drawn, using locations of an individual male (mean = 116 ± 77 per 3 month period) collected during tracking. Starting with May 1997, eight different polygons for each male are shown in each graph. MCP´s were used only for graphic presentation as conditions for independence were not met with the method. For orientation, the fence around the study area is shown. The dark coloured polygon in the graph "Schrägman" indicates the area used before territorial loss. The light coloured polygon indicates the core area used afterwards.

The size of the territories measured by drawing a line directly on a map around the outer positions of each animal was smaller compared to the 100 % minimum convex polygon method. It ranged between 54.4 km^2 and 74.5 km^2 (Table 5, excluding Schrägman). The proportions of the territories to each other were similar when comparing the males with the largest territories, Rambo and Amsterdam, but the smallest territory was here established for George and not for Kent.

The territories established with the 100 % minimum convex polygon method overlapped widely (Figure 15A). The mean overlap among territories (including the core area of Schrägman) was 42.3 % ± 12.2 % (n = 5) of an individual's territory. The mean overlap among territories established by drawing a line directly on a map around the outer positions of each animal was smaller (9.8 % ± 6.7 %, n = 5), but overlap among individual territories was still substantial: Amsterdam: 15.4 %, George: 4.9 %, Kent: 6.1 %, Rambo: 18.6 %, Schrägman: 3.8 %. The large territories of Amsterdam and Rambo overlapped more widely compared to the smaller territories of George, Kent and Schrägman.

The range used by the territorial males varied during the study period (Figure 16). The male who showed strongest variation in range was Schrägman who lost his territory in June 1997. Too few data were collected until that time to determine clearly what has happened. Rambo initiated several fights with Schrägman and followed him persistently every day. It is likely that he displaced him from his territory, but Amsterdam also took over part of the vacant territory. The other males also showed strong variations in range used, except for George, whose territory border was relatively stable over the observation period (Figure 16).

Morphological characteristics:

All body and horn measurements, except the distance between the eyes and the distance between the temples, were shown to reflect differences in size between sexes and age classes (Table 6). Subadult males were significantly smaller in size compared to adult males in all of the ten body and horn measurements which were analysed: distance between the eyes, circumference of the head, total length of the hornbase, circumference of the anterior and posterior horn, length of the anterior and posterior horn, girth of the neck and of the hump, and body length (results of Mann Whitney test with *a posteriori* sequential Bonferroni are given in Table 6). Adult males were also significant larger in size compared to adult females in all of the ten analysed horn and body dimensions (p - and Z - values are given in Table 6). No difference was found in the measurements of the front and hind foot between different sex and age classes (Table 6).

For comparison of morphological characteristics between individual adult males, only those measurements were used which showed significant differences between sexes and age classes (no. 3 – 12 in Table 6 and Figure 17).

Table 6: Head, body and foot dimensions (mean ± SD) of six different age and sex classes: calves (0 – 2 years), subadults (2 – 6 years) and adults (> 6 years). Dimensions from subadult males and adult males as well as adult males and ad. females were compared using Mann-Whitney test (Z). P-values were adjusted with sequential Bonferroni.

measurement [cm]	female calves		male calves		subadult female		subadult male		adult female		adult male		subad./adult male		adult male/ adult female	
	n	mean ± SD	n	mean ± SD	n	mean ± SD	n	mean ± SD	n	mean ± SD	n	mean ± SD	Z	p	Z	p
body measurements																
1. distance between ears	2	29 ± 6	9	31 ± 4	13	37 ± 3	10	38 ± 5	16	42 ± 3	5	48 ± 7	-2.6	0.09	-1.9	0.1
2. distance betw. temples	2	36 ± 4	8	37 ± 6	14	44 ± 3	9	47 ± 6	16	48 ± 4	5	52 ± 4	-2	0.5	-1.9	0.1
3. distance between eyes	2	29 ± 1	8	31 ± 4	11	37 ± 4	9	41 ± 6	14	43 ± 6	4	52 ± 3	-2.6	**0.02**	-2.3	**0.02**
4. head circumference	2	89 ± 1	9	88 ± 5	14	108 ± 7	10	115 ± 15	16	120 ± 9	5	140 ± 20	-2.1	**0.04**	-2.8	**0.01**
5. neck girth	2	140 ± 14	8	131 ± 6	14	162 ± 4	10	169 ± 20	16	175 ± 5	5	206 ± 11	-2.7	**0.007**	-3.3	**0.002**
6. hump girth	2	157 ± 9	8	150 ± 7	13	188 ± 8	10	205 ± 20	14	209 ± 8	5	256 ± 13	-3.1	**0.002**	-3.2	**0.002**
7. body length	2	183 ± 16	8	174 ± 8	14	214 ± 28	10	228 ± 24	16	244 ± 9	5	273 ± 15	-3.1	**0.002**	-3.2	**0.002**
horn measurements																
8. total length horn base	2	27 ± 1	9	27 ± 8	14	33 ± 3	10	36 ± 6	15	38 ± 2	5	44 ± 3	-2.6	**0.01**	-3.1	**0.004**
9. ant. horn circumf	2	36 ± 0	8	36 ± 5	13	51 ± 5	10	61 ± 15	16	61 ± 4	5	81 ± 3	-2.5	**0.01**	-3.3	**0.002**
10. post. horn circumf	2	25 ± 4	9	21 ± 9	13	38 ± 5	10	50 ± 9	15	49 ± 3	5	67 ± 7	-2.6	**0.008**	-3.3	**0.002**
11. ant. horn length	2	20 ± 3	9	15 ± 6	14	32 ± 10	10	40 ± 1	14	51 ± 9	5	62 ± 8	-3.1	**0.002**	-2.6	**0.002**
12. post horn length	2	5 ± 0	8	4 ± 1	13	10 ± 2	10	13 ± 5	15	17 ± 2	5	23 ± 3	-3.0	**0.003**	-3.2	**0.002**
foot measurements:																
13. fr.f. width lateral toes	1	19	7	22 ± 2	14	22 ± 2	9	25 ± 4	13	24 ± 4	4	26 ± 4	-0.2	0.9	-1.2	0.5
14. front foot length	1	25	8	24 ± 1	14	29 ± 3	8	29 ± 2	14	30 ± 2	5	31 ± 2	-1.8	0.2	-1.1	0.3
15. fr. f. width front toe	1	13	8	14 ± 1	14	14 ± 2	9	14 ± 2	15	15 ± 2	5	15 ± 2	-0.5	0.6	-0.6	1.2
16. h. f.width lateral toe	1	16	8	18 ± 2	13	19 ± 3	10	21 ± 3	15	22 ± 7	5	23 ± 3	-0.8	0.4	-1.2	0.4
17. hind foot length	2	25 ± 1	8	25 ± 5	14	29 ± 3	10	30 ± 2	15	30 ± 4	5	33 ± 4	-1.7	0.1	-1.8	0.1
18. h. f. width front toe	2	12 ± 2	8	11 ± 1	14	14 ± 1	10	14 ± 1	15	14 ± 1	5	15 ± 1	-0.9	0.4	-0.9	0.7

Rambo was the largest male of all (Fig. 21). He showed highest values in five out of ten analysed body and horn dimensions (length of the horn base, circumference of the 1. horn, head circumference, hump girth, body length, Fig. 17). Amsterdam was the second largest male (Fig. 18). He showed the largest deviation from the median value in the characteristics "distance between the eyes" and "circumference of the second horn". The other males (George: Fig. 19, Kent: Fig. 20, Schrägman: Fig. 22) showed highest values in only one of the ten analysed morphological characteristics (George in neck girth; Kent in length 1. horn, Schrägman in length 2. horn). They were therefore classified as equal in size.

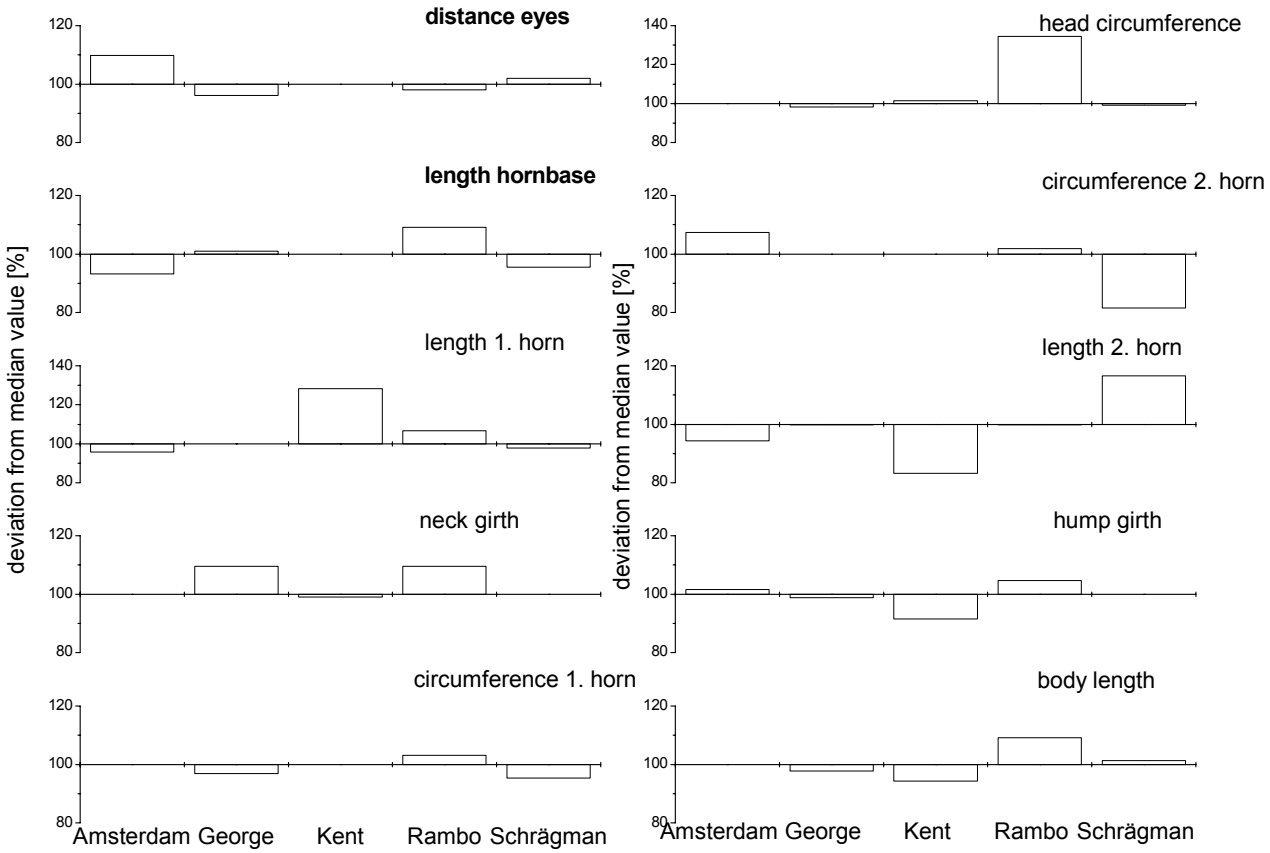


Figure 17: Comparison of body and horn dimensions between individual males. Data of adult males were compared by calculating the deviation of individual body and horn dimension from the median value of each morphological characteristic.

Figure 18: Picture of adult male named Amsterdam George

Figure 19: Picture of adult male named

Figure 20: Picture of adult male named Kent Rambo

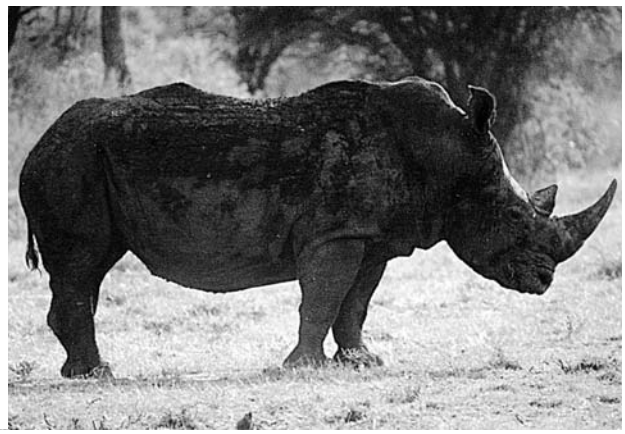


Figure 21: Picture of adult male named

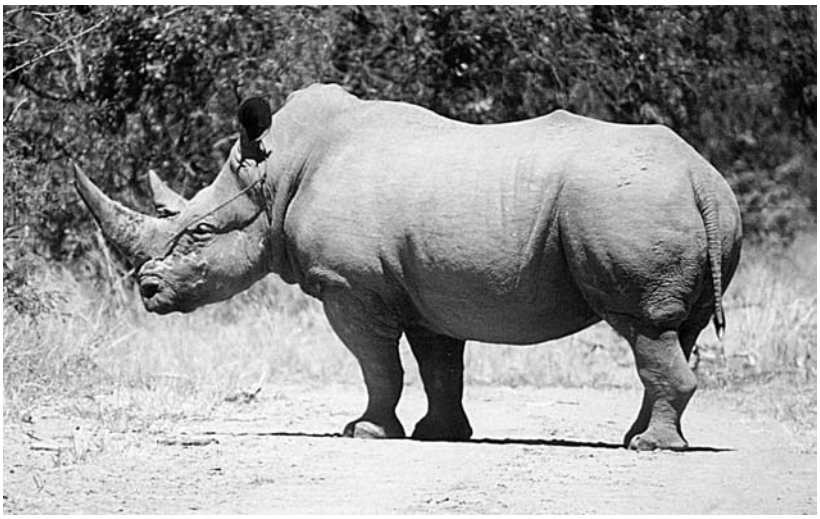


Figure 22: Picture of adult male named Schrägman

Territory quality:

The quality of the territories was established using measurements on transect points enclosed by the territory boundaries (Figure 23). The number of transect points used for each territory was as following: Amsterdam = 34, George = 28, Kent = 34, Rambo = 41, Schrägman = 6.

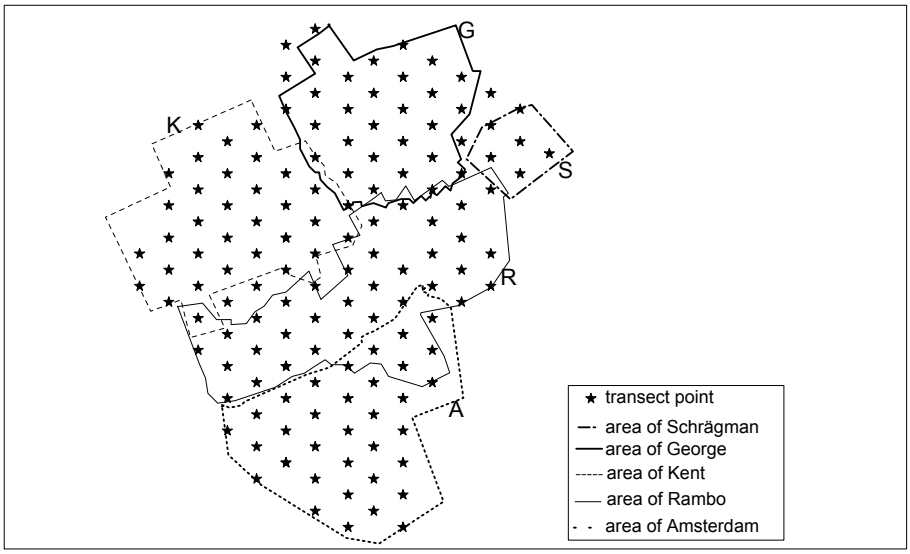


Figure 23: Distribution of transect points among the territories of five adult males. The lines indicate the border of the area occupied by each male. The letter symbolises the owner of the area.

Vegetation structure of the study site:

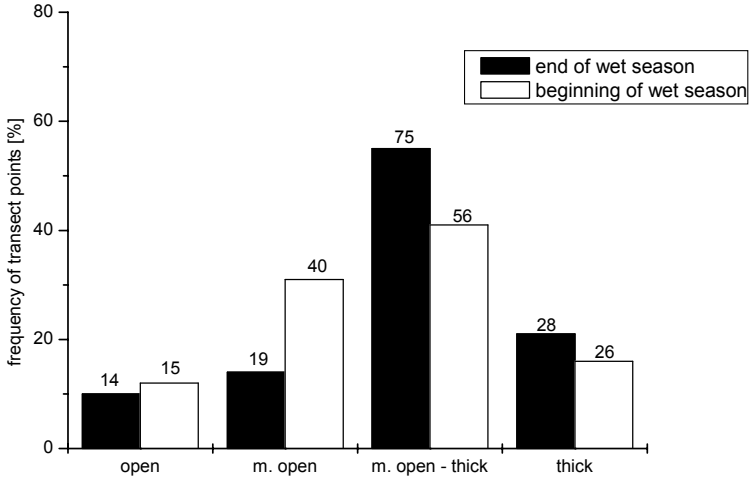


Figure 24: Frequency of four different categories of openness at the beginning of the wet season (Oct. 1998) and at the end of the wet season (Apr. 1999). The number of transect points per category is given on top of the bars.

The study area consisted mainly of „medium open to thick“ areas, both at the beginning of the wet season (41%, n = 56) and at the end of the wet season (55%, n = 75, Fig. 24). The degree of openness of the study area differed significantly between the seasons (G - test with Williams correction: df = 3, p = 0.016, G = 10.4), with a tendency towards thicker habitats at the end of the wet season.

Vegetation structure of the territories:

The territories of adult males were ranked according to their openness. Schrägman had a territory with a low degree of openness (rank = 325) closely followed by George (r = 319), Kent (r = 272) and Amsterdam (r = 267). Rambo had the highest degree of openness (r = 243) in his territory. The male Schrägman is left out for further comparisons because of the low number of transect points within his territory (n = 6).

All four categories of openness occurred in the territories of the four remaining males (Fig. 25). The category “m. open to thick” was the most frequent category in all territories, both at the beginning of the wet season and at its end. The category “thick” was most frequent in the territory of George compared to all other males, both at the end of the wet season (41 %) and at the beginning (33 %). A statistical comparison of the distribution of all categories between all territories was not possible as the conditions for contingency tables were not met. Therefore a new category was created, named „moderate open” (Table 7) and its frequency was tested against that of the category “thick” The results revealed significant differences between the territories at the end of the wet season (G - test with Williams correction: df = 3, p = 0.0007, G = 17.1). Rambo had a significantly higher number of moderately open transect points within his territory compared to

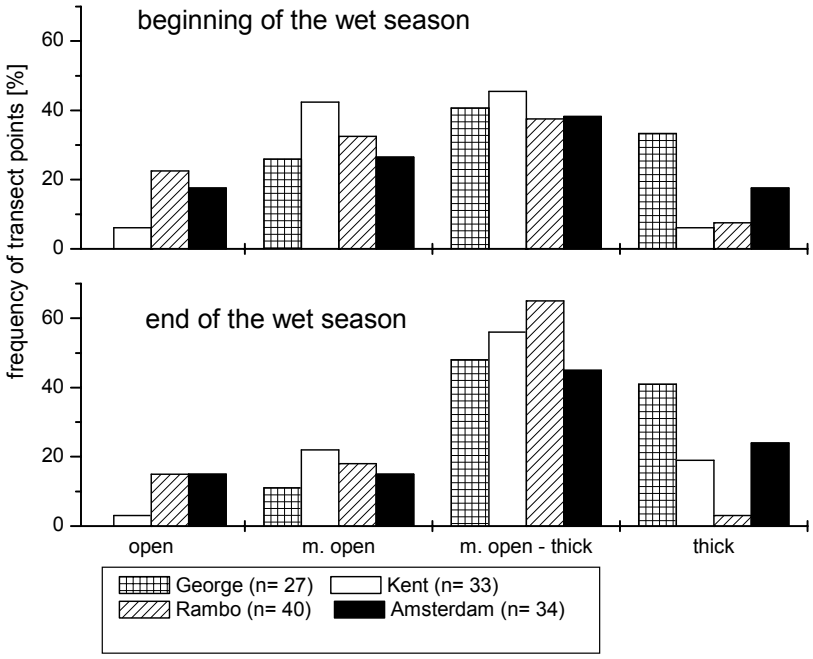


Figure 25: Comparison of the degree of openness between the territories of four adult males. The graph represents the frequency of transect points per category of „openness“. The total number of transect points in the territory of each male is given in the legend.

Amsterdam and George (Fisher exact test with *a posteriori* sequential Bonferroni correction: Rambo/Amsterdam p = 0.045, Rambo/George p = 0.0005). No difference was observed between any other pairs of males in the frequency of the two categories (Fisher exact test with a posteriori sequential Bonferroni correction: Rambo/Kent p = 0.16, G - test with Williams correction and a posteriori s. Bonf.: George/Amsterdam df = 1, p = 0.36, G = 1.8; George/Kent df = 1, p = 0.20, G = 3.4; Amsterdam/Kent df = 1, p = 0.60, G = 0.3). It was not possible to compare the territories at the beginning of the wet season as 25 % of the expected frequencies were below five percent.

Table 7: Number of the category „moderate open“ and „thick“ measured at transect points within the territories of four adult males at the end of the wet season.

study animals/categories	Amsterdam	George	Kent	Rambo
moderate open	25	16	26	39
thick	8	11	6	1

Comparison of vegetation structure between the male territories and the study area:

The frequency of the different categories of openness of each territory was in all cases similar to their overall frequency of the total study area. The results of the G - test or Fisher exact test are given in Table 8.

Table 8: Results of the G - test (df = 3) or Fisher exact test (∗), comparing the frequency of four categories of openness between the territories and the study area, both at the beginning and at the end of the wet season. P - values were adjusted with a posteriori sequential Bonferoni correction, after multiple comparison of the frequencies of each category with the study area.

	Amsterdam		George		Kent		Rambo	
	p - value	G	p – value	G	p - value	G	p – value	G
end of wet season	0.68	∗	0.25	∗	0.99	∗	0.08	10.0
beginning wet season	0.80	1.0	0.31	∗	0.44	0.1	0.51	5.9

Tree species composition of the study area:

Ten tree species constituted the main woody component of the study area. Three of these species - *Combretum apiculatum*, *Acacia erubescens*, *and A. tortilis* - occurred on average on 50 % of all transect points (Table 9). The average height of the tree species was 5 m.

Table 9: Scientific name* and common name* of the main tree species found at transect points (N = 139) at the end of the wet season. For each species its average height and its frequency are given. The frequency does not add up to 100% as several tree species could occur at each transect point.

scientific name	common name	average height [m]**	frequency on transect points [%]
Combretum apiculatum	Rooibos	5	68
Acacia erubescens	Bluethorn	5	56
A. tortilis	Umbrella thorn	4	47
Pterocarpus rotundifolius	Round-leaved teak	3	43
A. nigrescens	Knob thorn	8	38
Peltophorum africanum	Weeping wattle	5	17
Sclerocarya birrea	Marula	10	12
Terminalia sericea	Silver cluster-leaf	3	11
A. mellifera	Black thorn	5	6
C. imberbe	Leadwood	6	6

* According to van Wyk & van Wyk 1997
** Mean of the average heights of each species of all transect points

Comparison of tree species composition between the male territories:

A comparison between the frequency of tree species on transect points within the male territories could only be applied for the five most abundant species (Table 10). For the other species not enough records were found to allow statistical comparison. Therefore a new category was created including *Peltophorum africanum*, *Terminalia sericea*, *A. mellifera* and *C. imberbe*, called "others". *Sclerocary birrea* was not included in this category. It showed a striking difference in its frequency between the territories of two males (Amsterdam 3 %: George 33 %, Table 10) and was therefore tested separately. The frequency of *Sclerocary birrea* was significantly higher in the territory of George compared to that of all other males (Fisher exact test and a posteriori sequential Bonferroni: George/Amsterdam: $p = 0.01$, George/Kent: $p = 0.02$, George/Rambo: $p = 0.02$), while no difference was found between the frequency of the category "others" between males (G – test with Williams correction: $df = 3$, $p = 0.4$, $G = 2.8$).

Table 10: The frequency of each tree species on transect points within the territories of four adult males. The result of the G – test (df = 3), comparing the number of transect points found with or without a particular tree species between the territories of the males, is given in the table.

scientific name	Amsterdam [%]	George [%]	Kent [%]	Rambo [%]	G	p
Combretum apiculatum	76	81	62	59	5.5	0.14
Acacia erubescens	39	52	85	44	19.3	**0.0002**
A. tortilis	64	37	44	46	4.7	0.19
Pterocarpus rotundifolius	61	48	35	34	6.4	0.09
A. nigrescens	42	37	18	51	9.3	**0.02**
Peltophorum africanum	6	19	21	20	♦	♦
Sclerocarya birrea	3	33	6	10	♦	♦
Terminalia sericea	6	0	15	12	♦	♦
A. mellifera	3	7	3	12	♦	♦
C. imberbe	12	0	0	7	♦	♦

♦ Application of the G - test was not possible

A significant difference was found in the frequency of the tree species *Acacia erubescens* and *A. nigrescens* between the male territories (results of the G – test: Table 10). The frequencies of the tree species were therefore tested separately using a G - test with Williams's correction and a posteriori sequential Bonferroni. *A. nigrescens* occurred significantly less often in the territory of Kent (18 %) compared to the territory of Rambo (51 %, df = 1, p = 0.009, G = 9.3), but not to all other males (Kent/Amsterdam: df = 1, p = 0.054, G = 4.9; Kent/George: df = 1, p = 0.09, G = 2.8). *Acacia erubescens* was significantly more frequent in the territory of Kent (85 %) compared to those of Amsterdam (39 %), George (52 %) and Rambo (44 %, Kent/Amsterdam: G = 15.5, p < 0.001; Kent/George: df = 1, p = 0.005, G = 8.0; Kent/Rambo: df = 1, p < 0.001, G = 14.2).

Comparison of tree species composition between the study area and male territories:

The relative frequency of each tree species in each male territory was compared to that of the overall study area. A. *erubescens* was significantly more frequent in the territory of Kent compared to the study area (G - test with Williams correction and a posteriori sequential Bonferroni: df = 1, p < 0.01, G = 10.8, Table 11). The frequency of *A. nigrescens* within his territory was only slightly lower in proportion to the average frequency of the species in the study area (G – test with Williams correction and a posteriori sequential Bonferroni: df = 1, p = 0.057, G = 5.5). *Sclerocarya birrea* occurred significantly more often in the territory of George in proportion to its frequency on the study site (Fisher exact test and a posteriori sequential Bonferroni, p < 0.05). The frequency of other trees did not differ significantly between individual territories and the study area (Table 11).

Table 11: Comparison of the number of transect points found with or without a tree species between the study area and the territory of the male named in the Table. A G - test (df = 1) or Fischer exact test was used depending on the number of expected values.

	no. of transect points						
	on the study area		in the territory				
Common name	with tree sp.	without	with tree sp.	without	name of male	G	p
Combretum apiculatum	95	44	22	5	George	5.5	0.25
Acacia erubescens	78	61	29	5	Kent	10.8	**0.002**°
A. tortilis	66	73	21	12	Amsterdam	2.8	0.10
Pterocarpus rotundifolius	60	79	20	13	Amsterdam	3.2	0.07
A. nigrescens	53	86	6	28	Kent	5.5	0.057°
A. nigrescens	53	86	21	20	Rambo	2.2	0.14
Peltophorum africanum	24	115	2	31	Amsterdam	/	0.17∗
Sclerocarya birrea	17	122	9	18	George	/	**0.03**∗°
Terminalia sericea	15	124	0	27	George	/	0.13∗
A. mellifera	8	131	5	36	Rambo	/	0.18∗
C. imberbe	8	131	4	29	Amsterdam	/	0.25∗

°Sequential Bonferroni correction due to multiple comparisons of the values for comparison between males
∗Fischer exact test

Food quality of the study site assessed by plant characteristics:

A total of 31 grass species was recognised during vegetation analysis at the end of the wet season (Table 12). Most of the species (71 %) were perennial grasses, producing more leaf material compared to annual grasses. The most frequent species recognised at the end of the wet season was *Eragrostis rigidor* (on 91 % of all transect points). This species has a low grazing and a low palatability value (van Oudtshoorn 1992). At the beginning of the wet season nine grass species and nine grass categories, including several species, were identified (Table 13). The species *Eragrostis rigidor* and the category „thin grass" occurred most frequently. The category „thin grass" was of poor quality, as it constituted mainly of grasses with a low grazing and a low palatability value (e.g. *Aristida congesta*). Thus, the vegetation occurring at the study site was dominated by grass species of poor quality.

A similar trend was shown in the proportional grass volume at the study site. At the end of the wet season, species with a low or very low grazing value added up to 62 % of the total volume, while only 29 % of the volume consisted of grasses with a high to very high grazing value. The volume of palatable to very palatable grasses was slightly higher, adding up to 57 % of the total volume, while 43 % of the volume consisted of unpalatable to very unpalatable species. At the beginning of the wet season, the main grass volume (61 %) of all identified grasses consisted of *Eragrostis rigidor*, *Panicum maximum* and the category "thin grass". Only *Panicum maximum* had a very high grazing value and is very palatable (van Oudtshoorn 1992). It occurred less frequently on the study area, but contributed 15 % to the total volume due to its high average height.

Food quality of the territories assessed by plant characteristics:

The territories of the four males analysed differed in the frequency of grass species and grass volumes. At the end of the dry season, *Schmidtia pappophoroides* and *Eragrostis rigidor* were the most frequent grasses found in the territories of Amsterdam and Rambo (Table 14). *Schmidtia pappophoroides* has a high grazing value and a reasonably good palatability, and *Eragrostis rigidor* is of low grazing value and low palatability (van Oudtshoorn 1992). The most frequently occurring species in the territories of George (*Eragrostis rigidor*) and Kent (*Aristida spec*.) have a low (*E. rigidor*) or even a very low grazing value (*A. spec*.). Despite the differences found in the most frequent grass species, the number of grass species with equal plant characteristics showed no significant difference between the territories (number of perennial/annual species (Table 14): G - test with Williams correction: df = 3, p = 1, G = 0.1; number of palatable/unpalatable species: df = 3, p = 0.4, G = 3.0; number of species with a high/low grazing value: df = 3, p = 0.9, G = 0.5).
Eragrostis rigidor and *Schmidtia pappophoroides* also contributed the most to the total grass volume in the territories: *Eragrostis rigidor showed* highest proportional grass volume in the territories of George: 17 %, Kent 21 % and Rambo 27 %, and *Schmidtia pappophoroides* in the territory of Amsterdam 22 %, Table 14.

Table 12: Common name and scientific name of the main grass species found at transect points at the end of the wet season. For each grass species its frequency, proportion of the total volume and average height is given, as well as the grazing value, palatability and perenniality (according to van Oudtshoorn, 1992).

scientific name	common name	freq. of occurrence	prop. total volume [%]	av. height [m]	graz. value	Palatability	perenniality
Eragrostis rigidor	Broad-leaved curly leaf	91.4	20.80	0.25	l	U	p
A. adscensionis, A. congesta, A.	Aristida spec.	76.3	12.27	0.35	vl	U	a
Schmidtia pappophoroides	Sand quick	76.3	11.13	0.20	h	P	p
Melinis repens	Natal red top	57.6	8.59	0.20	l	P	a
Panicum maximum	Guinea grass	45.3	8.49	0.25	vh	VP	P
Enneapogon scoparius	Bottle brush grass	33.1	4.27	0.30	vl	P	p
Tragus berteronianus	Common carrot seed grass	74.8	4.17	0.10	l	P	a
Urochloa mosambicensis	Bushveld signal grass	49.6	3.47	0.15	h	P	p
Brachiaria deflexa	False signal grass	38.1	3.28	0.18	m	P	a
Enneapogon cenchroides	Nine-awned grass	18.7	3.16	0.60	m	P	a
Digitaria eriantha	Finger grass	30.2	2.84	0.30	h	P	p
A. stipitata	Long-awned three awn	26.6	2.64	0.45	vl	VU	p
Cymbopogon plurinodes	Narrow-leaved turpentine	5.0	2.30	0.53	l	U	p
Bothriochloa radicans	Stinking grass	6.5	2.27	0.50	l	U	p
Eragrostis pallens	Broom love grass	2.9	1.83	0.60	l	U	p
Heteropogon contortus	Spear grass	20.1	1.71	0.20	m	P	p
Panicum coloratum	White buffalo grass	18.7	1.19	0.24	vh	VP	p
Chloris virgata	Feathered chloris	22.3	1.03	0.24	l	P	a
Cenchrus ciliaris	Blue buffalo grass	1.4	0.94	0.69	h	P	p
Eragrostis lehmannia	Lehmann´s love grass	5.0	0.87	0.40	m	P	p
Pogonarthria squarrosa	Heringbone grass	10.8	0.83	0.30	vl	VU	p
Themeda triandra	Rooigras	0.7	0.65	0.80	h	P	p
Eragrostis biflora	Shade eragrostis	2.9	0.47	0.25	l	P	a
	Black-footed signal grass	8.6	0.25	0.10	vh	VP	p
Stipagrostis uniplumis	Silky bushman grass	2.2	0.17	0.15	m	v	p
Perotis patens	Cat´s tail	10.1	0.15	0.15	vl	U	a
Cynodon dactylon	Couch grass	0.7	0.07	0.25	m	P	p
Microchloa caffra	Pincushion grass	4.3	0.06	0.08	vl	P	p
Panicum natalense	Natal panicum	0.7	0.05	0.09	l	U	p
Setaria pallide-fusca	Garden bristle grass	0.7	0.03	0.07	l	P	a
Trichoneura grandiglumis	Small rolling grass	1.4	0.02	0.20	l	U	p

grazing value: vh = very high, h = high, m = medium, l = low; vl = very low palatability: VU = very unpalatable, U = unp., P = palatabl., VP = very palatable, v = variab. Perenniality: a = annual, p = perennial

Tab.13: Grass species and categories found during transect measurements at the beginning of the wet season. Common name and scientific name (van Oudtshoorn 1992) are given, as well as the frequency, the proportion of the total volume and the average height of the grasses and grass categories.

Common name	scientific name	freq. of occurrence [%]	prop. of total volume [%]	av. height [m]	grazing value	palatability	perenniality
Eragrostis rigidor	Broad-leaved curly leaf	82.3	30.20	0.27	l	U	p
Panicum maximum	Guinea grass	54.6	15.42	0.40	vh	VP	p
A. spec., A. stip., Stipagrostis uniplumis, Panicum natalense, Eragrostis biflora	"thin grass"	94.3	14.93	0.20	/	/	/
Schmidtia pappophoroides	Sand quick	75.9	8.43	0.21	h	P	p
Enneapogon scoparius, Enneapogon cenchroides	Enneapogon spec.	41.8	5.95	0.25	/	/	p
Heteropogon contortus	Spear grass	25.5	5.25	0.35	m	P	p
Melinis repens	Natal red top	38.3	5.23	0.36	l	P	a
Brachiaria deflexa, Urochloa mosambicensis, Panicum coloratum, Trichoneura grandiglumis	"broad grass"	38.3	2.85	0.20	/	/	/
Digitaria eriantha	Finger grass	37.6	2.60	0.07	h	P	p
Eragrostis lehmannia, Eragrostis plana	Eragrostis spec.	18.4	2.36	0.25	/	/	/
Pogonarthria squarrosa	Heringbone grass	19.9	2.09	0.50	vl	VU	p
Eragrostis pallens, Eragrostis gummiflua	"tough grass"	18.4	1.29	0.55	/	/	/
Bothriochloa radicans, Cenchrus ciliaris	"tuff grasses"	9.9	1.26	0.28	/	/	/
Cymbopogon plurinodes, Monocymbium ceresiiforme	"turpentine grasses"	5.7	0.94	0.20	/	/	/
Brachiaria nigropedata	Black-footed signal grass	16.3	0.38	0.06	vh	VP	p
Tragus berteronianus, Perotis patens, Setaria pallide-fusca	"short grasses"	10.6	0.28	0.06	/	/	/
	unidentified grasses	5.0	0.25	0.17	/	/	/
Chloris virgata, Cynodon dactylon	"creeping grasses"	7.1	0.17	0.12	/	/	/
Themeda triandra	Rooigras	0.7	0.11	0.80	h	P	p

grazing value: vh = very high, h = high, m = medium, l = low; vl = very low
palatability: VU = very unpalatable, U = unpalatable, P = palatable, VP = very palatable, v = variable

Tab.14: Grass species found in the territories of four adult males on transect measurements at the end of the wet season (Apr. 1999). The frequency of each grass species and their proportion on the total volume within each territory is given.

	Amsterdam		George		Kent		Rambo	
Common name	**frequency [%]**	**prop. t. volume [%]**	**frequency [%]**	**prop. t. vol. [%]**	**frequency [%]**	**prop. t. vol. [%]**	**frequency [%]**	**prop. t. vol. [%]**
Schmidtia pappophoroides	93.9	21.87	66.7	7.43	70.6	4.53	87.8	14.59
Eragrostis rigidor	93.9	19.42	88.9	16.92	88.2	21.39	92.7	26.79
A. adscensionis, A. congesta, A.	78.8	10.34	74.1	10.36	82.4	19.61	75.6	9.53
Panicum maximum	39.4	8.65	55.6	14.95	55.9	7.93	34.1	5.41
Enneapogon scoparius	39.4	7.76	40.7	2.09	32.4	2.41	31.7	3.15
Melinis repens	57.6	7.20	63.0	7.23	50.0	6.66	63.4	9.38
Tragus berteronianus	78.8	5.06	44.4	1.13	88.2	5.89	85.4	4.93
Cenchrus ciliaris	6.1	4.38	/	/	/	/	2.4	0.71
Urochloa mosambicensis	60.6	2.81	48.1	4.56	38.2	1.32	56.1	2.55
Bothriochloa radicans	6.1	2.75	11.1	5.89	8.8	1.90	2.4	0.11
Brachiaria deflexa	24.2	2.74	37.0	2.83	67.6	6.63	24.4	2.03
Cymbopogon plurinodes	6.1	1.66	3.7	2.53	/	/	9.8	6.16
A. stipitata	12.1	1.56	29.6	1.30	29.4	3.70	29.3	3.34
Panicum coloratum	21.2	1.18	22.2	1.03	5.9	0.31	19.5	1.83
Chloris virgata	15.2	0.87	7.4	0.07	52.9	2.53	12.2	0.33
Heteropogon contortus	15.2	0.92	18.5	1.62	11.8	1.02	31.7	3.67
Enneapogon cenchroides	3.0	0.47	14.8	0.50	35.3	8.60	22.0	2.86
Digitaria eriantha	12.1	0.28	63.0	8.88	20.6	0.22	39.0	1.85
Brachiaria nigropedata	9.1	0.10	14.8	0.76	8.8	0.25	4.9	0.07
Pogonarthria squarrosa	6.1	0.08	7.4	1.77	17.6	0.68	7.3	0.14
Perotis patens	3.0	0.11	22.2	0.24	5.9	0.10	4.9	0.07
Microchloa caffra	/	/	14.8	0.26	2.9	0.03	2.4	0.03
Eragrostis pallens	/	/	3.7	0.38	2.9	0.85	2.4	0.24
Cynodon dactylon	/	/	/	/	2.9	0.30	2.4	0.25
Panicum natalense	/	/	3.7	0.01	2.9	0.19	/	/
Stipagrostis uniplumis	/	/	/	/	5.9	0.46	/	/
Themeda triandra	/	/	3.7	3.50	/	/	/	/
Eragrostis biflora	/	/	3.7	0.01	8.8	1.85	/	/
Eragrostis lehmannia	/	/	14.8	3.71	5.9	0.60	/	/
Trichoneura grandiglumis	/	/	/	/	2.9	0.07	/	/
Setaria pallide-fusca	/	/	/	/	/	/	/	/

Tab.15: Grass species and grass categories found in the territories of four adult males during transect measurements at the beginning of the wet season. The common name of the species or the category is given as well as the frequency in each territory and the proportion of each grass volume on the total volume in each territory.

Scientific name	Amsterdam		George		Kent		Rambo	
	frequency [%]	prop. tot. volume [%]	frequency [%]	prop. tot. volume [%]	frequency [%]	prop. tot. volume [%]	frequency [%]	prop. tot. volume [%]
Eragrostis rigidor	94.1	25.82	92.9	28.54	100.0	40.12	97.6	28.84
Panicum maximum	41.2	20.76	60.7	14.44	61.8	13.70	48.8	10.00
A. spec., A. stip., Stipagrostis uniplumis, Panicum natalense, Eragrostis biflora	91.2	15.80	85.7	11.73	97.1	18.55	97.6	14.39
Schmidtia pappophoroides	85.3	13.97	67.9	6.86	73.5	6.15	87.8	10.48
Enneapogon scoparius, Enneapogon cenchroides	47.1	0.67	42.9	1.66	32.4	4.47	43.9	6.24
Heteropogon contortus	29.4	1.93	21.4	4.54	5.9	0.82	36.6	12.06
Melinis repens	32.4	4.05	50.0	8.08	29.4	6.44	34.1	4.29
Brachiaria deflexa, Urochloa mosambicensis, Panicum coloratum, Trichoneura grandiglumis	44.1	4.14	42.9	2.77	2.9	0.06	63.4	5.08
Digitaria eriantha	20.6	0.82	64.3	6.19	14.7	0.10	56.1	1.96
Eragrostis lehmannia, Eragrostis plana	23.5	3.76	17.9	1.11	17.6	2.69	9.8	0.95
Pogonarthria squarrosa	11.8	1.25	17.9	0.94	20.6	2.55	14.6	1.85
Eragrostis pallens, Eragrostis gummiflua	5.9	0.23	28.6	2.16	11.8	0.96	9.8	0.07
Bothriochloa radicans, Cenchrus ciliaris	8.8	6.60	10.7	7.80	14.7	1.44	7.3	0.42
Cymbopogon plurinodes, Monocymbium ceresiiforme	/	/	7.1	0.66	/	/	14.6	2.96
Brachiaria nigropedata	17.6	0.07	35.7	1.05	17.6	0.62	7.3	0.04
Tragus berteronianus, Perotis patens, Setaria pallide-fusca	2.9	0.13	17.9	0.66	5.9	0.05	7.3	0.05
unidentified grass	/	/	7.1	0.22	8.8	0.67	2.4	0.02
Chloris virgata, Cynodon dactylon	2.9	0.02	7.1	0.01	17.6	0.62	2.4	0.32
Themeda triandra	/	/	3.6	0.61	/	/	/	/

The territory of Kent showed the highest proportion of grass volumes of annual species (52 %) compared to all other males (Rambo = 29 %, Amsterdam = 27 %, George = 22 %), the lowest proportion of grass volumes with a high grazing values and very high grazing value (15 %, Amsterdam = 39 %, George = 41, Rambo = 27 %) and the lowest proportion of grass volumes of palatable species (Kent = 51 %, Amsterdam = 64 %, George = 61, Rambo = 54 %). All three plant characteristics are an indicator of a poor quality of food. Rambo still showed low proportion of grass volumes with a high grazing values and very high grazing value (27 %) compared to the others males (Amsterdam = 39 %, George = 41 %), suggesting a lower food quality.

At the beginning of the wet season, the most frequent grass in the territories of George, Kent and Rambo was the category "thin grass" which consisted mainly of unpalatable grasses with a low grazing value, while the most frequent occurring grass in the territory of Amsterdam was *Eragrostis rigidor* (Table 15). *Eragrostis rigidor* contributed most to the total grass volume in all four territories, but in a higher proportion in the territory of Kent (40 %), compared to the territories of the other males: Amsterdam (26 %), George (29 %), and Rambo (29%). A further description of the plant characteristics at the beginning of the wet season was not possible as grass categories combined grass species of varied values.

Comparison of food quality between the study area and male territories:

The territory of Kent showed a much higher proportion of grass volumes of annual species (52 %) compared to the study site (33 %). The proportion of grass volumes of palatable species was only slightly lower in his territory (51 %) compared to the study site (57 %) and slightly higher in the territory of Amsterdam (64 %) compared to the study site. The proportion of grass volumes having a high grazing value was half as much in the territory of Kent as at the study site and similar to the study site in the territory of Rambo.

Food quality assessed by foraging analysis:

A total of 130 feeding patches (39 of females and 91 of males) and 206 non – feeding patches (55 of females and 151 of males) were recorded. For each of the five adult males, total number of patches was distributed as follows: Amsterdam = 49, George = 36, Kent = 64, Rambo = 32, Schrägman = 61. Feeding preferences of individuals could not be established because of the low sample size. Data for different individuals were pooled because of the nearly similar amount of data obtained from different animals. Also feeding preferences of individuals of the same sex were expected to be similar, because of their similarity in body size.

The food of white rhinos consisted of 13 different grass species (Table 16). The composition of the forage varied slightly between the sexes. The main food resource of males consisted of five different species: *Eragrostis rigidor, Panicum maximum, Enneapogon scoparius, Digitaria eriantha* and *Heteropogon contortus*. These species were eaten very frequently and provided a high volume when eaten. The forage of

females consisted of two species: *Eragrostis rigidor, Panicum maximum*. The low frequency found for the other species might be due to the low number of feeding patches which were analysed for females (n = 39) compared to males (n = 91).

Table 16: The grass species ingested by male and female white rhinos. Frequency and estimated median volumes (calculated as the difference between grass height before and after it was eaten) are given for ingested grass species. N is the number of grass volumes analysed.

grass species	frequency foraged [%]		estimate of average volume foraged [%]			
			male		female	
	male	female	median	N	median	N
Eragrostis rigidor	31	46	20.2	26	16.8	18
Panicum maximum	27	44	20.5	22	17.6	17
Enneapogon scoparius	17	8	12.3	13	5.0	3
Schmidtia pappophoroides	12	15	2.7	10	10.1	6
A. adscensionis, A. congesta, A. canescens	8	3	8.0	7	17.0	1
Urochloa mosambicensis	8	5	4.4	6	5.0	1
A. stipitata	1	0	15.0	1	/	/
Melinis repens	7	/	4.1	6	/	/
Digitaria eriantha	6	/	23.4	5	/	/
Heteropogon contortus	6	/	27.7	5	/	/
Tragus berteronianus	1	0	2.9	1	/	/
Chloris virgata	0	3	/	/	8.0	1
Pogonarthria squarrosa	0	3	/	/	13.5	1

The most frequently occurring grass on the study area *Eragrostis rigidor* (91.4 % at the end of the wet season, 82.3 % at the beginning of the wet season Table 12 and 13) was also the grass most often foraged by males (31 %) and females (46 %). The average volume of the grass grazed (males: 20.2 cm^3, females: 16.8 cm^3, Table 16) was among the highest of all estimated volumes foraged by both sexes. The grass was not, however specifically selected for foraging (Table 17). The number of times the species was found on a feeding and non-feeding patch did not differ from the total number of analysed feeding and non–feeding patches. Additionally, the number of times the species was grazed (males: 26, females: 18) did not deviate from the average preference with which a grass species was grazed on a feeding patch (males: 0.46 times, females: 0.54 times). The decision to forage on the plant is most likely dependent on the volume of the species. Both sexes fed significantly more often on *Eragrostis rigidor* when it occurred in a high volume on the feeding patch (Mann-Whitney test: $p = 0.003$, Table 17).

Panicum maximum was grazed with a frequency similar to *Eragrostis rigidor* by both sexes (males: 27 %, females: 44 %) even though it occurred less often at the study site (45.3 % at the end of the wet season, 54.6 % at the beginning of the wet season Table 12 and 13). The estimated median volumes eaten by males (20.5 cm^3) and females (17.6 cm^3) were also similar to the volumes of *Eragrostis rigidor*. The difference in the frequency of occurrence of the plant and in the frequency foraged by rhinos indicates that both sexes selected places with *Panicum maximum,* which was confirmed by further analyses (Table 17). Males and females grazed significantly more often on patches where *Panicum maximum* occurred and less often on patches where it did not occur (G – test with Williams correction: males: $df = 1$, $p < 0.001$, $G = 24.6$, females: $df = 1$, $p = 0.002$, $G = 15.5$, Table 17).

Tab. 17: Analysis of food preferences for males and females. **A**) Comparison of the number of times a grass species was found on a feeding patch and non–feeding patch with the total amount of feeding (males = 91, females = 39) and non–feeding patches (males = 155, females = 55) **B**) Comparison of the number of times a species was foraged and not foraged with the average number of species and the average number of times species were foraged at a feeding patch. In A) and B) a G- test (DF = 1) or a Fisher exact test (⁕) was used. C) Comparison of the volumes of a grass species when the animal was grazing on it (Mann-Whitney test, n = number of analysed volumes).

grass species		A				B				C				
		number of times on		p- value	G	number of times		p-value	G	median volume [cm^3]		p	n	
		feed. pat.	non-feed.p.			eaten	not eaten			feeding	not feed.	value	feeding	not feed.
Eragrostis rigidor	male	45	101	0.21	1.5	26	15	0.12	2.4	28.0	6.1	**0.003**	25	16
	female	24	34	0.98	0.0	18	6	0.14	2.2	22.4	10.5	**0.04**	17	7
A. adscensionis, A. congesta,	male	31	81	0.09	2.9	7	21	0.09	2.8	6.0	2.6	**0.03**	7	21
A. canescens	female	9	30	**0.04**	4.2	1	8	0.14	⁕	21.0	4.1	/	1	8
Schmidtia pappophoroides	male	26	22	**0.03**	4.8	10	16	0.58	0.3	4.3	2.5	0.07	10	16
	female	14	15	0.52	0.4	6	8	0.46	0.5	10.5	5.0	**0.04**	5	9
Melinis repens	male	13	14	0.26	1.2	6	6	1	0.0	3.1	4.0	0.98	5	6
	female	0	5	0.08	⁕	0	0	/	/	/	/	/	0	0
Panicum maximum	male	29	7	**<0.0001**	24.6	22	3	**0.001**	10.3	23.6	7.0	0.14	22	3
	female	19	6	**0.002**	15.5	17	1	**0.02**	9.3	24.5	5.0	/	17	1
Enneapogon scoparius	male	17	6	**0.0007**	11.5	14	3	**0.03**	4.6	17.1	2.3	**0.01**	13	3
	female	5	1	0.05	⁕	3	2	1	⁕	7.7	5.0	0.40	3	2
Tragus berteronianus	male	10	6	**0.049**	3.9	1	9	0.14	⁕	3.9	0.6	/	1	9
	female	1	0	0.42	⁕	0	1	1	⁕	/	0.6	/	0	1
Urochloa mosambicensis	male	15	16	0.23	1.5	7	4	0.41	0.7	7.5	1.0	0.20	5	5
	female	3	3	0.69	⁕	2	1	1	⁕	5.4	1.1	/	1	1
Digitaria eriantha	male	16	10	**0.02**	5.7	5	11	0.29	1.1	34.0	1.1	**0.001**	5	11
	female	0	0	/	/	0	0	/	/	/	/	/	0	0
A. stipitata	male	4	22	**0.02**	5.3	7	21	0.10	2.8	20.0	5.0	/	1	3
	female	6	7	0.75	0.1	0	6	0.18	⁕	/	4.6	/	0	6
Heteropogon contortus	male	6	4	0.09	⁕	5	1	0.55	⁕	32.0	1.5	/	1	5
	female	0	2	0.51	⁕	0	0	/	/	/	/	/	0	0
Chloris virgata	male	2	5	0.29	⁕	0	2	1	⁕	/	0.9	/	0	2
	female	2	0	0.18	⁕	1	1	1	⁕	13.0	1.0	/	1	1
Pogonarthria squarrosa	male	2	19	**0.006**	7.6	0	2	1	⁕	/	7.6	/	0	3
	female	3	7	0.74	0.7	1	2	1	⁕	/	/	/	1	2
Perotis patens	male	1	6	0.17	⁕	0	1	1	⁕	/	/	/	0	0
	female	0	0	/	/	0	0	/	/	/	/	/	0	0

When foraging on a patch, *Panicum maximum* was grazed more frequently than expected by both males and females (G – test with Williams correction: males: df = 1, p = 0.001, G = 10.3, females: df = 1, p = 0.02, G = 9.3, Table 17). The strong preference for the species might be due to its high palatability and its high grazing value.

Males showed a highly significant selection of patches on which *Enneapogon scoparius* occurred (G – test with Williams´s correction, df = 1, p < 0.001, G = 11.5) and a significant selection of this grass species within a feeding patch (G-test, df = 1, p = 0.05, G =4.6, Table 17). In contrast, females foraged more frequently on *Schmidtia pappophoroides* (15 %) compared to *Enneapogon scoparius* (8 %) but they still showed a slightly but not significant preference to forage at patches where *Enneapogon scoparius* occurred (Fisher exact test: p = 0.05, Table 17). *Enneapogon scoparius*, is a palatable species of low grazing value (van Oudtshoorn 1992) which occurred less frequently in the study area (33 % at the end of the wet season, 41.8 % at the beginning of the wet season, Table 12 and 13) compared to *Schmidtia pappophoroides* (76 % at the end of the wet season, 75.9 % at the beginning of the wet season, Table 12 and 13). *Schmidtia pappophoroides* was not specifically selected for foraging by females (patch selection: G – test: df = 1, p = 0.52, G = 0.4; grass selection: df = 1, p = 0.46, G = 0.5). The decision to feed on the plant was likely dependent on the volume of the species, as females were found to forage significantly more often on the plant when it occurred in high volume on the feeding patch. In contrast to females, males showed a significant selection of places on which *Schmidtia pappophoroides* occurred for foraging (G – test: df = 1, p = 0.03, G = 4.8), but no significant difference was found in the observed number of times the species was grazed (n = 10) compared to expected numbers (n = 16, G – test: df = 1, p = 0.58, G = 0.3).

Patches where the grass species *Tragus berteronianus* and *Digitaria eriantha* occurred were significantly selected as feeding places by males (*T. berteronianus*: G – test: df = 1, p = 0.049, G = 3.9; *D. eriantha*: df = 1, p = 0.02, G = 5.7). *Tragus berteronianus* was the least frequently fed grass (1 %) and only a low average volume (2.9 cm^3) of the plant was foraged; in contrast, *Digitaria eriantha* was more often grazed (6 %) and the average volume fed by the plant was among the highest of all volumes established (23.4 cm^3). The highest average volume fed was that of the species *Heteropogon contortus* (27.7 cm^3). The species was grazed at a low frequency (6 %) and males did not show any preference for the species.

A negative selection was shown by females for the species *Aristida adscenionis, A. congesta* and *A. canescens*. Females foraged significantly less often on patches where the species occurred (G – test: df = 1, p = 0.04, G = 4.2). Males showed merely a tendency to avoid feeding in places where these species occurred (feeding: n = 31, non-feeding: n = 81, df = 1, p = 0.09, G = 2.9, Table 17). Another species of the same family, *A. stipitata* and the species *Pogonarthria squarrosa* were significantly avoided by males. They foraged less often in places where these species occurred (*A. stipitata*: G – test: df = 1, p = 0.02, G = 5.3; *P. squarrosa*: df = 1, p = 0.006, G = 7.6).

In conclusion, it can be said that males showed a preference for five different grass species: *Schmidtia pappophoroides*, *Panicum maximum, Tragus berteronianus, Digitaria eriantha* and *Enneapogon scoparius;*

these occurred significantly more often on feeding patches compared to non-feeding patches. Two of these species, *Panicum maximum* and *Enneapogon scoparius,* were particularly selected for foraging from all grasses available at the feeding patch. Females selected only one species for foraging, *Panicum maximum*, but this species was selected in two hierarchical orders (selection of the patch and selection of species within a patch). All of the selected grass species are categorised as of high palatability, but with different grazing values, while the species which were particularly avoided, *A. stipitata* (by males and females) and *Pogonarthria squarrosa (*by males only), were categorised as unpalatable.

Comparison of the frequencies of the most frequently ingested or selected grass species between male territories:

Foraging analyses showed a high similarity in feeding preferences and forage selection between males and females. The frequency of the grass species most frequently ingested or selected by males (*Eragrostis rigidor, Panicum maximum, Schmidtia pappophoroides, Enneapogon scoparius, Tragus berteronianus, Digitaria eriantha and Heteropogon contortus)* of males were therefore compared between territories. No difference was found in the concentrations of the main food resource, *Eragrostis rigidor,* between male territories, either at the beginning or at the end of the wet season (frequencies are given in Table 18 and 19, application of the G – test was not possible as more than 20 % of expected frequencies were below 5 %). Also no difference was found in the frequency of the grass species *Panicum maximum* during either season (end of the wet season: df = 3, p = 0.16, G = 5.1; beginning of the wet season: df = 3, p = 0.28, G = 3.9), this being identified as a highly selected feeding plant by males and females (Table 17). Significant differences between territories occurred in the grass species *Digitaria eriantha*, *Schmidtia pappophoroides* and *Tragus berteronianus* at the end of the wet season (G - and p – values, Table 18) and in the grass species *Heteropogon contortus* and *Digitaria eriantha* at the beginning of the wet season (G - and p – values, Table 19). The frequencies of these species were compared separately between male territories to establish individual differences.

Table 18: Comparison of the number of transect points found with or without a grass species between the territories of the males at the end of the wet season (G – test, df = 3). The most frequently ingested or selected grass species (either selectively eaten or selected as feeding patch) were used in this analysis.

scientific name/ territorial males	Amsterdam [%]	George [%]	Kent [%]	Rambo [%]	p – values	G
Eragrostis rigidor	94	89	88	93	♦	♦
Panicum maximum	39	56	56	34	0.16	5.1
Schmidtia pappophoroides	94	67	71	89	**0.01**	10.9
Enneapogon scoparius	39	41	32	32	0.82	0.9
Tragus berteronianus	79	44	88	85	**0.0006**	17.4
Digitaria eriantha	12	63	21	39	**0.0001**	20.6
Heteropogon contortus	15	19	12	32	0.16	5.1

♦ Application of the G – test was not possible as more than 20 % of expected frequencies were below 5 %

The frequency of *Schmidtia pappophoroides* was slightly higher in the territory of Amsterdam compared to the territory of George at the end of the wet season (Fisher exact test and a posteriori sequential Bonferroni: Amsterdam/George: df = 1, p = 0.05), while no difference was found between the frequencies in the other territories (G - test or Fisher exact test and a posteriori sequential Bonferroni: Amsterdam/Rambo: df = 1, p = 0.4, G = 2.7; Amsterdam/Kent: p = 1.0; George/Rambo: df = 1, p = 0.7, G = 1.5; George/Kent: df = 1, p = 0.8, G = 0.1; Kent/Rambo: df = 1, p = 0.3, G = 3.3). *Schmidtia pappophoroides* is a palatable grass with a limited leaf production (van Oudtshoorn 1992), which was frequently foraged by males and females (Table 16).

Digitaria eriantha also occurred more frequently in the territory of George compared to Amsterdam and Kent (G – test with Williams correction and a posteriori sequential Bonferroni: Amsterdam/George: df = 1, p = 0.0003, G = 17.2; George/Kent: df = 1, p = 0.01, G = 11.3) and significantly more often in the territory of Rambo compared to Amsterdam (df = 1, p = 0.04, G = 7.0). *Digitaria eriantha* occurred also more frequent in the territory of George and Rambo compared to the territory of Amsterdam and Kent at the beginning of the wet season (G – test with Williams correction and a posteriori sequential Bonferroni: df = 1, George/Kent: p = 0.0005, G = 16.4; George/Amsterdam: p = 0.004, G = 12.2; Rambo/Kent: p = 0.002, G = 14.2; Rambo/Amsterdam: p = 0.01, G = 9.9). *Digitaria eriantha* is a highly digestible and palatable pasture grass with a high leaf production (van Oudtshoorn 1992), which was frequently foraged by males (Table 16), but the species was never eaten by females (Table 16).

The territory of George showed a significantly lower frequency of *Tragus berteronianus* compared to the territory of Amsterdam, Kent and Rambo (G – test with Williams correction and a posteriori sequential Bonferroni: df = 1, George/Amsterdam: p = 0.03, G = 7.5; George/Kent: p = 0.002, G = 13.5; George/Rambo: p = 0.002, G = 12.5), while no difference was found between the other territories. *Tragus berteronianus* is a pioneer grass species growing in overgrazed areas. It has hardly any grazing value because of its low leaf production but it plays an important role in control of soil erosion (van Oudtshoorn 1992).

Table 19: Comparison of the number of transect points found with or without a grass species or grass category between male territories at the beginning of the wet season (G – test, df = 3). The most frequently foraged or selected grass species (either selectively eaten or selected as feeding patch when species occurred) were chosen for this analysis.

scientific name/territorial males	Amsterdam [%]	George [%]	Kent [%]	Rambo [%]	p - values	G
Eragrostis rigidor	94	93	100	98	♦	♦
Panicum maximum	41	61	62	49	0.28	3.9
Schmidtia pappophoroides	85	68	74	88	0.15	5.3
Enneapogon scoparius, E. cenchroides	47	43	32	44	0.63	1.7
Heteropogon contortus	29	21	6	37	**0.009**	11.6
Digitaria eriantha	21	64	15	56	**< 0.0001**	26.6
Tragus berteronianus, Perotis patens, Setaria pallide-fusca	3	18	6	7	♦	♦

♦Application of the G – test was not possible

The frequency of *Heteropogon contortus* was significantly lower in the territory of Kent compared to the territories of Rambo and Amsterdam (Kent/Rambo: $p = 0.007$, $G = 11.2$; Kent/Amsterdam: $p = 0.049$, $G = 6.7$). *Heteropogon contortus* is a relatively good, hardy and fast growing pasture grass with a declining grazing value as the season progresses (van Oudtshoorn 1992).

Comparison of the frequencies of frequently ingested or selected grass species between male territories and the study site:

Only the territories and grass species that differed most significantly were used in this analysis.
Amsterdam had a similar frequency of *Schmidtia pappophoroides* and of *Digitaria eriantha* in his territory compared to the overall frequency of these species at the study site at the end of the wet season (G - test with Williams correction and a posteriori sequential Bonferroni: *Schmidtia pappophoroides:* $df = 1$, $p = 0.08$, $G = 6.2$; *Digitaria eriantha:* $df = 1$, $p = 0.04$, $G = 7.0$). While the frequency of *Digitaria eriantha* did not differ between the study site and his territory at the beginning of the dry season ($df = 1$, $p = 0.16$, $G = 0.2$).

Digitaria eriantha occurred significantly more often in the territory of George compared to the study site at the end of the wet season (G – test with Williams correction and a posteriori sequential Bonferroni: $df = 1$, $p = 0.01$, $G = 9.9$) and nearly significantly more frequent at the beginning of the wet season (G – test with Williams correction and a posteriori sequential Bonferroni: $df = 1$, $p = 0.05$, $G = 6.6$). The territory of George also showed a significantly lower frequency of *Tragus berteronianus* compared to the study site at the end of the wet season (G – test with Williams correction and a posteriori sequential Bonferroni: $df = 1$, $p = 0.01$, $G = 9.0$). Kent had a significantly lower frequency of *Heteropogon contortus* in his territory compared to the overall occurrence of the species at the study site ($df = 1$, $p = 0.04$, $G = 7.5$). He had also a significantly lower frequency of *Digitaria eriantha* in his territory compared to the study site ($df = 1$, $p = 0.046$, $G = 7.1$). Rambo had a similar frequency of *Digitaria eriantha* in his territory *compared* to the study site ($df = 1$, $p = 0.14$, $G = 0.0$).

The vegetation structure at feeding and non-feeding patches:

The number of times with which a category was found in feeding and non-feeding patches of males did not differ from the number of analysed feeding and non-feeding patches ($df = 3$, $G = 6.9$, $p = 0.07$).

Table 20: Frequency of four different categories of openness [%] at feeding (n = 42) and non-feeding patches (n = 72) of males at the end of the wet season.

	open	m. open	m. open - thick	thick
feeding	29	19	26	26
non-feeding	14	30	41	15

Nutrient and mineral content in forage samples of territorial males:

The nutrient content of the forage eaten by male rhinos was analysed from grass samples collected along the feeding trails of three males in March 1999. The amount of grass collected for each male was as follows: Amsterdam: 2900 g and 1930 g, Schrägman: 2870 g and 4205 g, George: 1940 g and 2120 g.

Table 21: Concentrations of nutrients, macro-minerals and trace minerals (mean) in the forage of three territorial males measured along feeding trails (n = 2). The average concentration and the coefficient of variation (CV) are given.

	Amsterdam		George		Schrägman			
nutrient concentration [% DM]	mean	SD	mean	SD	mean	SD	mean	CV [%]
NDF	75.0	*0.5*	74.5	*1.7*	74.3	*1.2*	74.6	*0.5*
lignin	6.5	*0.2*	7.1	*0.6*	6.8	*0.9*	6.8	*4.6*
hemicellulose	31.7	*1.3*	32.5	*0.7*	31.8	*0.1*	32.0	*1.3*
cellulose	36.8	*1.6*	34.9	*0.4*	35.7	*0.3*	35.8	*2.7*
protein	5.3	*1.7*	3.8	*0.4*	4.9	*1.0*	4.7	*16.7*
macro-mineral concentration [g/kg DM]								
calcium	2.5	*0.2*	2.7	*1.4*	2.1	*0.2*	2.4	*14.0*
phosphorus	1.0	*0.1*	1.0	*0.0*	1.1	*0.1*	1.0	*2.4*
Ca : P	2.5	*0.4*	2.7	*1.3*	2	*0*	2.4	*15.0*
potassium	8.9	*2.7*	8.1	*1.0*	8.5	*2.0*	8.5	*4.9*
chlorine	2.7	*1.7*	4.1	*1.1*	3.6	*0.9*	3.5	*20.6*
sodium	0.3	*0.1*	0.3	*0.1*	0.3	*0.0*	0.3	*6.7*
trace mineral [mg/kg DM]								
zinc	21.1	*5.0*	16.1	*0.2*	31.4	*5.6*	22.8	*34.1*
copper	4.6	*1.5*	3.9	*0.3*	3.8	*0.4*	4.1	*10.9*
iron	184	*41*	132	*58*	214	*8*	177	*23.6*
manganese	814	*385*	848	*141*	818	*357*	827	*2.2*

The mean concentration of NDF (74.6 % DM), lignin (6.8 % DM), hemicellulose (32 % DM) and cellulose (35 % DM) in the forage of Amsterdam, George and Schrägman differed only slightly between males (coefficients of variation, Table 21). The mean concentration of protein (4.7 % DM) varied more noticeably (CV = 16.7 %). The forage eaten by Amsterdam showed the highest concentration of protein (5.3 ± 1.7) and the forage of George the lowest (3.8 ± 0.4). Concentrations of protein showed still high variation between individual forage samples (Table 21).

The mean concentrations of calcium (2.4 g/kg DM) and chlorine (3.5 g/kg DM) and the calcium to phosphorus ratio (2.4) varied noticeably between males. The calcium concentration and the calcium to phosphorus ratio was highest in the forage of George (calcium: 2.7 ± 1.4 g/kg DM; Ca : P: 2.7 ± 1.3 g/kg DM) and lowest in the forage of Schrägman (calcium: 2.1 ± 0.2 g/kg DM; Ca : P: 2.0 ± 0 g/kg DM). The

concentration of chlorine was highest in the forage of George (4.1 ± 1.1 g/kg DM) and lowest in the forage of Amsterdam (2.7 ± 1.7 g/kg DM). Again high variations in concentrations occurred between individual forage samples (Table 21).

Among trace minerals, the concentration of zinc (22.8 mg/kg DM) and iron (177 mg/kg DM) showed variations between males, with Schrägman showing the highest concentration in zinc (31.4 ± 5.6 mg/kg DM) and iron (214 ± 8 mg/kg DM) and George the lowest (zinc: 16.1 ± 0.2 mg/kg DM; iron: 132 ± 58 mg/kg DM) while the concentration of manganese showed high individual variation in concentration (Table 21).

Nutrient content in the faeces of territorial males:

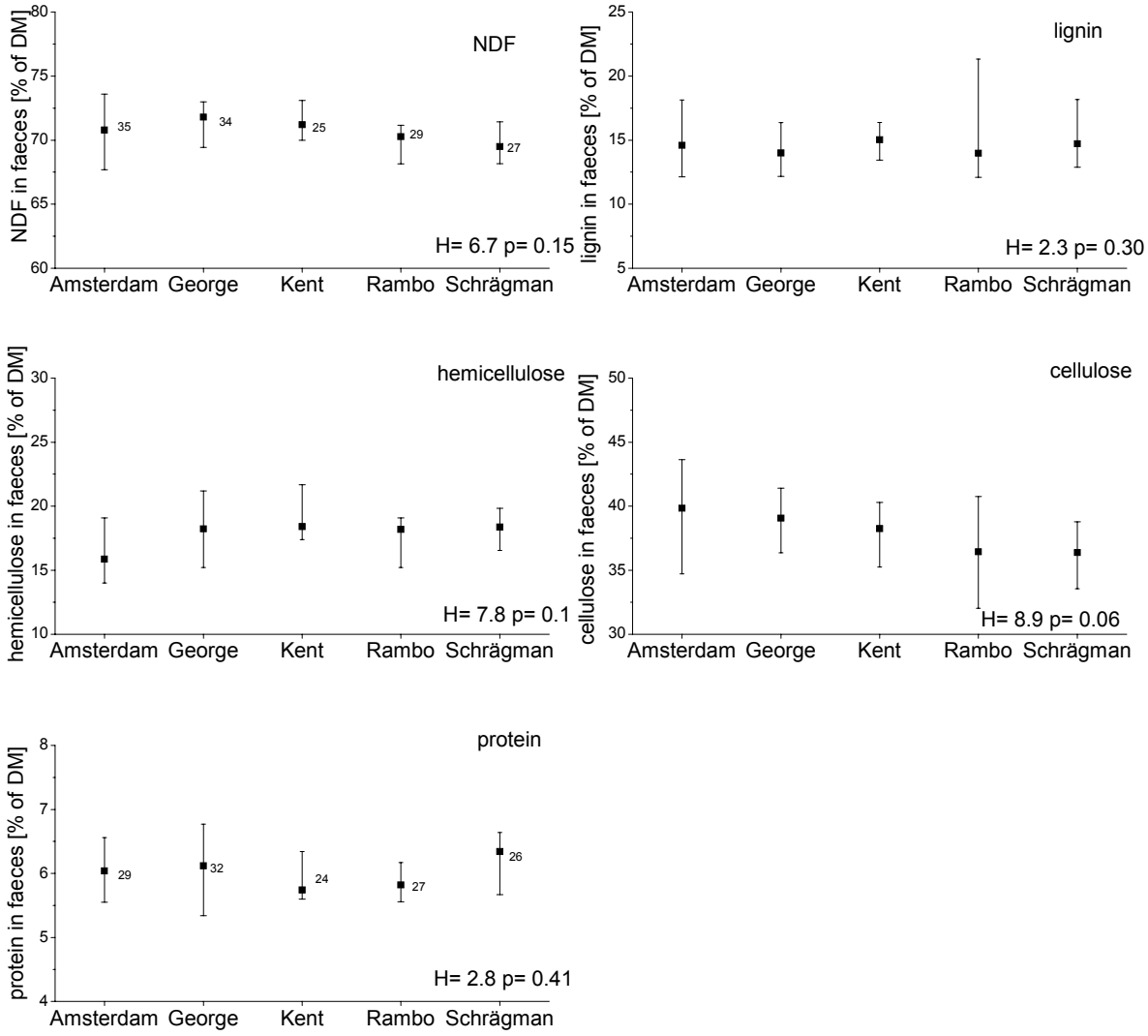


Figure 26: Comparison of NDF, lignin, hemicellulose, cellulose and protein content (Median ± IQ) in the faeces of five adult males between Nov. 1997 and March 1999. The sample sizes for each male are consistent throughout the first four graphs. The results of the Kruskal Wallis test (H and p – values) are given in each graph.

A total of 206 faecal samples was collected between November 1997 and March 1999, 54 samples of adult females and 152 samples of adult males (Amsterdam: 35, George: 34, Kent: 25, Rambo: 29, Schrägman: 27). On average two samples per month were collected per male (± 1 SD) and three samples (± 3 SD) per female.

The concentration of NDF, lignin, hemicellulose, cellulose and protein in the faeces varied only slightly between males (Kruskal Wallis test, NDF: $H = 6.7$, $p = 0.15$; lignin: $H = 2.3$, $p = 0.30$; hemicellulose: $H = 7.8$, $p = 0.10$; cellulose: $H = 8.9$, $p = 0.06$; protein: $H = 2.8$, $p = 0.41$, Fig. 26).

Cellulose concentrations of faeces collected during the dry season (April – September) varied significantly between males, while no other nutrients showed any differences in concentrations (Kruskal Wallis test, H and p- values Table 22). Multiple comparisons of single concentrations with Dunn´s test showed no significant results ($p > 0.05$).

Table 22: Nutrient concentrations (median) in the faeces of territorial males during the dry season (April – Sept.). The results of the comparison of the concentrations between males (Kruskal Wallis test, H and p-values) are given in the table.

nutrient concentration [% DM]	Amsterdam median	George median	Kent median	Rambo median	Schrägman median	p	H
NDF	69.9	72.3	70.8	69.1	68.6	0.08	8.2
lignin	14.9	11.8	14.1	13.7	14.7	0.11	7.5
hemicellulose	16.6	20.7	18.6	18.7	18.9	0.25	5.4
cellulose	37.2	38.9	37.9	35.2	34.8	0.02	10.9
protein	5.9	5.4	5.7	5.6	6.4	0.30	4.9

Comparison of the nutrient content in faeces between males and females:

Significant differences were recorded between the nutrient content of the faeces of males and females (Fig. 27). The faeces of males had significantly higher median NDF (70.7 % of DM) and hemicellulose concentrations (17.9 % of DM) compared to the faeces of females (NDF: 67.8 % of DM, Mann-Whitney test: $Z = -4.4$, $p = 0.0001$; hemic.: 16.2 % of DM, $Z = -2.4$, $p = 0.02$), whereas females had significantly higher protein content in their faeces (3.2 % of DM) compared to males (3.0 % of DM, $Z = -2.8$, $p = 0.01$). No difference was found in the lignin and the cellulose content between the faeces of males (lignin: 14.6 % of DM; cellulose: 37.9 % of DM) and females (lignin: 14.4 % of DM; $Z = -0.8$, $p = 0.4$, cellulose: 36.4 % of DM, $Z = -1.6$, $p=0.10$).

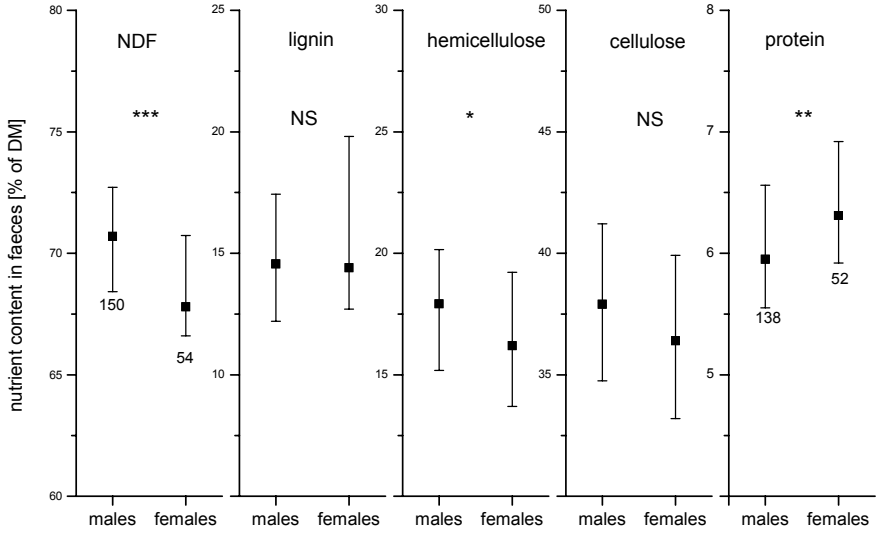


Figure 27: Comparison of the nutrient content in faeces of males and females (median and interquartiles) including samples from Nov. 1997 until March 1999. The sample size of lignin, hemicellulose and cellulose are equal to the numbers given for NDF. The result of the Mann-Whitney U-test are given in the graph: *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$.

Frequency of rhinos in male territories:

The frequency of rhinos in male territories was established out of the number of visits of rhinos at waterholes situated in the territories of the adult males.

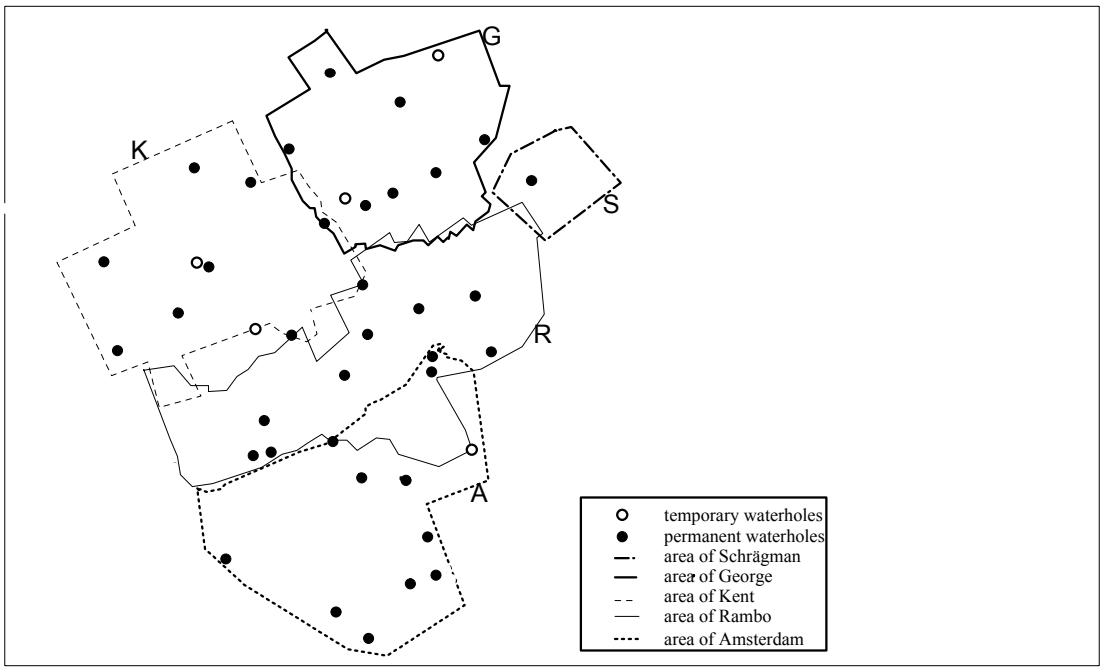


Figure 28: Distribution of permanent and temporary waterholes among the territories of five adult males. The lines indicate the border of the area occupied by each male. The letter symbolise the owner of the area.

The number of waterholes enclosed by individual territory borders differed between the animals: George = 12, including 2 temporary waterholes, Kent = 12 (2 temp.), Rambo = 15 (2 temp.), Amsterdam = 12 (1 temp.), Schrägman =1. The number of visits at the waterholes, however, was independent from the number of waterholes within each territory (Spearman rank correlation: rs = -0.15, p = 0.6, N = 13). Higher numbers of visits were found at waterholes during the dry season (mean = 38, interquartile range (IQR) = 18) compared to the wet season (mean = 29, IQR = 12).

The total number of visits at the waterholes within each territory differed significantly in the time period between February 1998 and April 1999 (Kruskal Wallis test: N = 13, H = 43.5, p < 0.001, Fig. 29). Between February 1998 and April 1999, Schrägman had a significantly lower frequency of visits per month (n = 0, IQR = 1) compared to all other males: Amsterdam (n = 7, IQR = 4), George (n = 7, IQR = 5), Kent (n = 13, IQR = 7), Rambo (n = 15, IQR = 4). Comparisons using a Mann-Whitney test and *a posteriori* sequential Bonferroni: N = 26, Schrägman/Amsterdam: p < 0.001, Z = -4.4; Schrägman/George: p < 0.001, Z = -4.3; Schrägman/Kent: p < 0.001, Z = -4.4; Schrägman/Rambo: p < 0.001, Z = 4.4. Amsterdam and George had a significantly lower frequency of visits per month compared to Kent and Rambo (Mann-Whitney test and *a posteriori* sequential Bonferroni: Amsterdam/Kent: p = 0.02, Z = -2.7; Amsterdam/Rambo: p = 0.01, Z = -3.4; George/Kent: p = 0.02, Z = -2.9; George/Rambo: p < 0.001, Z = -3.6).

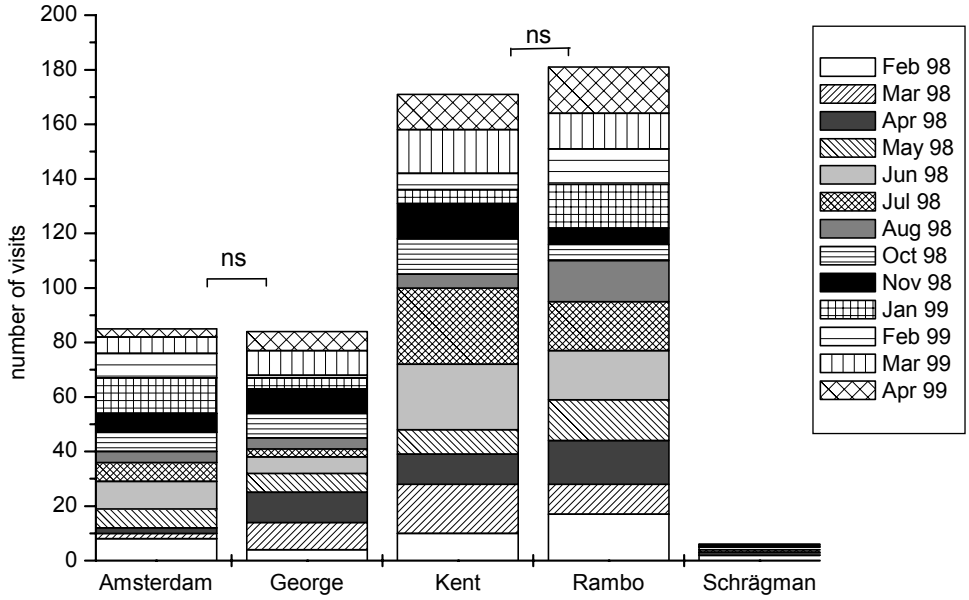


Figure 29: Number of visits in male territories, established once each month by counting the tracks of rhinos at each waterhole. The number of visits established each month is indicated by the different colour /pattern. Horizontal brackets give non-significant differences, according to Mann Whitney and *a posteriori* sequential Bonferroni.

Genetic analysis of fatherhood:

A total of 14 samples of calves were available for genetic analysis of fatherhood. Paternity could be established for 12 calves only, as two calves showed two possible sires (Amsterdam and Rambo, Table 23). For the others calves, four out of the five sires could be excluded with two bands or more (animals no. 212, 228, 241, 252, 257, and 259; Table 23) and by one band (animal no. 209, 214, 222, 236, 249, and 277).

Table 23: Number of loci, established with AFLP methods, for 14 offspring which exclude paternity of each of five possible males (Kellner 2000). The estimated time of birth is given for each animal. The bold number indicates the most probable father.

label number of calves	estimated time of birth	Amsterdam	George	Kent	Rambo	Schrägman
209	1994	**0**	2	1	2	2
212	Mar-97	**0**	5	7	2	5
214	Mar-97	1	3	5	1	**0**
218	1996	**0**	2	2	**0**	1
222	Mar-97	3	5	4	1	**0**
228	Mar-97	3	**0**	3	2	2
236	Dec-97	2	**0**	1	2	1
241	Jan-97	4	**0**	5	5	3
246	Jun-97	**0**	2	2	**0**	1
249	Dec-97	1	1	1	1	**0**
252	Mar-97	3	3	**0**	3	4
257	Jul-97	4	5	**0**	5	4
259	Mar-97	3	4	**0**	5	3
277	Sep-98	**0**	1	3	2	2

George, Kent and Schrägman had the same number of offspring (n = 3). The number of offspring for Amsterdam and Rambo could only be guessed because paternity could not be established for two calves. Amsterdam had either the highest number of offspring compared to all other males (n = 5/n = 4 in two of three possible mother-father-calf triad combinations, Amsterdam fathered both calves/one calf) or similar numbers compared to George, Kent and Schrägman (n = 3). Rambo had in all three possible mother-father-calf triads combinations the lowest number of offspring compared to all other males (Rambo fathered: two calves/one calf/no calf, n = 2/n = 1/ n = 0).

Positions of females with juveniles of known fathers

Females with juveniles of known fathers stayed most frequently in the territory of the sire of her juvenile (Fig. 30, Table 30, mean: 77 ± 17 %, n = 9, excluding the females staying in the territory of Schrägman whose territory borders could only be estimated). In the two cases were paternity could not be established clearly, the frequency of sightings of females with offspring was similar in the territories of Amsterdam and Rambo (female U: Amsterdam = 46: Rambo = 34; female R: Amsterdam = 6: Rambo = 16, Table 24). The frequency of sightings gives thus no further information about possible fatherhood.

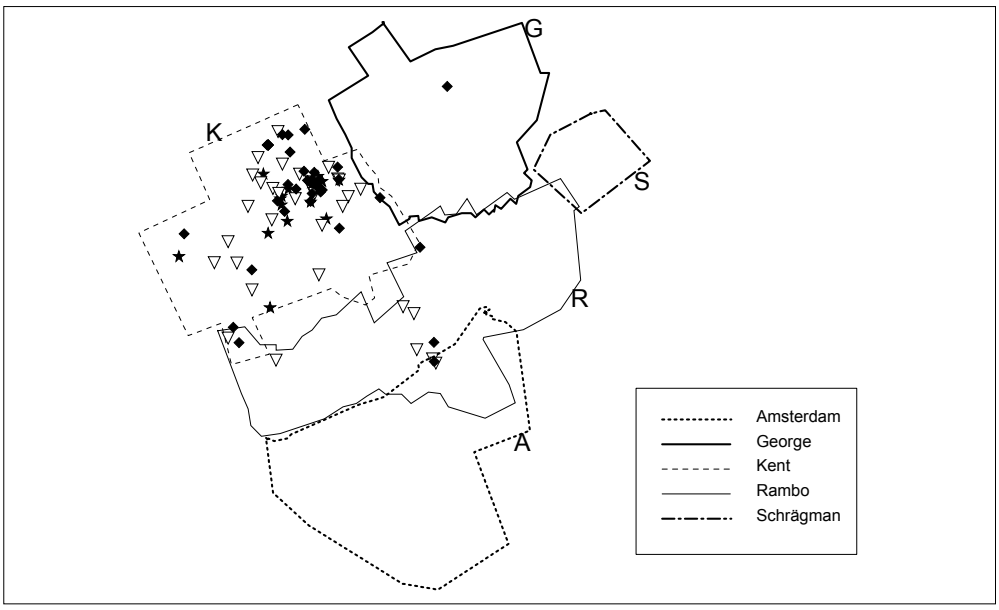


Figure 30: Sightings of females with offspring that were shown to be fathered by Kent using genetic analysis. Locations of different females are indicated by different symbols, the territory borders established using Map Info are indicated by different lines. Territories of males and locations of females include sightings between March 1997 and May 1999. The letters within the graph symbolise the name of the territory owner.

Table 24: Frequency of sightings of females in the territory of the sire of her offspring. Number of sightings of females was established by counting positions situated in the territory borders of males which were proved to be the father of her offspring. For Schrägman the territory borders were established for the period before he lost his territory.

females	total number of sightings	number of sightings in territory of male [%]
females in the territory of Amsterdam		
C	70	89
St	10	60
S	31	71
U *	50	46
R *	32	6
females in the territory of George		
G	27	85
Stu	28	46
Sa	31	71
females in the territory of Kent		
H	18	100
Sch	34	82
W	44	91
females in the territory of Rambo		
U *	34	34
R*	32	16
females in the old territory of Schrägman**		
X	48	48
K	32	41

- Offspring was either fathered by Rambo or Amsterdam,
- ** Area established out of data between April – June 1997

DISCUSSION:

The aim of this study was to assess whether female mate choice goes beyond the selection of territorial males in white rhinoceros and to determine factors influencing the mating success of territorial males. The study was conducted on a population of white rhinoceros living on a private game farm in South Africa. The study site proved very useful for this study. 1. The area was large (30.000 ha) in comparison to other field studies on grazing animals: Red deer, Isle of Rhum: 10.000 ha in size (Clutton-Brock et al. 1982), white rhino, Matobo National Park: 10.500 ha in size (Rachlow et al. 1998) which enabled the rhinos to develop a normal spacing system. The area was even large enough that the males were able to establish territories which were much larger (61 – 116 km^2) than those observed in other studies on rhinos: Matobo National Park, Zimbabwe: 15 – 50 km^2 (Rachlow et al. 1999); Krüger National Park, Republic of South Africa: 6 – 14 km^2 (Pienaar et al. 1993b), Umfolozi Game Reserve, Republic of South Africa: 1 – 3 km^2 (Owen-Smith 1973). 2. The study population was large enough for the study of the mating behaviour of white rhinos. Even though the number of animals in the population can not be given due to security risks, it can be revealed, that the population was larger than the population of black rhinos used for the study of the mating system and reproductive skew by Garnier et al. (2001). 3. The advantage of this study compared to studies on free-living white rhinos (Owen-Smith 1973) was that all individuals of the population were individually known. It is very difficult and time consuming to identify all animals in free-living populations. Garnier et al. (2001) mentioned that this might be the reason for the few studies that have been able to study female mating behaviour in free-living populations (Garnier et al. 2001).

A disadvantage of the study site was that the rhino population was managed to a certain degree. Three adult males were hunted between 1991 and 1994, and almost all of the subadult males were removed from the study site. As mentioned earlier (General Methods), removal and hunting were likely to have had only a minor influence on the territory system and mating activity of the rhinos. Subadult males were too young to take part in mating activity and to defend a territory. Hunting of adult males took place long before the study started, and adult males probably built up new territories within this time period. Mating activity was not negatively influenced by hunting and translocations. The annual growth rate observed in the study (15.0 %, Kretzschmar 2002) was among the highest rates reported for white rhinoceros: 10.4 % in Matobo National Park, Zimbabwe (Rachlow & Berger 1998), 9.5 % in the Umfolozi-Corridor-Hluluwe Complex, South Africa (Owen-Smith 1973), 8.4 % Krüger National Park, South Africa (Pienaar 1994). Hunting and translocations may even have even led to the high rates of population growth as it reduced the density of the population. This effect was desirable for the study as a high growth rate also means a high number of mating and juveniles, and thus a larger sample size.

Hunting has reduced the number of adult males, which led to a smaller number of males available for female choice, although the sample size, which is defined by the number of females and their calves, was not affected. Paternity was established for 13 different females and 14 different mother-calf relationships (one female had two calves). The sample size was further increased as in most cases the distribution of rhinos was used as a measure of mating success, rather than number of progeny (see below). Thus the sample size used in this study is comparable to or even greater than in a variety of field studies (mean sample size = 23, analysed field studies n = 81, Engel 1999). A higher number of males would have been desirable for the

study. Since, however, it is very time consuming to accumulate data on territory size, vegetation composition and food quality, it would not have been possible to describe the quality of a territory adequately for a higher number of males.

Territory size:

The ranges established for the adult males in the study overlapped widely, it is therefore questionable whether the can be referred to as territories. In general, territories do not overlap, while home ranges show more, or completely overlap (Schenkel 1966) but there is no formal degree of overlap that separates a territory from a home range in literature (Maher & Lott 1995). It emerged that the degree of overlap was dependent on the method used. Mean overlap of the ranges established with the minimum convex method was four times as high as established with Map Info. The range boundary established by the minimum convex polygon method encompasses all the fixes, including occasional fixes well beyond the main area of activity (Harris et al. 1990), the range may thus include large areas which the animal never visited. Range boundaries drawn in by hand allow a more precise interpretation of spatial relationships between animals (Macdonald et al. 1980 cited in Pienaar et al. 1993b) but the minimum convex polygon is the only technique that is strictly comparable between studies (Harris et al. 1990), so both methods were used in the study.
The overlap established with MCP 100 % in my study (42 % ± 12 %) was nearly five times as high as the overlap established for rhinos with the same method in Matabo National Park, Zimbabwe (9.4 % ± 3.7 %, Rachlow et al. 1999). The difference in overlap between the study sites was most likely due to the differences in territory size. Male territories established in my study, 61 – 116 km^2, were much larger than those observed in other studies: Matobo National Park, Zimbabwe: 15 – 50 km^2 (Rachlow et al. 1999); Krüger National Park, Republic of South Africa: 6 – 14 km^2 (Pienaar et al. 1993b), Umfolozi Game Reserve, Republic of South Africa: 1 – 3 km^2 (Owen-Smith 1973). The large territory possibly enabled intruders to cross borders without being detected immediately, as the ability to defend a territory depends on the ability of an animal to monitor the boundary of its ranges (Mitani & Rodman 1979). With increasing size of a territory, distances between scent marks increase and thus the amount of missed detection also increases (Gosling & Robert 2001). Despite the loose structure of their borders, the males in the study were often engaged in fighting with neighbouring bulls when they met at their boundaries (chapter 2) and showed site specific dominance. They scent marked along the border with faeces and urine, which is a common form of signalling territorial status (review Gosling & Robert 2001) by male white rhinos (Owen-Smith 1971, 1973, 1975) and other species*:* e.g. Grévy's zebra (Klingel 1974a, 1974b), H*ippopotamus amphibius* (Klingel 1991), African and Asian wild asses (Klingel 1998). It appears thus justified to refer to the areas established by the males in the present study as territories.

The territories established in the study were much larger than those observed in other populations of white rhinoceros (see below). The difference appears to be almost directly connected with the differences in population density, which becomes clearly in the following list:

TERRITORY SIZE:	WHITE RHINO DENSITY:	STUDY SITE AND AUTHOR:
61 – 116 km^2	0.23 animals/km^2	Northern Transvaal, Kretzschmar 2002
15 – 50 km^2	app. 0.4 animals/km^2	Matobo National Park in Zimbabwe, Rachlow et al. 1999
5 – 11 km^2	0.7 animals/km^2	Kyle National Park in Zimbabwe, Condy 1973 cited in Pienaar et al. 1993b
6 - 14 km^2	0.5 – 1.4 animals/km^2	Krüger National Park, Pienaar et al. 1993b
3 - 14 km^2	0.6 – 1.8 animals/km^2	Ndumu Game Reserve, Conway & Goodman 1989
1 - 3 km^2	3 – 5.7 animals/km^2	Umfolozi Game Reserve, Owen-Smith 1973

Thus males tended to increase the size of their territories when population density and thus competition between males was low.

Distribution of animals and mating success:

The number of offspring per male could not be established clearly, due to the fact that only a few samples could be included in the analysis - the samples of known mother-offspring dyads-, and because for two calves two potential fathers were established. The ambiguous determination of fatherhood was likely due to the „Amplified fragment length polymorphism“ (AFLP) method used. This method is based on the selective PCR amplification of restriction fragments from a total digest of genomic DNA. It has the disadvantage that it is difficulty to identify homologous markers (Queller et al. 1993, Mueller & Wolfenbarger 1999) but its advantage is that it produces fingerprints without prior sequence knowledge (Vos et a. 1995). Up to so far too few markers have been developed for white rhinoceros so that it is impossible to conduct microsatellite analysis. Lately additional samples have been collected and microsatellite analyses are being developed (van Coeverden de Groot et al. 2001) which will allow more precise conclusions in the near future.

Despite the mentioned problems, the method, for the first time, made it possible to combine long-term behaviour observations with genetic analysis of fatherhood. It revealed that females were more likely to mate with males in whose territory they spent most of their time. This indicates that males having a high concentration of females in their territory also have a high level of mating success. This corroborates the hypothesis put forward by Emlen and Oring (1977), which suggested that the distribution of females influences the reproductive success of males.

To assess reproductive success of the males it would have been desirable to measure the distribution of females but only the number of visitors in male territories could be established. However, it is more than likely that the number of visitors in male territories was connected with the number of females. The number of visitors was established by counting the footprints of individual animals along the waterholes. Adult females, subadults and calves of both sexes were included in the analysis. All of the described classes are usually able to move between the territories during most of the time (Owen-Smith 1973) and were often found walking together in groups. It is thus very unlikely that females did concentrate in a different area from subadults and calves and it is thus very likely that the number of visitors represents the number of females. In the following, the number of visitors is therefore referred to as number of females.

Based on the established fact that regular presence of females in male territories was correlated with conception it would have been expected that those males with the highest frequency of females in their territory also have the greatest reproductive success. Contrary to expectations, the male with the highest number of females in his territory, Rambo, had the lowest number of offspring compared to all other males, while the number of juveniles of the other males varied only slightly. It is very likely that the results obtained from genetic analysis actually reflect a territorial situation that was different to the one observed in the study. The skin samples were collected in July 1998 from animals of one to two years of age; the juveniles were thus fathered between 1996 and 1997. From the period of mating to the time of observations, territorial conditions might have changed. For instance Rambo was observed to take over the territory of Schrägman in 1997; the territory he had before may have been less attractive to animals, which would explain the low number of juveniles he fathered. Due to the high frequency of females observed within his territory it is assumed that Rambo may sire more offspring now. The distribution patterns are therefore better suited to establish current male and territory qualities than the results obtained from the genetic analysis.

Morphological characteristics, territory size and mating success:

All body and horn measurements, except the distance between the eyes and the distance between the temples, showed differences in size between sexes and age classes. The body and horn measurements taken for the study thus proved to reflect differences in size and were thus best suited for the comparison of morphological characteristics between adult territorial males.

The male with the largest body and horn size, Rambo, turned out to have the largest territory. The second largest male had the second largest territory, suggesting that body and horn size was correlated with territory size. This relationship was less clear for the other males, but, they all showed smaller body and territory size compared to Rambo and Amsterdam. The low correlation for the other males was maybe due to the fact that the territorial situations constantly changed, as it was observed for Schrägman. It is thus very likely that large body and horn size had an advantage in the intra-sexual competition for large territories in male white rhinoceros, as it has been shown elsewhere that morphological characteristics do influence the outcome of contests in various invertebrates (e.g. shore crabs: Sneddon et al. 1997) and vertebrates (e.g. antelopes: Gosling 1986, fallow deer: McElligott et al. 2001).

The question arises why males strive to increase the size of their territory, as defending and patrolling a large territory requires a great deal of energy. A possible explanation could be that they strive to increase the number of females in their territories and thus to increase their mating success. Rambo and Kent showed the highest frequency of rhinos in their territories compared to the other males but the territory of Rambo was nearly twice as large as the territory of Kent. Territorial size was thus not directly correlated with the frequency of animals. The density of rhinos was higher in the territory of Kent compared to the territory of Rambo, due to its smaller size. His territory was therefore likely more attractive to other rhinos. It may be that a large territory and an attractive territory lead to the same result, a high frequency of rhinos in the territory. Yet the question arises why such an attractive territory as Kent's can be defended by a male who has low values in most of the measured body and horn measurements. It might be that it is not the overall

body size which is the crucial point but a different feature: horn size. Kent had the longest horn of all males. He killed an intruder with this horn during a territorial fight just at the beginning of the study. It is thus likely that overall horn and body characteristics, as well horn size, do play a role in intra-sexual competition for territories and that males do adopt different strategies in order to increase number of animals in their territories: 1. They try to increase the size of their territory and/or 2. They defend a small but attractive area. In the following it will be discussed whether the frequency of animals within the territories was correlated with vegetation structure, vegetation composition or food quality at the study site and whether the territory of Kent was of a higher quality compared to all other males.

Territory quality described by:

Vegetation structure:

Vegetation structure changed, as expected, towards thicker vegetation during the end of the wet season compared to its beginning. Although the method was based on a rough categorising of habitat structures it appeared to be adequate to detect differences between different seasons. The method thus served well as an illustration of possible differences between male territories.

The animal possessing the most open territory (Rambo) also showed the highest number of animals in his territory suggesting that the vegetation structure may have influenced the distribution of animals; the other males' territories, however, did not differ in vegetation structure even though they showed varying frequencies of animals within their territories. This indicates that there must be additional factors influencing the frequency of animals. Nevertheless the result raised the question why the amount of open area influenced the frequency of rhinos within the territory of Rambo. Trees and shrubs limit grass cover and grass production (Ben – Shahar 1992, Van Rooyen et al. 1996). The quality of feed would thus be increased in an open area, compared to a closed area resulting in a more favourable territory, but males ingested in all four categories of openness categories with frequencies similar to those expected by random feeding. Vegetation structure therefore seemed to have no influence on the feeding behaviour. Vegetation density plays an important role in anti predator behaviour in birds: Lima (1987a, 1987b) and mammals: Underwood (1982a), Bowyer (1998), Burger et al. (2000). Dense vegetation can either increase the risk of predation (shorebirds: Metcalfe 1984, antelopes: Underwood 1982a, springbok: Burger et al. 2000) or decrease it (yellow – eyed junco: Caraco et al. 1980, house sparrow: Barnard 1980, eastern grey kangaroo: Heathcote 1987, Kretzschmar 1995). White rhinos show little fear of non – human predators and predatory losses of young are rare (Owen-Smith 1973). Protection from a predator is therefore less likely to influence the frequency of rhinos.

The vegetation structure is likely to be important as a shelter from climatic extremes. Rhinos prefer an open to moderate low-shrub stratum and a moderate tree stratum (Pienaar et al. 1993a, Pienaar 1994) while they avoid areas that consist of open plains with no shade (Pienaar 1994). It was often observed in the study that rhinos hide in thick areas during cold and windy days and that they moved into open areas during hot days. Since the "moderate open" territory of Rambo consisted of "open", "medium open" and "medium open to thick areas". His territory had the advantage of offering the rhinos open areas to cool down in a soft breeze

during hot days as well as some thicker areas as protection against cold wind. Thus the high frequency of rhinos within Rambo's territory could possibly be explained by microclimate. Further studies are needed to confirm this observation.

Plant characteristics:

Females were expected to prefer areas containing large quantities or high qualities of food resources as described in studies on pronghorn (Kitchen 1974), horses (Duncan 1983), bighorn sheep (Festa-Bianchet 1988), Grévy's zebra (Ginsberg 1988) and Kudu (Fabricius 1994); just the opposite, however, was shown in the present study. Territories containing the highest numbers of animals, those of Kent and Rambo, had the highest proportional grass volumes of plant species of low quality. An explanation for this result might be that the plant characteristics analysed are not based on the digestive ability and feeding preferences of white rhinos, but on those of cattle and other ruminants, which may have quite different nutritional requirements. Foraging analysis of male and female white rhinos did, however, show selection for grass species of high palatability and selection against unpalatable grass species. They thus show preferences similar to cattle, for which the categorisation of the grass species was developed.

Another explanation for the unexpected correlation between frequency of animals and proportional grass volumes of plant species of low quality might be that there are a number of grasses of which the grazing value and palatability varies to a greater or lesser extent within the same plant. This particularly happens in grass species with a wide geographical distribution, adapted to a variety of environmental conditions (van Oudtshoorn 1992). This variation can be attributed to differences in rainfall, temperature, soil, geology, slope and humidity or habitat management practices, like overgrazing, which will reduce the growth vigour and leaf production and therefore also the grazing value of a grass (van Oudtshoorn 1992). The grass species *Eragrostis rigidor*, for example, shows a low palatability in areas with high rainfall and higher palatability in areas of low rainfall such as in the study site (pers. comment: game manager at the study site). Therefore feeding preferences were established, and territory quality was described, by frequently foraged or selected grass species.

Feeding preferences of males and females:

The feeding preferences of rhinos were established separately for male and females; in a variety of other mammals there are noticeable differences in feeding preferences between males and females: red kangaroos (Newsome 1980), red deer (Clutton-Brock et al. 1982a), white-tailed deer (McCullough 1989), soay sheep (Peréz-Barbería & Gordon 1999), feral house mice (Torre & Bosch 1999) and Malagasy primates (Hemmingway 1999). Two different methods were used: observation of foraging behaviour in the field, and comparison of faecal composition. The two methods yielded different results:

1. The most frequently eaten grass species were identical in males and females, only the composition of the forage varied slightly between the sexes. The predominant food sources of males consisted of five different grass species while the forage of females consisted of two grass species only.

2. Faecal analysis indicated that differences in forage selection existed. Females showed significantly higher protein concentrations in their faeces and significantly lower concentrations of hemicellulose and neutral detergent fibre compared to males. This corresponds with the result of studies on faeces in white tailed deer (Beier 1987) and elephants (Greyling 2001). The higher protein concentration in the faeces of females was likely due to a higher intake of plants high in protein as faecal nitrogen levels are a good indicator of protein intake in ruminants (cattle: Zimmermann 1979, Wofford et al. 1985, various species: Grant 1995, white tailed deer: Howery & Pfister 1990) and non-ruminants (horse: Mésochina et al. 1998, elephants: Greyling 2001). Predictability of the concentration of other dietary components in faeces is more difficult due to the influence of fibre and lignin on digestibility (Foose 1982), but the high digestibility of the forage eaten by females and low cell wall content could explain the low hemicellulose concentration found in the faeces of females. The protein content in plants inversely correlates with the concentration of the cell wall constituents: hemicellulose, cellulose and lignin (Schwartz & Rennecker 1998, Foose 1982). Thus plants higher in crude protein concentration have low concentrations of the cell wall components. The similarity of lignin concentration found in the faeces of males and females could possibly be a result of the varying digestibility of foods different in lignin content. Lignin is indigestible and represents a barrier to digestion (Schwartz & Renecker 1998). The high digestibility of the cell wall components of the forage eaten by females and a the faster rate of digestion of foods high in fibre and lignin eaten by males may lead to similar lignin concentrations in the faeces of the two sexes. Consequently, faecal composition suggests that differences in foraging between males and females did exist. The different results of the different methods were most likely due to the small amount of data collected on the foraging behaviour of females.

Despite differences in the nutrient composition in the forage males and females showed considerable similarity in plant species selection. They selected for highly palatable grass species and against unpalatable grass species.

The high selectivity shown within the study was striking. White rhinos are hindgut fermenters, adapted to feed on coarse grassland, characterised by high fibre and low protein content (Sneddon & Argenzio 1998). They are able to maintain themselves on low fibre diets. The high selectivity demonstrates that even a large megaherbivore such as the white rhino was not only capable of selecting a feeding habitat or grassland type (as has been shown in previous studies - Owen-Smith 1975, Pienaar et al. 1993a, Pienaar 1994, Meister & Owen-Smith 1997), but also certain patches for feeding or even certain grass species within a feeding patch. The ability of the rhinos to graze selectively on plants is remarkable considering their broad lip with which they pluck grass, but grasses usually grow in tufts. This facilitates selection of individual species (Owen-Smith 1973). The preferred food items were most likely identified by olfactory information, the nostrils being placed close to the mouth (Owen-Smith 1973).

The result raised the question of how females achieved a higher protein intake while showing a similar level of plant species selectivity. It may be that the female metabolism operates in a different manner from that of males. It could also be that females are more selective within a patch and feed more on the more protein-rich parts of the plants, although this is unlikely because such a level of selection may be difficult for this particular large mammal because of the broad lip. Further samples need to be collected in order to draw conclusions about differences in foraging preferences of male and female white rhinoceros.

This high selectivity for individual plant species of high palatability was probably due to the low concentration of proteins in tropical grasses compared to temperate ones and the often chronic deficiency in mineral elements (Mc Dowell 1985). The crude protein concentration in the forage (mean 4.7 % DM) was below the critical level of 5 % given for African ungulates (Tainton 1988). The critical level for nonruminants is probably lower than 5 %, as they are more effective in extracting proteins per unit time from fibrous vegetation than ruminants (Foose 1982). Nevertheless the protein concentration was established at the end of the wet season and protein concentration generally decreases with increasing age of the plant (Schwartz & Rennecker 1998). Animals are expected to be more selective when nutrient intake falls below maintenance (Melton 1987). The selectivity of individual animals for their feeding sites was thus likely due to the low protein concentration in the forage. Individuals having higher protein requirements, such as lactating females and growing young (National Academy of Science 1989), are likely to be more selective compared to others. Females with growing young and lactating females are thus likely to select areas or grass species high in protein concentration, but this has to be confirmed by further analysis.

Territory quality described by:

Frequently ingested or selected grass species:

Forage selection requires much time and energy to search for the preferred item, but a large species such as a rhino needs substantial amounts of food for maintenance. The grass species which was most frequently eaten by rhinos, *Eragrostis rigidor*, was also the most frequently occurring grass at the study site. Rhinos have most likely chosen an abundant plant species of relatively good quality that requires low energy to search for their main food resource. No difference was found in the quantity of *Eragrostis rigidor*, at the end and at the beginning of the wet season; this indicates a similar distribution of the main food between male territories regardless of the season. Also no difference was found in the frequency of the grass species, identified as a highly selected feeding plant by females (*Panicum maximum*) during both seasons.

Significant differences between territories occurred in four different grass species that were either frequently ingested or especially selected for by males. The territory of Amsterdam was characterised by a significantly higher frequency of a palatable grass species (*Schmidtia pappophoroides*, van Oudtshoorn 1992), which was frequently foraged on by males and females. Males selected a feeding patch according to its availability, and females in particular grazed high amounts of this grass species. The species was not significantly different in its overall frequency at the study site. It is therefore less likely that the occurrence of this grass species had an influence on the frequency of animals in the territory of Amsterdam.

The territory of George showed a significantly lower frequency of a pioneer grass species (*Tragus berteronianus)* growing in overgrazed areas. The plant has hardly any grazing value because of its low leaf production, but it plays an important role in control of soil erosion. Low frequency of this grass could be an indication of a territory which was less overgrazed compared to the other territories. The territory of this male

also showed the highest frequency of a highly digestible and palatable pasture grass (*Digitaria eriantha*) during both seasons, which is characterised by a high leaf production (van Oudtshoorn 1992). This grass species was frequently selected for feeding by males, but the plant was never grazed on by females, most likely due to its relatively low frequency at the study site. Both grass species thus indicated a high quality territory, but this was not reflected in the number of animals in his territory. This suggested that there are other factors that influence females to prefer a territory.

The territory of Kent was characterised by a low frequency of the *Heteropogon contortus* at the beginning of the wet season; this is a relatively good, hardy and fast growing pasture grass (van Oudtshoorn 1992). This species occurred less often in his territory than at all other transect points in the study site. The differences in frequency occurred only at the beginning of the wet season, when the grass was likely to be less preferred compared to the wet season due to its declining grazing value as the season progressed (van Oudtshoorn 1992). Thus the differences most likely had no influence on the distribution of animals.
The territory of Rambo showed the highest frequency of the nutritious grass, *Digitaria erianthia*. The number of animals was comparatively high in his territory indicating a connection between the frequency of the grass species and the number of animals.
The territory of Rambo showed a connection between animal density and forage, while the results for George´s territory stand in contrast to those for Rambo´s. Amsterdam and Kent showed no connection. These opposing results do not allow conclusions about a correlation between the frequencies of frequently ingested or selected grass species and rhino distribution.

Nutritional analysis:

The protein content in plants varies depending on the species, the age of the plant, and the soil on which the grass is growing (Schwartz & Rennecker 1998). Young plants and plants growing in the shade tend to have higher protein concentrations and low concentrations of the cell wall components, compared to older plants and plants growing in full sunlight (Hjeljord et al. 1990 cited in Schwartz & Rennecker 1998). Females selected forage high in protein content, and it is likely that they prefer a territory with high availability of high protein content.
To describe forage quality appropriately, the protein content, digestible energy, minerals, and fibre characteristics of the territorial males' intake were established. The intake was expected to reflect the quality of the forage available.
The concentration of crude protein in the food of the three analysed males differed, showing highest concentration in the forage of Amsterdam and lowest in the forage of George. Individual forage samples, however, showed high variability in concentration indicating that differences between individual forage samples were too high to draw conclusions about differences in crude protein concentrations between territories. Faeces were collected to substitute for the low number of forage samples, and these showed no differences in faecal crude protein concentrations between males. Due to the relatively good predictability of dietary crude protein from the faecal protein levels (Mesochina et al. 1998), generalisation of forage quality from faeces appears justified.

Thus no difference was found in the concentration of crude protein measured in the forage of the five territorial males and the differences in number of animals could not be explained by differences in protein concentrations of forage between individual male territories.

Faecal analysis of neutral detergent fibre, lignin, hemicellulose and cellulose also showed no differences in concentration between males, although predictability of dietary concentrations from faeces is here more difficult due to the influence of fibre and lignin on digestibility (Foose 1982), but forage samples confirm the trend shown in faeces, indicating a high similarity in the food available in the territories of the five males. Mineral concentrations in the forage showed variation between territories in terms of calcium, calcium to phosphorus ratio, chlorine, zinc, copper and iron; but the number of samples was too low to draw conclusions about differences in mineral concentration between individual male territories.

Tree species composition:

The territory of Rambo had the highest frequency of *Acacia nigrescens*. This is a medium to large tree, which is abundant on deep heavy soils and does not occur on sandy soils (van Wyk 1994). These soils have a relatively high pH and consequently produce more palatable grass with a high nutrient content (Van Rooyen & Theron 1996a, Ben-Shahar 1995). The high frequency of this tree species indicates a high nutrient content in his territory. This might explain the high number of animals found in his territory. The territory of Kent had significantly fewer *A. nigrescens* compared to Rambo. Also his territory had a significantly higher frequency of *Acacia erubescens* compared to all other male territories; this is a many-stemmed shrub or small tree occurring in dry bushveld, often on rocky outcrops or along sandy banks of dry watercourses (van Wyk & van Wyk 1997). The low frequency of *A. nigrescens* and the high frequency of *Acacia erubescens* in the territory of Kent could thus be an indicator for a predominance of sandy soils. Sandy soils have a low water and nutrient holding capacity (Van Rooyen & Theron 1996a) which results in a low nutrient concentration in the vegetation. The high number of animals in Kent´s territory can not be explained by the tree species frequency.

The territory of George showed a significantly higher frequency of the tree species S*clerocarya birrea* compared to all other males. This is a medium to large tree occurring in bushveld and woodland. It occurs on places with medium to shallow sandy soils (van Wyk & van Wyk 1997). The tree could be an indicator of low nutrient concentration in the soil, which would correlate with the low number of animals in his territory.
In summary in two out of three cases a direct correlation was found in the frequency of trees and the number of animals occurring in the territories of the males. This suggests a possible correlation between soil quality, indicated by tree species and numbers of animals in territories of males. Further studies with direct measurements of soil quality should be conducted to confirm this observation.

Conclusion:

Two factors, vegetation structure and tree species composition, possibly influenced the frequency of animals within male territories. These factors did not, however, explain the frequency of animals in the territory of Kent compared to Rambo; thus the hypothesis that the territory of Kent was more attractive compared to the territories of the other males could not be confirmed by the study. The study has shown that it is very difficult to determine a single factor that may influence the distribution of rhinos, because of their influence on each other. Three possibilities exist 1. Factors not established in the study were influencing the frequency of the animals. 2. Several factors influence the distribution of animals which makes it difficult to determine a single factor. 3. The distribution of animals does not follow any pattern except randomness. Further studies need to be conducted to clarify these points. For further studies it would be interesting to investigate whether 1. The quality of the water in male territories or 2. the age of the territorial males has an influence on the distribution of females.

CHAPTER 2: THE INFLUENCE OF SEASON, MATING BEHAVIOR AND FIGHTING ON GONADAL ACTIVITY IN MALE WHITE RHINOCEROS (*CERATOTHERIUM SIMUM SIMUM*)

INTRODUCTION:

Androgen plays a major role in social and sexual behaviour of mammals (reviewed in Bronson 1989 and Nelson 1995). They mediate sexual behaviour and affect the likelihood of mating. The testosterone concentration is correlated with mating success, attractiveness of males to females and status, as shown for many animals like African buffalo (Brown 1991a), plain zebra, Grevy´s zebra (Chaudhuri & Ginsberg 1990), wild dog (Monfort et al. 1997), various bird species (Enstrom et al. 1997, Poiani et al. 2000), African elephants (Rassmussen 1998). It can be modulated by various environmental and social factors (Bronson 1989, Brockman et al. 2001). Day length (e.g. fallow deer Asher et al.) food availability (impala: Brown et al. 1991b), rainfall (in African buffalo: Brown et al. 1991a) or temperature can influence the onset and cessation of hormone secretion in mammals. Social stimuli such as the sight, sound and smell of a female in oestrus can promote endocrine changes in males e.g. in rhesus monkeys (Bernstein 1977), domestic sheep (Gonzales et al. 1988) and grey lag goose (Kotrschal et al. 2000) and can reactivate the sexual activity of a satiated male („Coolidge effect" Lott 1991). Social stress on the other hand has suppressive effects on gonadotropin secretion (von Holst 1998).

Knowledge of the interaction between environmental factors, behaviour and androgens is critical for captive management of the white rhinoceros as its breeding success in captivity is very poor (Meister 1998, Rieches 1998). In zoos different strategies are used to improve reproduction of the species, e.g. long-term endocrine monitoring, assessment of the reproductive soundness using ultrasonography and electroejaculation, oestrus induction in acyclic females and development of artificial insemination (Schwarzenberger et al. 1998, Schaffer et al. 1998, Patton et al. 1999, Göltenboth et al. 2000, Hermes et al. 2001), but no distinct increase in the reproduction rate has been obtained yet (Emslie & Brooks 1999). Basic information about the reproduction of natural living white rhinoceros is urgently needed to develop management strategies for the species.

The southern white rhinoceros occurs south of the Zambesi (Penny 1987), in a region of dry winter and rainy summer. Fluctuation in rainfall and food availability may force temporal clustering of reproduction, but a seasonal pattern of hormone secretion has not been described for the white rhinoceros yet. Longitudinal hormone profiles of adult males were therefore established to analyse annual rhythm in androgen secretion.
The reproductive activity of female white rhinoceros has been studied for several years, revealing unregular oestrus cycle lengths ranging from 25 to 90 days or a total lack of cycling activity (Hindle et al. 1992, Schwarzenberger et al. 1998, Roth et al. 1998, Patton et al. 1999). However, information about the reproductive activity of males is still scarce. The low investigation effort is surprising, as male infertility

contributes significantly to reproductive failure in many zoo maintained species (Wildt 1996) and might be one reason for poor breeding success of white rhinoceros in captivity.

To study reproductive activity in wild and in captivity kept animals practicable and applicable methods are needed. Seasonal variations in androgens concentrations are usually measured by analysing blood samples that are collected at different times of the year (Brown et al. 1991a, b; Monfort et al. 1993a, Price et al. 2000). However, frequent capturing of rhinos is expensive, dangerous for the animals (Du Toit 1998, Alibhai et al. 2001) and causes stress which can interfere with the animals´ hormone balance (Brown et al. 1991a, Place & Kenagy 2000). Therefore, non-invasive methods using faecal or urinary steroid metabolites are more appropriate to determine reproductive activity. These methods were already used in various zoo and wildlife species (Grevy´s and plain zebra: Chaudhuri & Ginsberg 1990, sifaka: Brockman & Whitten 1996, wild dog: Monfort et al. 1997; hanuman langurs: Ziegler et al. 2000) and have been successfully established to monitor reproductive activity in female rhinoceros (black rhinoceros: Schwarzenberger et al. 1993, 1996; white rhinoceros: Hindle & Hodges 1990, Meister 1998; Indian rhinoceros: Schwarzenberger et al. 2000b and Sumatra rhinoceros: Roth et el. 2001). In contrast non-invasive measurements for male white rhinos are scarce. Testosterone-like immunoreactivity was measured once without further characterisation of the metabolite (Rachlow et al. 1998). Therefore, new methods are urgently needed to determine the reproductive status of male rhinoceros and to understand the relationship between behaviour and endocrine parameters affecting reproductive fitness and success in free living populations (Hindle et al. 1992).

The objectives of this study were (1) to validate an enzyme immunoassay (EIA) to quantify androgen metabolites in the faeces of white rhino, (2) to assess the potential of this assay to monitor changes in androgen secretion in faeces after gonadotropin administration, (3) to detect differences between different age classes, (4) to investigate seasonal fluctuations in testosterone metabolite concentrations and (5) to correlate testosterone metabolite concentrations with mating and territorial behaviour.

METHODS:

The collection of faeces:

A total of 378 faecal samples were collected from May 1997 until April 1999. Samples of adult males (n = 301) were gathered weekly during tracking of the animal. On this occasion the animal was followed along its track by a game tracker and all individually assignable faeces were collected. Fresh faecal samples of individual males could be identified, by collecting them along the tracks, without seeing them excrete. Probes were only taken when its origin was certain.
Samples of females, subadults and juveniles were collected on an unregular basis by chance of sighting of a defecating animal during car patrols. Only fresh samples – based on colour and moisture- were taken. The samples dated from the night before to early morning were collected during morning until midday, so that exposure to sun, heat and rain was low. Approximately 100 g of faeces were collected from different parts of

the dung heap and mixed in a plastic bag. Out of this amount 0.5 g were weighted into a plastic tube and mixed with 5 ml methanol (90 %). The tube was sealed with a screw lid and parafilm, in order to eliminate evaporation of methanol, and stored at –12 °C. The storage time lasted from 7 months up to 22 months depending on the time of sample collection. Faecal testosterone concentrations of each individual collected during the same period (January – March) did not differ significantly in concentrations between 1998 and 1999 (Wilcoxon paired sample test $T_{-} = 46.5$ $p = 0.16$, $n = 11$. Thus, prolonged storage times did not lead to a time dependent increase of individual faecal testosterone concentrations and thus did not affect seasonal trends. During the transport to Germany samples were kept in a cold box.

Collection of blood samples and administration of GnRH:

In July 1998 rhinos were caught for management purposes allowing to collect faecal and blood samples from tranquillised animals. The faecal samples were collected from the animals rectum (juvenile males n = 5, subadult males n = 6, adult males n = 5) while blood samples (n = 12) were obtained from the ear vein. The rhinos were kept tranquillised for shortest periods possible, maximum 15 – 30 minutes, in order to avoid unnecessary stress. The blood samples were gathered in vacutainer and kept in a cooler box until the evening. Serum was obtained after centrifugation and stored at – 12 °C. The samples were kept in dry ice during the transport to Germany and then kept frozen at – 12 °C until further analysis.

To stimulate the gonadal secretion of testosterone 20 ml Receptal ® containing 84 µg Buserelin (Hoechst, Midrand, South Africa) were administered to an anaesthetised territorial bull. Starting on the day of treatment all faecal samples were collected by tracking this animal continuously for three days and additionally on the fifth day. Faecal samples obtained prior to Buserelin treatment served as control. Those were taken out of the rectum of the anaesthetised male (n = 1) as well as from sample collections on the tracks 7 days (n = 2) and 8 days (n = 1) before the treatment. In addition one sample was collected 14 days after treatment. Due to the intensive monitoring effort needed to obtain consecutive samples, only one male was chosen for this part of the study.
The estimated time of defecation after Buserelin injection and the number of samples which has been collected is given in Table 25.

Table 25: Day of sample collection, number of samples and time after injection of Buserelin.

day of collection	no. of samples	time after injection [h]
07/09/98	1	± 5 minutes before injection
07/10/98	1	± 12
07/11/98	3	± 36
07/12/98	5	± 56
07/14/98	3	± 109

Determination of testosterone concentration in faeces and serum:

The samples were analysed in the laboratory of Dr. Dehnhard, Institute for Zoo and Wildlife Biology, Berlin, Germany. After centrifugation (15 min at 1200 g) the supernatant was transferred into a new tube, diluted 1 : 1 with water and aliquot portions of 20 µl was subjected to the enzyme immunoassays (EIA) for testosterone metabolites. For a second extraction, the faecal sediment was suspended in 90 % methanol, vortexed for 30 minutes and prepared for EIA as described above. With the second extraction 30 - 50 % of the metabolites were still recovered. Both extracts were individually analysed in duplicate using a microtitre plate EIA procedure. After extraction faecal sediments were fully lyophilised and faecal hormone levels were expressed as mass/g dry weight, which rules out the dietary effects on steroid excretion (Wasser et al. 1993). The testosterone metabolite concentration of each faecal sample was calculated by summing up the concentrations of both extracts. The antibody (provided by Prof. Meyer, Weihenstephan, Germany) was raised in rabbits immunised against 17α-OH-testosterone-HS-RSA. The cross-reactivities of the antibody to different androgens were as follows: 4-androsten-17β-ol-3-one (testosterone: 100 %), 5α-androstan-17β-ol-3-one (dihydrotestosterone: 13.6 %), 5α-Androst-2-en-17β-ol (1.5 %), and <0.1 % for 5α-androstan-3β-ol-17-one (epi-androsterone), 5α-androstan-3α-ol-17-one (androsterone), 5α-Androst-2-en-17-one. Testosterone-3-CMO-peroxidase was used as enzyme conjugate. The testosterone calibration standards were prepared by dilution with 40 % methanol and ranged from 0.2 to 100 pg/well. For EIA 20 µl sample extract, 100 µl of the antibody solution (1:500 000) and of the enzyme solution (1:50 000) were added to the plate. After incubation for 24 h at 6 – 8 °C, the plates were washed four times before 150 µl of substrate buffer (1.2 mM H_2O_2, 0,4 mM 3,3´,5,5´-tetramethylbenzidine in 10 mM sodium acetate, pH 5.5) was added to each well and incubated for 40 min at 25 °C. The enzymatic reaction was arrested with 50 µl 4 M sulphuric acid to each well and the absorbency at 450 nm was measured. The sensitivity of the assay was defined as two standard deviations from the signal given by the zero blank. Precision and reproducibility were calculated from multiple measurements of pooled samples. Serial dilutions of faecal extracts yielded displacement curves parallel to those of the testosterone standard. The intra-assay coefficients of variation were 9 % (n = 8) and 8.9 % (n = 8) and the inter-assay coefficients were 20.8 % (n = 32) and 21.29 % (n = 32) for two pooled samples containing low and high concentrations, respectively. The detection limit of the assay was 0.4 pg/well. The inter-assay coefficients were slightly elevated, however they were in a range reported for measurements of different faecal steroid metabolites in birds (14 – 19.6 %; Hirschenhauser et al. 1999) and mammals (8 – 20 %; Matsumuro et al. 1999). To minimise inter-assay variations we tried to measure individual animals within one assay.

To determine testosterone in bloodplasma 0.1 ml of plasma was extracted with 2 ml of solvent consisting of 30 % butylmethylether and 70 % petroleum ether. After freezing at -80 °C, the organic phase was decanted, dried at 50 °C, dissolved in 1 ml 40 % methanol and analysed with the same EIA technique as described for the faecal samples.

Three series of data analysis:

The faecal samples were collected from April 1997 until March 1999 but only samples from January 1998 until March 1999 (n = 224) were used for analysis as previous samples ran out during transportation. The hormone metabolite concentration of the residues was determined under the assumption, that the concentration should not vary within the liquid but comparison of median testosterone metabolite concentration for each male revealed significant differences between the samples (Friedman test: $\chi^2 = 10$, a = 3, b = 5, $p < 0.001$; a posteriori Dunn´s test: $p = 0.05$ $Q = 3.2$). The monthly concentrations of the year 1997 were significantly lower than those from the same month of the following year (Wilcoxon paired sample test: first series: T = 0, n = 8, p = 0.01; second: T = 19, n = 10, p = 0.002), which could have been due to the animals increasing age. A comparison of the monthly concentration of samples from the year 1998 and 1999, which did not run out, showed not differences (T = 47, n = 17 p = 0.16). The data from 1997 were therefore neglected.

Age classes:

For analysis animals were assigned to three different age classes: calves (0 – 2 years of age), subadults (2 – 6 years of age) and adults (> 6 years). For further description on age estimation see general methods.

Fighting activities:

The seasonal distribution of inter- and intrasexual territorial conflicts was established out of sightings during tracking. Broken trees and long scratch marks on the ground gave indications to fights. The tracks, size and the pattern of lines underneath their feet, gave clues to distinguish characters such as the individuals and number of participants. Nineteen fighting events occurred between May 1997 until April 1999, nine between territorial males, ten between territorial males and females. The number of fights between all five territorial males or between the territorial males and females were summarised according to the month they occurred. Additionally the frequency of fights between January 1998 and April 1999 was established for each male separately out of the number of fighting (between males only) in which this male was involved divided by the total number of sightings of each particular male. The frequency of fighting for each male was than compared with the median testosterone metabolite concentrations measured for this male during that time period.

Conceptions:

To represent a seasonal distribution of conceptions, the time of conception was established for individual females and conceptions of subsequent years were summed up for each month. The time of conception was established by subtracting 16 months, the length of pregnancy in white rhinoceros (Owen-Smith 1973), from the time of birth of the calf. The times of birth were established by direct observations, either of the female

with her new-born or of the previous calf having left the mother (n = 31 births occurred between Jan. 1997 and Dec. 1999, personal data were supplemented by observations of game wardens).

Receptive females:

It was analysed whether the presence of a receptive female had an influence on the testosterone concentrations of the male. The receptive phase of a female was defined by the age and sex of her calf, backdated to the observation. Since receptivity of a female was found to be dependant upon the age and sex of her calf, (females having a male calf conceive ± 7.5 months after their previous young was born while females having a female calf conceive only after ± 18.5 months, Kretzschmar 2002), it was defined that all females with a male calf of 7 months or older and a female calf of >18 months were classified as receptive in the following analysis. However, it can not be ruled out that some females were receptive beforehand.
Based on the assumption, that the presence of a receptive female was likely not a single event as consorting and courtship behaviour usually take up to several days or weeks (Owen-Smith 1973), median concentrations of faecal samples collected on the day of sighting of a male together with a receptive female were compared to concentrations of samples of the same male without a female. However, the number of animals was too small for statistical comparison. Data of adult males were pooled after it was checked, whether individual differences in concentrations occurred (see results) and compared using a Mann-Whitney test.

Used Range:

The range used by an animal was determined out of the area established from the GPS coordinates obtained during tracking using Map Info Professional (see chapter 1). It is not comparable with the territory size as it only includes sightings within a certain period of time. A time interval was chosen in dependence on the seasonal testosterone fluctuations which comprises periods of high (Sept. – Nov.) medium (Dec. – Feb., March – May) or low testosterone metabolite concentrations. For each time period the size of the used range was calculated for each male (UA_2) and the size of the range of the whole study period (UA_1) was than subtracted from UA_2. From these deviations a median was calculated for each period including the ranges of all males.

Marking activity in connection with androgen status:

The median distance between scent marks was calculated for each male and day and compared with the hormone concentrations of this male and day. The distance between scent marks was calculated out of the distance between positions of urine and faecal markings per male and tracking session. The distance was calculated by using following formula:

$[(Lo_1 - Lo_2)^2 + (La_1 – La_2)^2]^{0.5} / 1000$ Lo = longitude, La = latitude

Between January 1998 and May 1998 the male "Schrägman" occasionally stopped spray marking and scattering of dung and defecated like a subdominant β-bull (n = 10). These TM concentrations were compared with the concentration on days while he defecated like a territorial male (n = 8). For comparison the same period of time was chosen including data from 1998 and 1999, as it has been shown, that concentrations do not increase in successive years (see three series of data analysis).

Statistical analysis:

For data analysis nonparametric statistics based on two-tailed tests were used only. The calculation of the statistical tests was carried out using Microsoft ® Excel 1997, SPSS 8.0 and SsS 1.0. For descriptive statistics the median and interquartile ranges (IQR) were calculated, giving 25 and 75 % of the data range (Zar 1996). For further description of statistical testes used see chapter 1.

RESULTS:

Stimulation of GnRH production:

After administration of Buserelin to one adult male, the testosterone metabolite (TM) secretion increased one day after treatment from a baseline of 64.8 ng/g faeces (IQR = 19.6, n = 5) to 165 ng/g faeces by 154 % (n = 1, Figure 31). Within five days post treatment the values decreased slowly (102 ng/g faeces, IQR = 28, n = 11). Measurements on day 14 showed testosterone metabolite concentrations comparable to starting levels (49.6 ng/g faeces, n = 1).

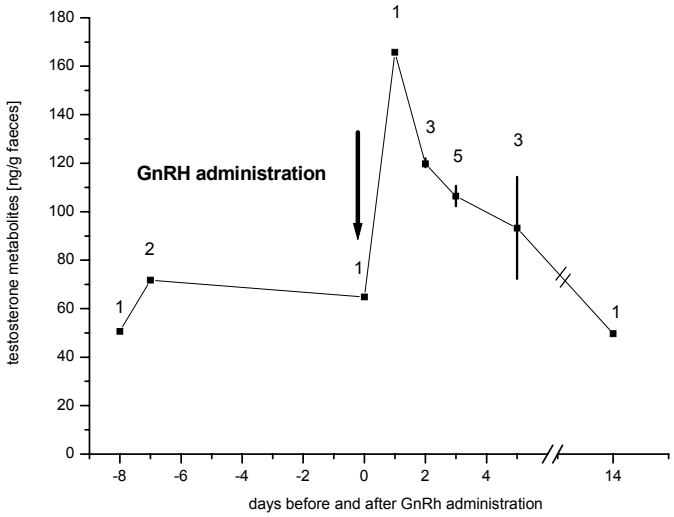


Figure 31: Testosterone metabolite concentration (median ± IQR) before and after administration of Buserelin. The numbers indicate the number of faecal samples. The arrow indicates the date of administration.

Comparison of faecal and blood testosterone concentrations:

A positive correlation was found between plasma hormone and faecal testosterone metabolite concentrations (Spearman rank correlation: $r_s = 0.59$, $p = 0.042$, $n = 12$, Fig. 32) both collected at the same time from one immobilised male ($n_{adult} = 5$, $n_{subad.} = 6$, $n_{calf} = 1$).

The circles around the data of Figure 32 demonstrate that testosterone concentrations in blood and faecal samples differed between adult males and male calves/subadult males. Adult males had significantly higher serum testosterone concentrations than male calves/subadult males (Mann-Whitney test: BLOOD: $Z = -2.8$, $n_a = 5$, $n_{c/sa} = 7$ $p = 0.004$). The differences in faecal testosterones were tested in the following chapter.

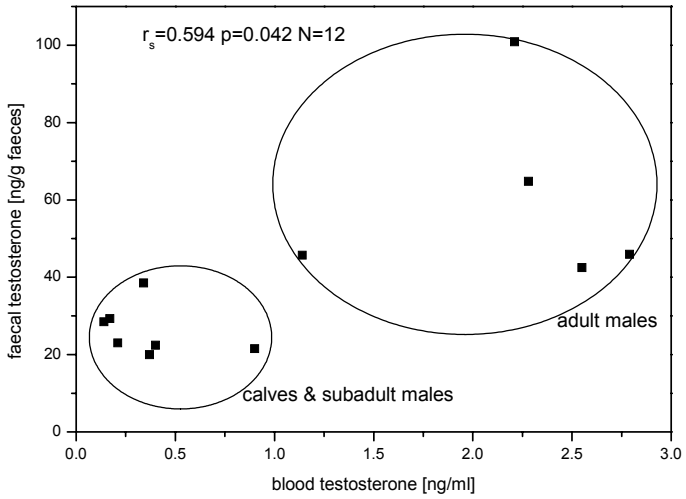


Figure 32: Faecal TM concentrations in relation to blood testosterone concentration. A circle is drawn around measurements of adult males as well as around male calves together with subadult males. The result of the Spearman rank correlation is given in the graph.

Comparison of faecal testosterone concentrations between different sexes and age classes:

Data of adult males of similar testosterone metabolite levels (Kruskal Wallis test $H = 7.5$, $p = 0.11$ see below), were significantly higher compared to testosterone metabolite concentrations of male calves (median = 28.4 ng/g faeces, IQR = 8.2, $n = 8$) and subadult males (28.5 ng/g faeces, IQR = 30.5, $n = 11$, Mann – Whitney test with a posteriori standard Bonferroni correction: adults/calves: $Z_c = -3.84$, $p = 0.0002$, $n_a = 215$, $n_c = 8$; adults/subadults: $Z_s = -2.8$, $p = 0.01$, $n_a = 215$, $n_s = 11$, Fig. 33). Subadult males have slightly but not significantly higher testosterone metabolite concentrations compared to male calves ($Z = -0.6$, $n_c = 8$, $n_S = 11$, $p = 1$).

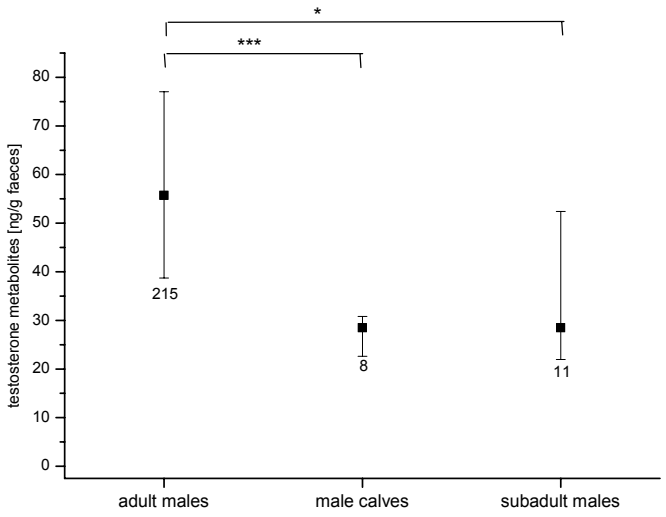


Figure 33: Comparison of faecal TM concentrations of adult males, male calves and subadult males. (median ± IQR). Numbers indicate the number of faecal samples. (Mann-Whitney test and Bonferroni correction *: $p < 0.05$, ***: $p<0.001$).

Comparison of testosterone levels between territorial males:

The testosterone levels of the adult territorial males did not differ significantly from each other (Kruskal Wallis test $H = 7.5$, $p = 0.11$, Fig. 34). Their median testosterone metabolite concentration was 55.7 ng/g faeces (IQR = 38.3, n = 205). Kent showed a higher variation in concentrations and had slightly elevated values compared to all other males while the testosterone metabolite level of Schrägman was slightly lower compared to the others. According to this result the testosterone concentrations of adult males were pooled if necessary.

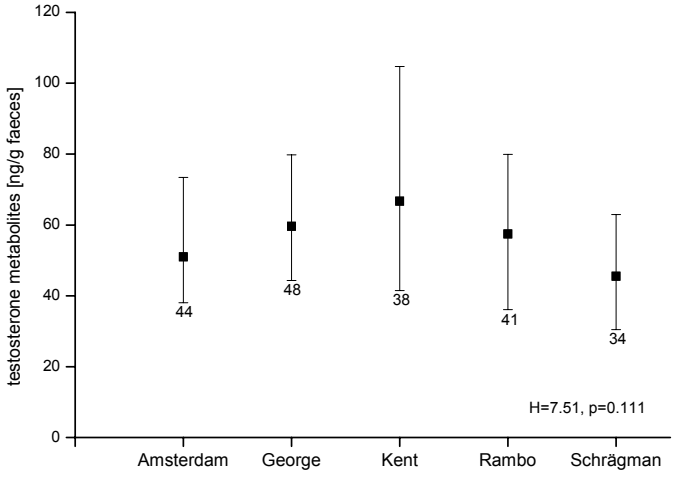


Figure 34: Faecal TM concentrations of adult males in the year 1998/1999 (medians ± IQR). Numbers indicate the number of faecal samples. The result of the Kruskal-Wallis test is given in the graph.

Seasonal testosterone fluctuations:

The testosterone concentrations of each male were significantly higher during the period from September to December compared to January to August (Wilcoxon paired sample test $T_- = 0$, $n = 5$, $p = 0.043$). Based on the findings of similar testosterone concentrations of individual males and similar concentrations within certain time periods, data of adult males were pooled and monthly median testosterone concentrations were established.

The median testosterone levels of all males fluctuated around 45 ± 15 ng/g between January and August (median = 47.4 ng/g faeces, IQR = 37.5, n = 124). Beginning in September faecal metabolite levels increased, reaching significantly higher levels between September to December (87 ng/g faeces, IQR = 62.8, n = 38) compared to data from January till August (Mann - Whitney test: $Z = -2.0$, $n_{J-A} = 124$, $n_{S-D} = 38$, $p = 0.043$, Fig. 34). Maximal faecal testosterone concentrations were found in October (median = 120 ng/g faeces, IQR = 12.1, n = 4).

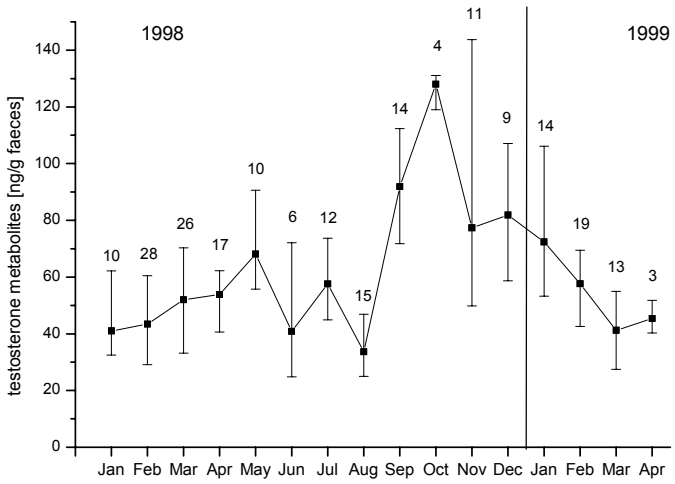


Figure 35: Faecal TM concentration of all adult males for each month of the years 1998 and 1999. Numbers indicate the number of faecal samples. The vertical line indicates the beginning of a new year.

Gonadal activity and behaviour:

In the previous chapters it was shown that changes in blood testosterone level were well reflected in faecal testosterone metabolites: Stimulation by a GnRH analogous substance led to an increase up to 154 % of testosterone metabolite, serum testosterone concentrations showed to be correlated with faecal testosterone concentrations and differences between age classes were detectable with faecal analysis. In the following the seasonal pattern of gonadal activity is being investigated further and hormone concentrations are related to behaviour, such as mating or territorial activity.

Seasonal variations in gonadal activity in correlation with behaviour:

The number of conceptions showed a tendency to be increased during the period of rising androgen titers (Fig. 36D). Most births occurred between December and June with an increase in February and March. Consequently, most conceptions took place between August and February (74 %) with an increase in October and November (Fig. 36C). The number of conceptions within the four months of increased hormone levels was twice as large (n = 14) as the number of conceptions during the same time span prior to increasing androgen concentrations (n = 7). In contrast decreasing androgen level do not necessary coincide with the number of conceptions. Given the low number of samples due to the known limitations in field studies, no statistical analysis was applied.

Median testosterone concentrations increased with the first rain, and reached highest concentrations two months before highest precipitation occurred (Fig. 36E).

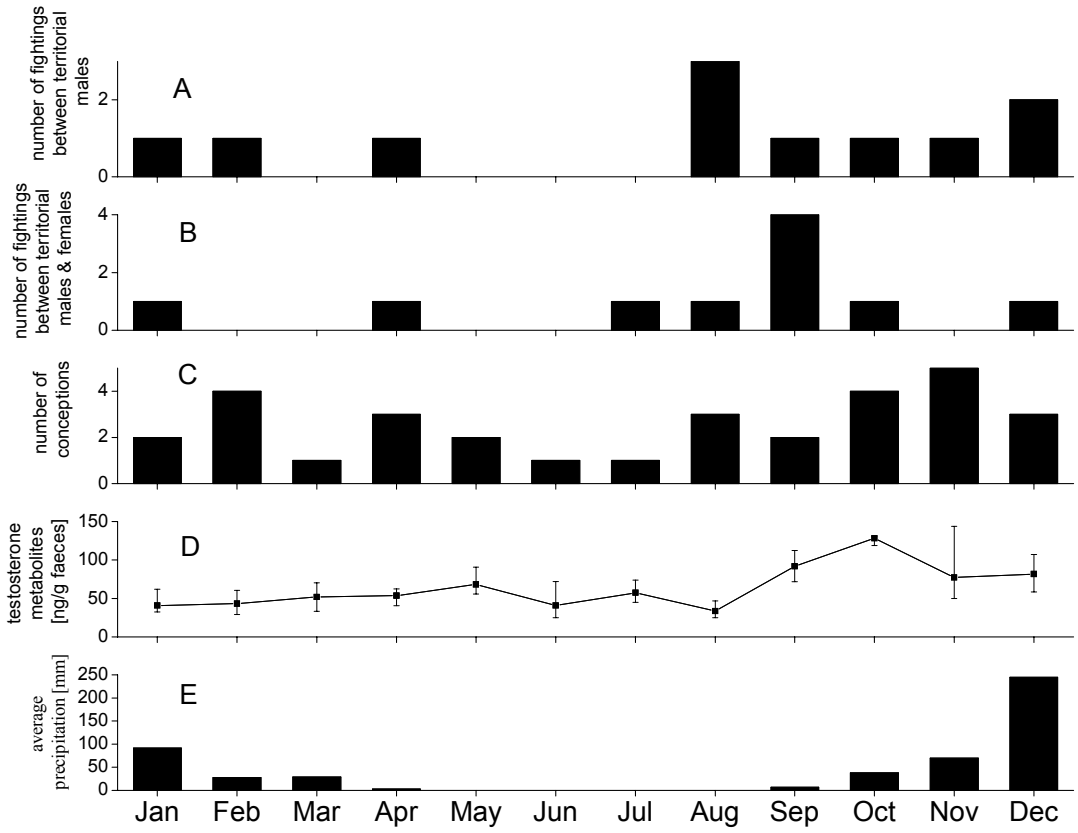


Figure 36: Seasonal distribution of fights between territorial males (A), fights between territorial males and females (B), number of conceptions (C) faecal testosterone concentrations of males (D) and average precipitation (E). Fig. A, B include data from two years, Fig. C comprises data from 3 years while Fig. D, E are based on data from one year.

Territorial conflicts were observed between August and April, with the highest number in August (n = 3, Fig. 36A), just before testosterone concentrations increased. Maximal intersexual conflicts between territorial males and females (78 %) occurred between July and December (80 %, n = 8, Fig. 36B) with a peak in September, when faecal androgen metabolite levels increased.

Gonadal activity and presence of receptive females:

Median testosterone concentrations of samples collected on the day of sighting males together with a receptive female were on average 24.2 % higher (IQR = 26, n = 4, range: 47.9 – 57.7 ng/g faeces) compared to median concentrations of individual males being alone (58.4 – 76.5 ng/g faeces, Fig. 37). The number of individuals was to small for statistical comparison of individual data. In pooled data, faecal samples of adult males collected on the day of sighting males together with a receptive female had significantly higher testosterone metabolite concentrations compared to samples being collected when males were alone (Mann-Whitney test: $Z = -2.1$, $n_{alone} = 95$, $n_{rec.\ female} = 17$, $p = 0.04$).

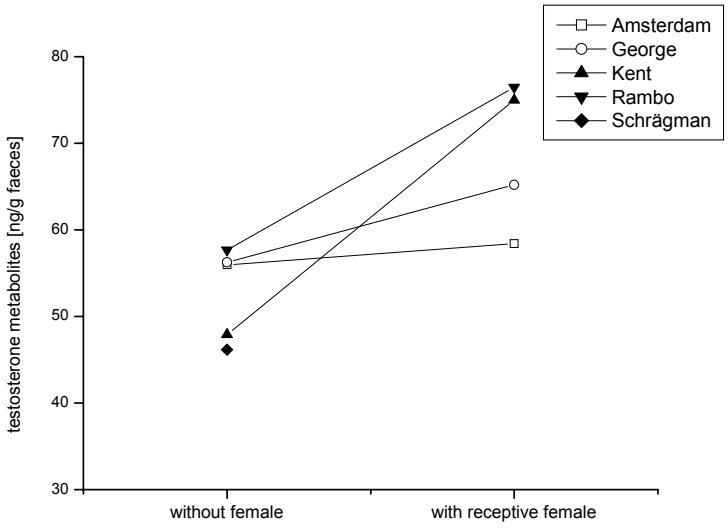


Figure 37: Median testosterone concentration of each male in dependence on presence of receptive females. No data were available for Schrägman as he was never seen together with a receptive female.

Faecal testosterone concentrations and fighting activity:

The frequency of fights which occurred between January 1998 and April 199 for each male were significantly correlated with the median testosterone metabolite concentrations measured for this male during that time period (Spearman rank correlation $r_s = -0.90$, $n = 5$, $p = 0.037$, Fig. 38).

Lower testosterone metabolite concentrations occurred in males with high fighting activity. Among all males, Schrägman was involved in the largest number of fights after he lost his territory, while Kent was involved in the lowest number.

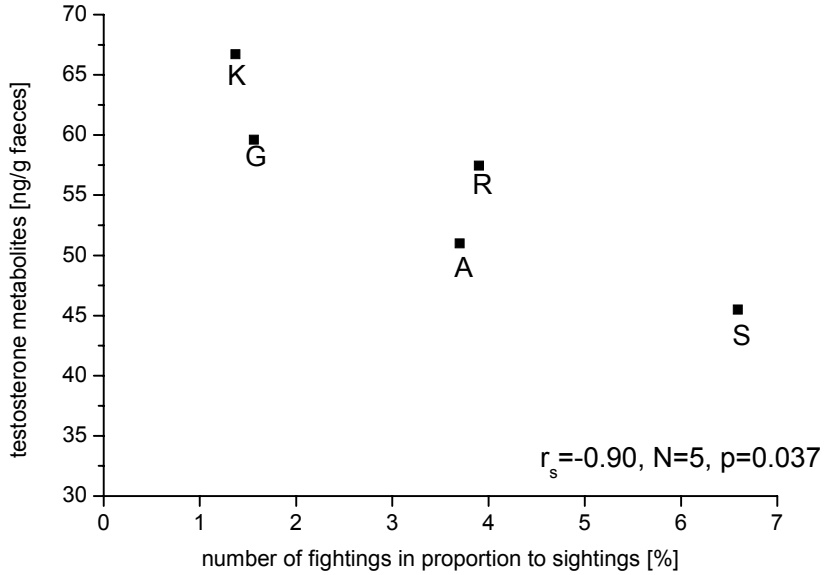


Figure 38: Testosterone concentration plotted against relative number of fight activities of each male. The letters refer to the name of each animal. The result of the Spearman rank correlation is given in the graph.

Testosterone concentrations and the utilisation of territory area:

The size of the utilised area was calculated for periods of three months (Table 26). The periods based on high and low TM concentrations being established for the years 1998/99 (see Fig. 35).

All males showed an increase in utilised area in the period from September to November 1997 and 1998 (Fig. 39), while it decreased compared to the median area between December and August. Highest average utilised area seemed to coincide with highest seasonal testosterone concentrations (see Fig. 35), but no direct correlation between both was found for any individual male (tested for the period January 98 until February 99; Spearman rank correlation, n = 5: Amsterdam: $r_s = 0.4$, $p = 0.50$; George: $r_s = 0.6$, $p = 0.29$; Kent: $r_s = 0.6$, $p = 0.29$; Rambo: $r_s = 0.7$, $p = 0.19$; Schrägman: $r_s = 0.3$, $p = 0.62$).

Table 26: Size of utilised area within a 3 months period, given in square kilometres. The area was established with Convex Polygon 100 % (Map Info).

Male/3 months period	6. - 8.97	9. - 11.97	12.97 – 2.98	3. - 5.98	6. - 8.98	9. - 11.98	12.98 – 2.99
Amsterdam	13.7	58.0	40.8	56.2	76.7	49.2	56.7
George	31.6	55.2	62.7	49.4	52.8	54.4	50.2
Kent	19.9	30.9	40.4	47.4	49.6	64.1	50.3
Rambo	96.6	98.5	53.8	70.3	85.5	95.1	92.5
Schrägman	21.9	5.9	53.7	8.4	11.5	75.3	35.0

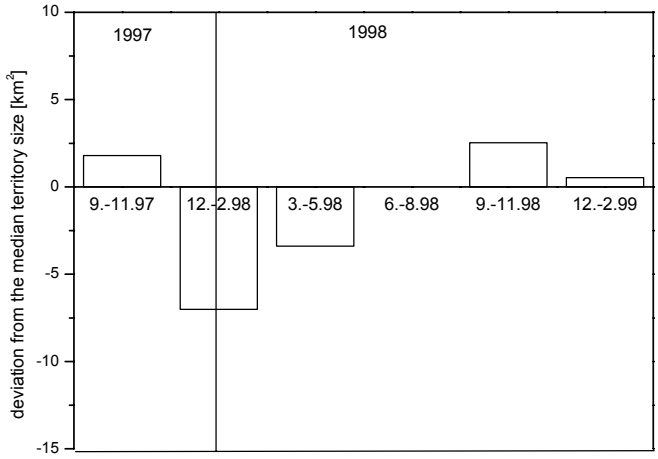


Figure 39: Average deviation (median) from the median size of utilised areas in all males between September 97 and February 99. The total study period was separated into three months periods. The vertical line indicates the beginning of the year 1998.

Territorial marking activity and androgen concentrations:

No correlation was found between the distance of territorial markings and the testosterone metabolites for the two animals being analysed (Kent: r_s = - 0.3, n = 22, p = 0.18; George: r_s = - 0.03, n = 19, p = 0.89).

A comparison of TM concentrations between January and May of the male "Schrägman" while he stopped spray marking and scattering of dung (n = 10) with concentration on days while he defecated like a territorial male (n = 8) showed no difference in androgen concentrations (Mann-Whitney test: Z = - 0.04, p = 0.24).

DISCUSSION:

Assessment of the reliability of non-invasive faecal measurement:

The study aimed to investigate whether measurements of faecal testosterone metabolites are a suitable tool to monitor gonadal production of the sexual hormone testosterone in the white rhinoceros. Three lines of evidence suggest that metabolite measurements clearly reflect gonadal activity: (1) GnRH administration led to an increase of 154 % of testosterone metabolites of an individual rhinoceros one day after treatment. (2) Distinct differences were obtained between male calves/subadult males and adult males. (3) There was a considerable correlation between testosterone levels in blood plasma and the concentration of fecal metabolites.

Testosterone and dihydrotestosterone (DHT) were tentatively identified a faecal metabolites, based on their identical retention time with the authentic standards when two HPLC systems with different selectivity were

used (Kretzschmar et al. subm.). However, I cannot exclude unknown androgen metabolites with structures similar to testosterone and DHT which probably cross-react with the used antibody

The stimulation of the pituitary by synthetic GnRH increased faecal metabolite testosterone levels by 154 % within 12 hours after administration and dropped slowly but continuously thereafter, reaching basic levels five days after injection. The gut passage time is responsible for the time lag between injection and excretion. The delay of one day in excretion is consistent with the intestinal transit time described for androgen and gestagen excretion of white rhinoceros (Hindle & Hodges 1990) as well as other species: e.g. baboons (Wasser et al. 1993), wild dogs (Monfort et al. 1997) and maned wolves (Velloso et al. 1998). The elevation time of androgen concentrations appears long compared to 48 h in African wild dogs (Monfort et al. 1997) and 16 h in maned wolves (Velloso et al. 1998). However, it is likely that species-specific or individual-specific differences exist, considering the steroidal clearance and the pattern of excretion. In female white rhinoceros radiolabelled gestagen was still excreted four days after administration (Hindle & Hodges 1990), while yellow baboons showed high individual variance in excretion patterns after an ACTH-challenge (Wasser et al. 2000).

The conclusions on the stimulation of the pituitary are based on data of one single animal only and temporal course and amount of androgen secretion can not be generalised. However two additional lines of evidence suggest that metabolite measurements clearly reflect gonadal activity: 1) Concentrations of testosterone metabolites correlated significantly between faeces and serum testosterone concentrations taken on the same day from the same animals. This is consistent with a study on sable antelopes, reporting a significant correlation between serum and faecal progestagen measurements (Thompson & Monfort 1999). 2) Differences in testosterone concentrations between animals of different age classes were reflected both in serum and faecal samples. Significantly higher testosterone concentrations were found in adult males than in male calves and subadult males. Subadult males had slightly but not significantly higher faecal testosterone concentrations than male calves. These findings support the general hypothesis of increasing androgen secretion during sexual maturity (Asa 1996).

Androgen concentrations of adult males:

Androgen concentrations of male white rhinos were expected to differ, in connection with mating success, attractiveness of males to females or status, as it has been shown in studies on African buffalo (Brown 1991a), plain zebra, Grevy zebra (Chaudhuri & Ginsberg 1990), wild dog (Monfort et al. 1997), birds (Enstrom et al. 1997, Poiani et al. 2000), African elephants (Rassmussen 1998). However, faecal androgen concentrations did not differ between adult territorial male rhinos. The median TM concentration of all males was 57.5 ng/g faeces (IQR = 41.7), which corresponds well with the concentrations being reported for territorial males in another free-living population (54.3 ng/g faeces, Rachlow et al. 1998). However, a direct comparison can only be done under reservations as it is not clear whether the same antibody has been used in both studies.

The resemblance in male's androgen level is believed to reflect the similarity in their status. All males were defending a territory and showed mating activities (see chapter 2). They could be classified as dominant α-bulls according to the definitions of Owen-Smith (1973, 1975). Non-territorial males (subdominant β-bulls) in contrast have lower testosterone metabolite concentrations (31.3 ng/g faeces, Rachlow et al. 1998) and do not take part in mating. Unfortunately it was not possible to compare the androgen status of Schrägman, when he lost his territory as these samples ran out during transport. It is expected, that his androgen concentrations dropped after loss of territory. In 1998 he established a new territory but occasionally stopped spray marking and scattering of dung and defecated like a subdominant β-bull. A comparison of androgen concentrations before and after this change in behaviour revealed no change in testosterone metabolite concentrations. The temporary change was maybe not connected with a change in status. It is rather believed that he was insecure and unfamiliar with the new area which he recently occupied. However it is conspicuous that insecurity which was most probably connected with stress had no influence on the androgen concentrations. More samples are necessary in order to draw further conclusions.

Fighting activity and androgens:

Testosterone metabolite concentrations were significantly higher in males that were less often involved in fighting activity. The highest fighting activity was observed for Schrägman who established a new territory, which resulted in several territorial conflicts with other males. The decrease in androgen concentration in connection with increasing aggression contrast to studies on rhesus monkeys (Rose et al. 1971), red deer (Lincoln et al. 1972), boars (Liptrap & Raeside 1978), humans (Harris et al. 1996) and spotted antbirds (Hau et al. 2000) which describe an inverse relationship. However, the relation between androgens and aggression is not simple (review Nelson 1995). Androgens act synergistically with many other factors regulating aggressive behaviour, such as social experience or motivation (Ruiz-de-la-Torre & Manteca 1999). Winning or losing a fight for example decides about the influence of aggression on testosterone secretion in humans (Nelson 1995). Aggressive encounters on the other hand have been shown to increase corticoid secretion of white rhinoceros in captivity (Schmidt 1995), which could result in a reduction of androgen concentrations (von Holst 1998). The restriction of aggression to the beginning of the reproductive season is in general a useful means of avoiding stress reactions (von Holst 1998). The white rhinoceros appears to exhibit this stress avoiding pattern. However further data need to be collected to confirm this observation. Stress hormone analyses are on the way in order to throw light on the problem.

Territorial activity and androgen concentrations:

Highest testosterone concentration tended to coincide with an increase in the range used within the territory of individual males. Males inhabit a larger range between September and November compared to the rest of the year. The trend is consistent with studies on avian species (Wingfield et al. 1990, Wingfield 1984, Wada et al. 1999), where males had larger territories, when they were experimentally maintained at peak testosterone levels (Wingfield 1984). Adult male white rhinoceros are generally solitary and only associated

with a cow during her oestrus (Owen-Smith 1975). The enlargement of the range being used could result from increased sexual motivation, due to which males are searching for mating partners.

The frequency of scent-markings showed only slight variations over the year and was independent from seasonal changes of androgen secretion. This is contrary to studies on small mammals showing an increase in frequency of scent-marking in connection with an increase in aggressiveness (Brown 1975, Johnson 1976).

Presence of receptive females and androgens:

Individual adult males showed a tendency of increased testosterone metabolite levels when they were accompanied by a receptive female compared to being alone. Pooled data confirmed that trend. Courting could possibly have induced an increase in androgen concentrations in adult males similar to studies on rabbit (Agmo 1976), domestic sheep (Sanford et al. 1974), boar (Liptrap & Raeside 1978), rat (Kamal & Frankel 1978), domestic cattle (Katongole et al. 1981), rhesus monkeys (Herndon et al. 1981) or grey lag geese (Kotrschal et al. 2000). These studies revealed that sexual activity or merely exposure to females (in rhesus monkeys: Rose et al. 1972, Bernstein et al. 1977; domestic sheep: Gonzales et al. 1988, domestic geese: Kotrschal 2000) or to their scent (hamster: Macrides et al. 1974) led to elevated concentrations of serum testosterone levels. This so called "Coolidge Effect" (Nelson 1995) could possibly be used for management purposes in order to stimulate the copulatory activity of a satiated male. The introduction of a new female might led to elevated testosterone concentrations. However, further data are needed before recommendations can be given.

Seasonal testosterone secretion:

White rhinoceros exhibit a seasonal pattern of androgen secretion with highest testosterone concentrations between September and December and lowest between January and August. This trend was consistent throughout all males. The increase in concentrations coincided with the beginning of the rainy season suggesting a seasonal pattern of gonadal activity in white rhinoceros following the rainy season. However, data must be interpreted cautiously, as the conclusion is based on five males only.

A seasonal increase in testosterone concentration has been reported for several mammal species e.g. African buffalo (Brown et al 1991a), impala (Brown et al 1991b), rhesus monkeys (Robinson et. al. 1975), black bear (McMillin et al. 1976), roe deer (Göritz 2000) and domestic sheep (Price et al 2000). It is characterised by testicular increase and begin of spermatogenesis (Clarke 1981 in Spinks 1997, Brown et al. 1991b), an increase in ejaculate volume, seminal quality and sperm motility (in buffalo and impala by Brown et al. 1991a, b, roe deer Göritz 2000). In the present study, the number of conceptions showed a tendency to be increased during the period of rising androgen concentrations, suggesting that testosterone concentration induced a change in mating behaviour. In contrast decreasing androgen concentrations did not necessarily coincide with the number of conceptions. The fact that a few matings still occurred throughout the year, suggests that low hormone concentrations do not abolish spermatogenesis. Therefore I conclude that white

rhinos are not strictly seasonal, but they show a tendency to concentrate reproductive activities between September and December. It is likely that putative hormone effects outlast increased hormone concentrations. Steroid induced changes in behaviour are known to involve cellular changes even in the central nervous system (Arnold & Gorski 1984, Breedlove 1992, Breedlove & Jordan 2001) and changes in cellular properties are not as quickly reversible as changes in blood hormone concentrations. However, further studies are needed to confirm these observations.

Other studies on free-living white rhinos in South Africa (Groves 1972, Owen-Smith 1975) support the concept, showing an increase of mating and courtship activity, in November and February in Transvaal (Owen-Smith 1975) and between July and September in Zululand (Groves 1972). Variations in the onset of reproductive activity between those study sites are likely due to variations in climatic or dietary factors. Phytohormones, nutritional composition or a change in food supply could possibly have induced seasonal reproduction in white rhinos, such as in e.g. antelopes (Gosling 1986), impala (Brown et al. 1991b), African buffalo (Brown et al. 1991a), hanuman langurs (Ziegler et al. 2000) and domestic sheep (Blache et al. 2000), leading to variation in breeding pattern in dependence on the availability of these factors. Owen-Smith (1975, 1998) suggested that the growing of fresh grass after the rain is inducing the oestrus of female white rhinoceros. High food intake has been shown to stimulate the GnRH-LH pulse frequency and to promote the testicular growth in domestic sheep (review: Blache et al. 2000), whereas a deficit in zinc, mangan and selenium triggered off reproductive failure in males and females of different species (Wildt 1996). Captive white rhinos do not show any seasonal trend in breeding (Frädrich 1997). Suggesting, that intrinsic seasonal physiological triggers such as photoperiodic e.g. in black bear (McMillin et al. 1976), blue fox (Mondain-Monval et al. 1988), eld´s deer (Monfort et al. 1993a) and fallow deer (Asher et al 1989) are less important in white rhinos.

Intra-sexual conflicts coincided with the beginning of the mating season during a phase of low testosterone metabolite concentrations, while inter-sexual conflicts peaked during elevated androgen concentrations. These observations support the concept of seasonal breeding in white rhinoceros. The increase in intra-sexual conflict was maybe induced by changes in sexual libido and mating behaviour as observed in ungulates (Fraser 1968 cited in Monfort et al. 1993b) or by a change in testosterone concentration similar to red deer (Nelson 1995) and rabbits (Girolami et al. 1997). Inter-sexual fights on the other hand might be induced by high androgen concentrations and are likely to be more sexually motivated (Owen-Smith 1973). However, further data is needed to confirm this correlation.

Why do rhinos breed seasonally? Reproductive patterns should have evolved, that youngsters are born when environmental conditions are most favourable for their growth and survival. (Gosling 1986, Estep & Dewsbury 1996). White rhino calves are being borne during the early dry season following 16 months of gestation (Owen-Smith 1975). This seems to be a selective disadvantage given the high nutritional demand of lactation. New borne calves weigh approximately 40 kg and increase in weight by estimated 1250 g during the first three months. (Dittrich 1972, Puschmann 1989). In the first four months they drink 15 l of milk per day, start to eat substantial amounts of solid food with 4 to 6 six months and are totally weaned at about twelve months of age (Dittrich 1971, Owen-Smith 1975, Nelson & Fowler 1986). The post birth period is therefore a high energy demanding period and it is surprising that this period is coinciding with low food supply. The female can cope with the situation as the cost of lactation and postweaning growth of the

offspring are usually spread out over longer periods of time (Robbins 1983 cited in Bronson 1989) and body reserves built up during the preceding wet season could help to sustain lactation through the dry season (Meyer et al. 1993, Owen-Smith 1998). A more critical period for the offspring is the time just after dissolvement of the zone pellucida before placentation of the embryo. Shortage in energy, vitamins and amino acids during that time can lead to the deformity and death of the embryo (Meyer et al. 1993). Seasonal breeding timed by rainfall guarantees the female high food supply during this period. Another critical time for the survival of the new-borne is the time just after weaning. Young animals require high amounts of energy and proteins (Schwartz & Rennecker 1998, Watson & Dawson 1993) during their growth. Due to the lower gut size in small animals (Van Soest 1996), young animals are not good in digesting the high share of fibres in their food (Dawson 1989). They need grass of high quality and low fibre content, which is occurring in young growing grass (Schwartz & Rennecker 1998). During the study, most births occurred between December and June, given a weaning period of 12 months in white rhinoceros, the postweaning period falls into the raining period where young grass is abundant. The availability of adequate food for the growing offspring immediately after weaning could therefore be another important reason for seasonal reproduction in white rhinoceros.

GENERAL CONCLUSIONS:

The overriding aims of the study are, firstly, to establish why rhinos do not breed well in captivity and, secondly, to identify the characteristics of those males which breed successfully. The results should make it possible not only to improve breeding in captivity, but also to assess the number of breeding males in free living populations and the ability of such populations to maintain genetic variability.
The main findings of the study are: 1. Females are more likely to mate with those males in whose territory they spend most of their time. 2. The distribution of rhinos in male territories varies, which suggests that there are different degrees of male mating success. 3. The male with the longest first horn and the male with the largest body and horn size had the highest number of rhinos in their respective territories. 3. The two largest males also had the largest territories. 4. The territory with the lowest density of trees and bushes had the highest number of rhinos. 5. Those territories with the highest density of certain tree species also had the highest number of rhinos. 6. There is a seasonal variation in testosterone metabolite concentrations. 7. There is a correlation between testosterone metabolite concentrations and fighting activity. 8. Males had significantly higher testosterone metabolite concentrations when they were in the company of a receptive female than when they were alone.

The mating behaviour of white rhinos was studied using a combination of different disciplines and approaches: ecology, genetics, behaviour, endocrinology and dietetics and field work and laboratory work. While the present study has been able substantially to increase our knowledge and understanding of the behaviour of white rhinos, it should be borne in mind that it covers only a limited number of years for a species with a lifespan of up to fifty years. Moreover, given the long gestation and lactation periods among white rhinoceros, a lengthier period of observation will be needed to confirm the mating patterns observed in this study. Nevertheless, the study reveals a large number of previously unknown facts about the reproductive behaviour of the white rhino and should therefore help considerably to improve species management.

The non-invasive endocrine monitoring technique, which was developed in the course of the present study in order to analyse the concentrations of testosterone metabolites in the faeces, is ideally suited to the study of free-living white rhinoceros. It reveals a link between environmental factors, territorial activities, fighting and courtship on the one hand, and testosterone concentrations in faeces on the other hand. It is more than likely that all of these factors play an important role in the mating behaviour of white rhinoceros. The data showed that mating activity varies seasonally, and is very probably influenced either by rainfall or nutrition, or by both. This suggests that the low rate of breeding success in captivity may result from failure to take account of the influence of seasonal variations in the food supply. The study also showed that although white rhinos select high quality grasses, the mineral content of the plants consumed was considerably lower than that of plants fed to white rhinos in zoos (Kiefer et al 2002). It is possible that the high food quality in zoos causes excess weight, which in turn may result in low reproductive performance.

It would therefore be worth considering whether a seasonal reduction in food intake followed by a diet of fresh grass would help to avoid the accumulation of body reserves and, by simulating natural conditions, help to stimulate reproductive activity.

The study used a novel method to establish paternity (AFLP method) which, for the first time, made it possible to combine long-term behaviour observations and genetic analysis of fatherhood in white rhinoceros. This method revealed that females were more likely to mate with those males in whose territory they spent most of their time. This corroborates the hypothesis put forward by Emlen and Oring (1977), which suggested that the distribution of females influences the reproductive success of males. The results also indicate that a high concentration of females is a clear sign of a high level of male mating success. If the distribution of the females in small free-living populations is uneven, this will distort breeding patterns and result in excessive inbreeding. This could, however, be avoided if the successful males were replaced every few years. The results of the study suggest that successful breeders can be identified clearly by monitoring the distribution of rhinos. This could be done either by patrolling all waterholes, as was done in the present study, or by patrolling along transect lines through the whole area once a month, or at least every three months, as the preferences of females may change with the season. Since the study indicated that the male with the largest body and horn size and the male with the longest first horn had the highest level of reproductive success, it might also be possible to use these criteria to identify dominant breeders. An alternative approach to reducing inbreeding might be to manipulate female distribution. Since the study shows that the largest concentration of rhinos is found in areas of low bush and tree density, clearance of areas with dense growth may enhance their attractiveness.

The study reveals a correlation between male body and horn size and territory size, suggesting that morphological characteristics play a role in male intra-sexual competition for large territories and that a large territory is related to mating success, although the nature of this relationship remains unclear. At all events, possession of a territory is crucial to mating behaviour. In captivity, however, space is often restricted. Males are often released into the same enclosure alternately, with the result that they do not have the chance to establish their own territory and the status on which successful mating depends. Breeding success of captive white rhinos could be increased if males were given their own areas. Since the presence of other males is important for the establishment of territories, they should however, be able to see and smell each other. This could be done by using bars to separate the different areas. Females should be allowed to move between different male “territories” to choose their favourite male. Another way of increasing breeding success in captivity would be to stimulate sexual activity in situations where only a single male is kept with several females. This could be done by simulating the presence of another bull by placing the urine and faeces of another bull in the enclosure. As was shown in a study by Kolar et al. (2002), this can stimulate territorial behaviour.

To gain further insight into the mating behaviour of white rhinos it is recommended that the approach by Tinbergen (1973, cited in Gansloßer 2000) be adopted. Tinbergen suggests that the solution to any problem in behavioural biology depends on finding the answers to four questions: 1) Where does the observed

behaviour comes from and how did it evolve phylogenetically? 2) Why did it evolve and which function does it have? 3) Which mechanism does it use? 4) Through which mechanism did it evolve?

These questions can be applied to the observed type of mate choice – females mate with males having a large territory and/or horn and body size - as following: Was this type of mate choice a characteristic behaviour pattern of the predecessors of the white rhino, or did it develop with this species? 2) How does the individual rhino benefit from this type of mate choice 3) What are the mechanisms through which this type of mate selection is practised. 4) How is this trait carried from one generation to the next?

1) Since it is not possible to investigate the behaviour of the predecessors of the white rhino, the first question can only be answered by making comparisons within the wider rhino family. For black rhinos, it has already been shown elsewhere that male reproductive success has varied (Garnier et al. 2001), suggesting that mate choice was already present in the ancestors of African rhinoceros. However, it is also possible that such behaviour has developed independently in both species. Neither the characteristics of successful males nor the factors which may have influenced the female's choice were established in the study by Garnier et al. (2001). For this reason, it is important to carry out further studies on mate choice in black rhinos as well as in other rhino species in order to establish whether females choose their mates and, if so, which factors influence their choice.

2) The present study has shown that a large body and horn size and a large territory are of benefit to male rhinos – i.e. by contributing to high reproductive success. However, it was not possible to show how females profit by concentrating in particular areas. Food is a possible explanation, although none of the nutritional factors analysed was found to influence the distribution of females. One possible advantage is that, by congregating in the territories of males with a large body and horn size, they are better protected against harassment by other males. To establish whether this is the case, it will be necessary to monitor females more closely. Another possible research task might be to manipulate environmental factors in male territories, for example by changing the vegetation structure or by introducing higher quality feeding plants into a certain areas. Monitoring would then show whether this influenced the distribution of females and the reproductive success of males.

3) Males gain greater reproductive success if they defend a large territory. A large horn and body size enables them to defend these areas against rivals. It is highly unlikely that testosterone influences their ability to defend large territories. This mechanism is clear and easy to implement. Males need only to increase the size of their territories as much as possible, but not to assess their quality. The relationship between a large horn size and a high reproductive success is not yet clear. It emerged that the male with a largest horn was extremely successful in defending his territory against intruders. It could not be established, however, why he was so attractive for females. Is it his territory, or the fact that he is good at protecting females against other males? If it should be the case that he was defending an attractive area, it needs to be established how he could assess the quality of the area attractive for females. It is also needs to be established how females can recognise a large territory or males with a large body size. It has been described how males blockade a female in oestrus when she tries to leave their territory. This might

provide her with an opportunity to assess the males´ body and horn size. These questions still need to be investigated in more detail.

4) To answer this question it needs to be established whether the reproductive success of one generation of males is carried on to the next, for example whether the offspring of a male with a large territory or/and a large body and horn size has got the same characteristics and the same reproductive success as its father or whether young males hold smaller or less attractive territories then older ones. A study conducted in co-operation with Kolar et al. (2002) revealed that females showed a higher reaction after introduction of urine marks from old males compared to younger ones. This suggests that females could well discriminate between scent marks of different age classes and different rank, as an increase in age is usually correlated with an increase in rank. Since it is very difficult to establish the age of fully grown animals in free ranging animals, long term monitoring would be necessary to establish this. It also needs still to be established whether young females prefer other males compared to old ones.

REFERENCES:

Aberham A (2001). Stimulation des Markier- und Paarungsverhaltens durch Einbringung von Kotproben beim südlichen Breitmaulnashorn (*Ceratotherium simum simum*). Diplom thesis, Paris-Lodron-Universität Salzburg.

Acocks JPH (1988). The veld types of South Africa. 3rd ed. Government Printer, Pretoria.

Adams NR, Hearnshaw H, Oldham CM (1981). Abnormal function of the corpus luteum in some ewes with phyto-estrogenic infertility. Australian Journal of Biological Science 34:61-65.

Agmo A (1976). Serum luteinizing hormone and testosterone after sexual stimulation in male rats. Acta Physiologica Scandinavica 96:140-142.

Alibhai SK, Jewell ZC (2001). Hot under the collar: the failure of radio-collars on black rhinoceros *Diceros bicornis*. Oryx 35:284-288.

Alibhai SK, Jewell ZC, Towindo SS (2001). Effects of immobilisation on fertility in female black rhino (*Diceros bicornis*). Journal of Zoology, London 253:333-345.

Andersson M (1994). Sexual selection. Princeton University Press, Princeton.

Andersson M, Iwasa Y (1996). Sexual selection. Trends in Ecology and Evolution 11:53-58.

AOAC (1965). Official methods of analysis of the association of official agricultural chemists. 10th ed.

Association of official agricultural chemists, Washington, D.C.

Arnold AP, Gorski RA (1984). Gonadal steroid induction of structural sex differences in the central nervous system. Annual Review Neuroscience 7:413-442.

Asa CS (1996). Reproductive physiology. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S (eds) Wild mammals in captivity. Principles and techniques. The University of Chicago Press, Chicago, pp 390-417.

Asher GW, Peterson AJ, Bass JJ (1989). Seasonal pattern of LH and testosterone secretion in adult male fallow deer, *Dama dama*. Journal of Reproduction and Fertility 85: 657-665.

Baker PJ, Funk SM, Harris S, White PCL (2000). Flexible spatial organisation of urban foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. Animal Behaviour 59:127-146.

Balshine-Earn S (1996). Reproductive rates, operational sex ratios and mate choice in St. Peter´s fish.

Behavioral Ecology and Sociobiology 39:107-116.

Barnard CJ (1980). Flock feeding and time budgets in the house sparrow (P*asser domesticus* L.). Animal Behaviour 28:295-309.

Bart J, Earnst SL (1999). Relative importance of male and territory quality in pairing success of male rock ptarmigan (*Lagopus mutus)*. Behavioral Ecology and Sociobiology 45:355-359.

Batzli GO (1994). Special feature: mammal-plant interactions. Journal of Mammalogy 75: 813-815.

Baur B, Studer P (1995). Inbreeding in captive Indian rhinoceros. International Zoo Yearbook 34:205-211.

Beier, P (1987). Sex differences in quality of white-tailed deer diets. Journal of Mammalogy 68:323-329.

Ben-Shahar, R (1992). The effects of bush clearance on African ungulates in a semi-arid nature reserve. Ecological Applications 2:95-101.

Ben-Shahar R (1995). Habitat classification in relation to movements and densities of ungulates in a semi-arid savanna. African Journal of Ecology 33:50-63.

Bernstein IS, Rose RM, Gordon TP (1977). Behavioural and hormonal responses of male rhesus monkeys introduced to females in the breeding and non-breeding seasons. Animal Behaviour 25:609-614.

Blache D, Chagas LM, Blackberry MA, Vercoe PE, Martin GB (2000). Review. Metabolic factors affecting the reproductive axis in male sheep. Journal of Reproduction and Fertility 120:1-11.

Brandt CA (1989). Mate choice and reproductive success of pikas. Animal Behaviour 37:118-132.

Breedlove SM (1996). Sexual dimorphism in the vertebrate nervous system. Journal of Neuroscience 12:4133-4142.

Breedlove SM, Jordan CL (2001). The increasingly plastic, hormone-responsive adult brain. Proceedings of the National Academy of Science USA 98:2956-2957.

Brockman DK, Whitten PL (1996). Reproduction in free-ranging *Propithecus verreauxi*: oestrus and the relationship between multiple partner matings and fertilisation. American Journal of Physical Anthropology 100:57-69.

Brockman DK, Whitten PL, Richard AF, Benander B (2001). Birth season testosterone levels in male Verreaux´s sifaka, *Propithecus verreauxi*: insights into socio-demographic factors mediating seasonal testicular function. Behavioral Ecology and Sociobiology 49:117-127.

Bronson FH (1989). Mammalian reproductive biology. The University of Chicago Press, Chicago.

Brown JL (1975). The evolution of behaviour. W.W. Norton & Company, New York.

Brown JL, Wildt DE, Raath JR, de Vos V, Howard JG, Janssen DL, Citino SB, Bush M (1991a). Impact of season on seminal characteristics and endocrine status of adult free-ranging African buffalo (*Syncerus caffer*). Journal of Reproduction and Fertility 92:47-57.

Brown JL, Wildt DE, Raath CR, de Vos V, Janssen DL, Citino SB, Howard JG, Bush M (1991b). Seasonal variation in pituitary-gonadal function in free-ranging impala (*Aepyceros melampus*). Journal of Reproduction and Fertility 93:497-505.

Bowyer RT, Kie JG, van Ballenberghe V (1998). Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? Journal of Mammalogy 79:415-425.

Bronson FH (1989). Mammalian reproductive biology. The University of Chicago Press, Chicago.

Brown S, Houlden B (1999). Isolation and characterisation of microsatellite markers in the black rhinoceros (*Diceros bicornis*). Molecular Ecology 8:1559-1561.

Burger J, Safina C, Gochfeld M (2000). Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. Acta Ethologica 2:97-104.

Byers JA, Moodie JD, Hall N (1994). Pronghorn females choose vigorous mates. Animal Behaviour 47:33-43.

Caraco T, Martindale S, Pulliam HR (1980). Avian time budgets and distance to cover. The Auk 97:872-875.

Carranza, J, Fernandez-Llario P, Gomendio M 1996. Correlates of territoriality in rutting red deer. Ethology 102:793-805.

Chaudhuri M, Ginsberg JR (1990). Urinary androgen concentrations and social status in two species of free ranging zebra (*Equus burchelli and E. grevyi*). Journal of Reproduction and Fertility 88:127-133.

Clarke JR (1981). Physiological problems of seasonal breeding in eutherian mammals. Oxford Reviews of Reproductive Biology 3:244-312.

Clutton-Brock TH, Harvey PH (1978). Mammals, resources and reproductive strategies. Nature 273:191-195.

Clutton-Brock TH (1982). The functions of antlers. Behaviour 79:108-125.

Clutton-Brock TH, Guinness FE, Albon SD (1982). Red deer. Behaviour and ecology of two sexes. The University of Chicago Press, Chicago.

Clutton-Brock TH, Iason GR (1986). Sex ratio variation in mammals. The Quaterly Review of Biology 61:339-374.

Clutton-Brock TH, Albon SD Guinness FE (1988). Reproductive success in male and female red deer. In: Clutton-Brock TH (ed) Reproductive success. Studies of individual variation in contrasting breeding systems. The University of Chicago Press, Chicago, pp 325-343.

Condy PR (1973). The population status, social behaviour and daily activity pattern of the white rhino in Kyle National Park, Rhodesia. University of Rhodesia.

Conway AJ, Goodman PS (1989). Population characteristics and management of black rhinoceros *Diceros bicornis minor* and white rhinoceros *Ceratotherium simum simum* in Ndumu Game Reserve, South Africa. Biological Conservation 47:109-122.

Davies NB (1978). Ecological questions about territorial behaviour. In Krebs JR, Davies NB (eds.) Behavioural Ecology: an evolutionary approach. Blackwell Scientific Publications, Oxford, pp 317-350.

Dawson TJ (1989). Diets of macropodoid marsupials: General patterns and environmental influences. In: Grigg G, Jarman P, Hume I (eds) Kangaroos, Wallabies and Rat-Kangaroos. Surrey Beatty & Sons, New South Wales, pp 129-142.

Dittrich L (1971). Beobachtungen zur Jungendentwicklung eines Breitmaulnashorns (*Ceratotherium simum simum*) im Zoo Hannover. Zeitschrift des Kölner Zoo 14:73-81.

Dittrich L (1972). Birth and growth of a male white rhinoceros at Hanover Zoo. International Zoo Yearbook 12:122-125.

Dörgeloh WG (1999). Assessment of veld conditions with multivariate techniques in mixed bushveld, South Africa. African Journal of Ecology 37:194-201.

Downing BH (1972). A plant ecology survey of the Umfolozi Game Reserve Zululand. PhD thesis, University of Natal.

Duncan P 1983. Determinants of the use of habitat by horses in a Mediterranean wetland. Journal of Animal Ecology 52:93-109.

Duncan P (1992). Horses and grasses. The nutritional ecology of equids and their impact on the Camargue. Springer - Verlag, New York.

du Toit JG (1998). Rhino ranching. A manual for owners of white rhinos. Africa Publishers, Pretoria.

EEC (1998). Vegetation description and veld condition assessment of the study site. Euclea Ecological Consultants CL, Pretoria.

Emlen ST, Oring LW (1977). Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Emslie R, Brooks M (1999). African rhino. Status survey and conservation action plan. IUCN, Gland, Switzerland.

Engel J (1999): Eine Übersicht über die Vor- und Nachteile von Verhaltensstudien im Zoo. In: U. Gansloßer U (ed) Tiergartenbiologie II Filander Verlag, Fürth, pp 194-215.

Enstrom DA, Ketterson ED, Nolan V Jr (1997). Testosterone and mate choice in the dark-eyed junco. Animal Behaviour 54:1135-1146.

Estep DQ, Dewsbury DA (1996). Mammalian reproductive behaviour. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S (eds) Wild mammals in captivity. Principles and techniques. The University of Chicago Press, Chicago, pp 379-389.

Festa-Bianchet M (1988). Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia (Berlin) 75:580-586.

Fisher RA (1958). The genetical theory of natural selection. 2d ed. Dover, New York.

Foose T (1978). Digestion in wild species of ruminant versus non-ruminant ungulates. AAZPA Conference, AAZPA, Wheeling, pp 74 - 84.

Foose TJ (1982). Trophic strategies of ruminant versus nonruminant ungulates. Dr. Phil. diss. University of Chicago.

Foose TJ (1991). Global Management of rhinos. In: Ryder OA (ed) International Rhino Conference. Zoological Society of San Diego, San Diego, pp 32-47.

Fournier F, Festa-Bianchet M (1995). Social dominance in adult female mountain goats. Animal Behaviour 49:1449-1459.

Fraser AF (1968). Reproductive behaviour in ungulates. Academic Press, New York.

Gansloßer U (2000). Tinbergens vier Fragen. Ein Plädoyer für eine saubere Trennung von Erklärungsebenen in der Biologie. Praxis der Naturwissenschaften - Biologie 6:38-39.

Garnier JN, Bruford MW, Goossens B (2001). Mating system and reproductive skew in the black rhinoceros. *Molecular Ecology* 10:2031-2041.

Ginsberg JR (1988). Social organisation and mating strategies of an arid adapted equid: the Grevy´s zebra. Dr. Phil. diss. Princeton University.

Ginsberg JR (1989). The ecology of female behaviour and male mating success in the Grevy´s zebra (*Equus grevyi*). Symposium of the Zoological Society London 61:89-110.

Girolami L, Fontani G, Lodi L, Lupo C (1997). Agonistic behaviour, plasma testosterone, and hypothalamic estradiol binding in male rabbits. Aggressive Behavior 23:33-40.

Goering HK, Van Soest PJ (1970). Forage fibre analysis. Agricultural Handbook, Vol. 379. USDA, Washington, D.C.

Göltenboth R, Klös HG (1995). Krankheiten der Zoo- und Wildtiere. Blackwell-Wissenschafts-Verlag, Berlin, Germany.

Göltenboth R, Göritz F, Blottner S, Hildebrandt TB, Ochs A, Faßbender M, Hermes R (2000). Management tools for the improvement of reproduction in rhinoceros at the Berlin zoo. Paper presented at the 3rd scientific meeting of the European Association of Zoo and Wildlife Veterinarian, 31. May - 4. June, Paris.

Gonzales R, Poindron P, Signoret JP (1988). Temporal variation in LH and testosterone responses of rams after the introduction of oestrus females during the breeding season. Journal of Reproduction and Fertility 83: 201-208.

Göritz F, Broich A, Quest M, Hildebrandt TB, Lengwinat T, Wagener A, Fassbender M, Hermes R, Blottner S (2000). Seasonal changes in morphology and function of the male reproductive tract in roe deer. In: Lechner-Doll M, Hofer H, 3rd international symposium on physiology and ethology of wild and zoo animals. Blackwell Wissenschafts-Verlag, Berlin, p 86.

Gosling LM (1974). The social behaviour of Coke´s hartebeest (*Alcelaphus buselaphus cokei*). In: Geist V, Walther FR (eds) The behaviour of ungulates and its relation to management. IUCN, Morges, Switzerland, pp 488-511.

Gosling LM (1986). The evolution of mating strategies in male antelopes. In: Rubenstein DI, Wrangham RW, (eds), Ecological aspects of social evolution in birds and mammals. Princeton University Press, Princeton New Jersey, pp 244-281.

Gosling LM, Roberts SC (2001). Scent-marking by male mammals: cheat proof signals to competitors and mates. Advances in the study of behavior 30:169-217.

Grant CC, Meissner HH, Schultheiss WA (1995). The nutritive value of veld as indicated by faecal phosphorous and nitrogen and its relation to the condition and movement of prominent ruminants during the 1992-1993 drought in the Kruger National Park. Koedoe 38:17-31.

Greig-Smith P (1957). Quantitative plant ecology, London.

Greyling MD, Owen-Smith RN, du Toit JT (2000). Use of near infrared reflectance spectroscopy on faecal samples to test for age and sex related differences in the quality of diets selected by African elephants. Project report, University of the Witwatersrand, Johannesburg, pp 1-24.

Groves CP (1972). *Ceratotherium simum*. Mammalian Species 8:1-6.

Gunn IM, Thorne A, Trounson A (1998). Infertility/subfertility in the southern white rhinoceros (*Ceratotherium simum simum*) and the evaluation of their reproductive parameters as to other related species. Paper presented at workshop on problems associated with the low rate of reproduction among captive-born female southern white rhinoceros (*Ceratotherium simum simum)*, 29-31 October, San Diego, pp 37-45.

Halliday TR (1978). Sexual selection and mate choice. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell Scientific Publications, Oxford, pp 180-213.

Halliday TR (1983). The study of mate choice. In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge, pp 3-32.

Hamilton WD (1964). The genetic evolution of social behaviour. Journal of theoretical Biology 7:1-52.

Harris JA, Rushton JP, Hampson E, Jackson DN (1996). Salivary testosterone and self-report aggressive and pro-social personality characteristics in men and women. Aggressive Behavior 22:321-331.

Harris S, Cresswell JW, Forde PG, Trewhella WJ, Woollard T, Wray S (1990). Home-range analysis using radio-tracking data - a review of problems and techniques particulary as applied to the study of mammals. Mammal Review 20:97-123.

Hau M, Wikelski M, Soma KK, Wingfield JC (2000). Testosterone and year-round territorial aggression in a tropical bird. General and Comparative Endocrinology 117:20-33.

Heathcote CF (1987). Grouping of eastern grey kangaroos in open habitat. Australian Wildlife Research 14:343-348.

Hemingway CA (1999). Time budgets and foraging in a Malagasy primate: do sex differences reflect reproductive condition and female dominance? Behavioural Ecology and Sociobiology 45:311-322.

Hermes R, Göritz F, Blottner S, Walzer C, Göltenboth R, Schwarzenberger F, Rudolph M, Hildebrandt TB (2001). Evaluation of fertility in captive male white rhinoceros (Ceratotherium simum)- semen assessment and preservation. Verhandlungsberichte zu Erkrankungen von Zootieren 40:173-176.

Herndon JG, Perachio AA, Turner JJ, Collins DC (1981). Fluctuations in testosterone levels of male rhesus monkeys during copulatory activity. Physiology & Behaviour 26:525-528.

Hillman-Smith K (1997). Das Nördliche Breitmaul-Nashorn. In: Die Nashörner. Begegnung mit urzeitlichen Kolossen. Filander Verlag, Fürth, pp 173-183.

Hillman-Smith AKK, Owen-Smith N, Anderson JL, Hall-Martin AJ, Selaladi JP (1986). Age estimation of the white rhinoceros (*Ceratotherium simum*). Journal of Zoology, London (A) 210:355-379.

Hindle JE, and Hodges JK (1990). Metabolism of oestradiol-17ß and progesterone in the white rhinoceros (*Ceratotherium simum simum*). Journal of Reproduction and Fertility 90:571-580.

Hindle JE., Möstl E, and Hodges JK (1992). .Measurement of urinary oestrogens and 20α-dihydroprogesterone during ovarian cycles of black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceroses. Journal of Reproduction and Fertility 49:237-249.

Hjeljord ON, Hovik N, Pedersen HB (1990). Choice of feeding sites by moose during summer: The influence of forest structure and plant phenology. Holarctic Ecology 13:281-292.

Hochberg Y (1988). A sharper Bonferroni procedure for multiple tests of significance. Biometrika 75:800-802.

Howery LD, Pfister JA. (1990). Dietary and faecal concentrations of nitrogen and phosphorus in penned white-tailed deer does. Journal of Wildlife Management 54:383-389.

Hume I (1982). Marsupial metabolism and nutrient requirements. Cambridge University Press, Cambridge.

Hundertmark KJ (1998). Home range, dispersal and migration. In: Franzmann AW, Schwartz CC (eds) Ecology and management of the North American moose. Smithonian Institution Press, Washington, pp 303-335.

International Rhino Foundation 2002. www.rhinos-irf.org/rhinoinformation/populationtable.htm

Itô, Y (1980). *Comparative ecology*. Press Syndicate of the University of Cambridge, Cambridge.

Jamieson A, Taylor SCS (1997). Comparison of three probability formulae for parentage exclusion. Animal Genetics 28:397-400.

Jarman PJ (1983). Mating systems and sexual dimorphism in large terrestrial mammalian herbivores. Annual Review 58:485-520.

Jewell ZC, Alibhai SK, Law PR (2001). Censusing and monitoring black rhino (*Diceros bicornis*) using an objective spoor (footprint) identification technique. Journal of Zoology, London 254:1-16.

Johnson RP (1976). Scent marking with urine in two races of the bank vole (*Clethrionomys glareolus*). Behaviour 55:81-93.

Johnson DH (1980). The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Kamal F, Frankel A (1978). Hormone release during mating in the male rat: time course, relation to sexual behaviour, and interaction with handling procedures. Endocrinology 103:2172-2179.

Katongole CB, Naftolin F, Short RV (1971). Relationship between blood levels of luteinizing hormone and testosterone in bulls, and the effects of sexual stimulation. Journal of Endocrinology 50:457-466.

Kellner K (2000). Amplified Fragment Length Polymorphism (AFLP) bei Nashörnern (*Ceratotherium simum*, *Diceros bicornis, Rhinoceros unicornis*): Ein Modell zum genetischen Wildtiermanagement. Schüling Verlag, München.

Kellner K, Kretzschmar P, Förster M (2002). AFLP as an economical method to correct field observations for genetic wildlife management in rhinoceros. In: Schwammer HM, Foose TJ, Fouraker M, Olson D (eds) A research update on elephants and rhinos. Schüling Verlag, München, pp 183-189.

Kiefer B (2002). Qualität und Verdaulichkeit der vom Breitmaulnashorn (*Ceratotherium simum simum*) aufgenommenen Nahrung. Freilandaten und experimentelle Studie im Vergleich. DVM thesis, Ludwig-Maximilians-University.

Kiefer B, Ganslosser U, Kretzschmar P, Kienzle E (in press). Feeding selection and food quality in territorial males of a free ranging population of white rhinoceros in South Africa. In: Fidgett A (ed), European Zoo Nutrition II. Filander Verlag, Fürth.

Kitchen DW (1974). Social behaviour and ecology of the pronghorn. Wildlife monographs 38:1-96.

Klein SL, Gamble HR, Nelson RJ (1999). *Trichinella spiralis* infection in voles alters female odour preference but not partner preference. Behavioral Ecology and Sociobiology 45:323-329.

Klingel H (1974a). A comparison of the social behaviour of the equidae. In: Geist V, Walther F (eds) The behaviour of ungulates and its relation to management. IUCN Publication new series, pp 124-132.

Klingel H (1974b). Soziale Organisation und Verhalten des Grevy Zebras (*Equus grevyi*). Zeitschrift für Tierpsychologie 36:36-70.

Klingel H (1991). The social organisation and behaviour of *hippopotamus amphibius*. African Wildlife: Research and Management, pp 73-75.

Klingel H (1998). Observations on social organisation and behaviour of African and Asiatic wild asses (*Equus africanus* and *Equus hemionus).* Applied Animal Behaviour Science 60:103-113.

Kolar D, Kretzschmar P, Gansloßer U (2002) Do urinary scent marks influence behaviour of male and female white rhinoceros (*Ceratotherium simum simum*)? In: Dehnhard M Hofer H (eds.) 4th International Symposium on physiology and ethology of wild and zoo animals. Blackwell Verlag, Berlin: 46.

Komdeur J, Deerenberg C (1997). The importance of social behaviour studies for conservation. In: Clemmons JR, Buchholz R (eds) Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, pp 262-276.

Kotrschal K, Dittami J, Hirschenhauser K, Möstl E, Peczely P (2000). Effects of physiological and social challenges in different season on faecal testosterone and corticosterone in male domestic geese (*Anser domesticus*). Acta ethologica 2:115-122.

Kretzschmar P (1995). Untersuchungen zur Streifgebietsgröße, Habitatselektion und Gruppengröße von weiblichen Östlichen Grauen Riesenkänguruhs *Macropus giganteus* Shaw. Diplom thesis, Friedrich-Alexander Universität, Erlangen-Nürnberg.

Ketzschmar P (2002): Population growth, sex ratio and reproduction of a natural living population of white rhinoceros.In: Schwammer HM, Foose TJ, Fouraker M, Olson D (eds). A research update on elephants and rhinos. Proceedings of the International elephant and rhino research symposium, Vienna, June 7 – 11, 2001. Schüling Verlag, Münster, pp 196-201.

Kretzschmar P, Gansloßer U, Dehnhard M (subm.). Relationship between androgens, environmental factors and reproductive behavior in male white rhinoceros (*Ceratotherium simum simum*). Hormones and Behavior.

Kuwamura T, Karino K, Nakashima Y (2000). Male morphological characteristics and mating success in a protogynous coral reef fish, *Halichoeres melanurus*. Journal of Ethology 18:17-23.

Kvarnemo C, Ahnesjö I (1996). The dynamics of operational sex ratios and competition for mates. Trends in Ecology and Evolution 11:404-408.

Lechner-Doll M, Deutsch A, Lang D (2000). Nutritional management of ungulates in captivity - should we learn from natural seasonality of the vegetation? In: Nijboer J, Hatt J-M, Kaumanns W, Beijnen A, Gansloßer U (eds) Zoo Animal Nutrition, Filander Verlag, Fürth, pp 205-212.

Lee AK, Cockburn A (1985). Evolutionary ecology of marsupials. Cambridge University Press, Cambridge.

Leger DW, Didrichsons IA (1994). An assessment of data pooling and some alternatives. Animal Behaviour 48:823-832.

Leite ER, Stuth JW (1990). Value of multiple faecal indices for predicting diet quality and intake of steers. Journal of Range Management 43:139-143.

Lightbody JP, Weatherhead PJ (1988). Female settling patterns and polygyny: Test of a neutral mate-choice hypothesis. American Naturalist 132:20-33.

Lima SL (1987a). Vigilance while feeding and its relation to the risk of predation. Journal of theoretical Biology 124:303-316.

Lima SL (1987b). Distance to cover, visual obstructions, and vigilance in house sparrows. Behaviour 102:231-238.

Lincoln GA, Guinness F, Short RV (1972). The way in which testosterone controls the social and sexual behaviour of the red deer stag (*Cervus elaphus*). Hormones and Behavior 3:375-396.

Lindemann H (1982). African rhinoceroses in captivity. M.Sc. thesis, University of Copenhagen.

Liptrap RM, Raeside JI (1978). A relationship between plasma concentrations of testosterone and corticosteroids during sexual and aggressive behaviour in the boar. Journal of Endocrinology 76:75-85.

Lott DF (1991). Intraspecific variation in the social systems of wild vertebrates, Cambridge University Press, Cambridge.

Macdonald DW, Ball FG, Hough NG (1980). The evaluation of home range size and configuration using radio tracking data. In: Amlander CJ, Macdonald DW (eds), A handbook on telemetry and radio tracking. Pergamon Press, Oxford.

Macrides F, Bartke A, Fernandez F, SïAgelo W (1974). Effects of exposure to vaginal and receptive females on plasma testosterone in the male hamster. Neuroendocrinology 15:355-364.

Maher CR, Lott DF (1995). Definitions of territoriality used in the study of variation in vertebrate spacing systems. Animal Behaviour 49:1581-1597.

Manley, BFJ, McDonald LL, Thomas DL (1993). Resource selection by animals. Chapman & Hall, London.

McClintock MK (1983). Pheromonal regulation of the ovarian cycle: Enhancement, suppression, and synchrony. In: Vandenbergh JG (ed) Pheromones and reproduction in mammals. Academic Press, New York, pp 113-149.

McCullough DR, Hirth DH, Newhouse SJ (1989). Resource partitioning between sexes in white-tailed deer. Journal of Wildlife Management 53:277-283.

McDowell LR (1985). Nutrition of grazing ruminants in warm climates. Academic Press, New York.

McElligott AG, Gammell MP, Harty HC, Paini DR, Murphy DT, Walsh JT, Hayden TJ (2001). Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? Behavioral Ecology and Sociobiology 49:266-272.

McNaughton SJ (1988). Mineral nutrition and spatial concentrations of African ungulates. Nature 334:343-345.

McQueen RE, Nicholson JWG (1979). Modification of the Neutral-Detergent-Fiber procedure for cereals and vegetables by using alpha-amylase. Journal of the Association of Analytical Chemists 62:676-680.

McMillin JM, Seal US, Rogers L, Erickson AW (1976). Annual testosterone rhythm in the black bear (*Ursus americanus*). Biology of Reproduction 15:163-167.

Meister J, Owen-Smith N. (1997). Das Breitmaul-Nashorn. In: Die Nashörner. Filander, Fürth, pp 163-172.

Meister J (1998). Research on social and reproductive behaviour in captive female white rhinos (*Ceratotherium simum*). PhD thesis, University Erlangen-Nürnberg, Germany.

Melton DA (1987). Habitat selection and resource scarcity. South African Journal of Science 83:646-651.

Mésochina P, Martin-Rosset W, Peyraud J-L, Duncan P, Micol D, Boulot S (1998). Prediction of the digestibility of the diet of horses: evaluation of faecal indices. Grass and Forage Science 53:189-196.

Metcalfe NB (1984). The effects of habitat on the vigilance of shorebirds: is visibility important? Animal Behaviour 32:981-985.

Meyer H, Bronsch K, Leibetseder J (1993). Supplemente zu Vorlesungen und Übungen in der Tierernährung. 8th ed. M+H Schaper Alfeld, Hannover.

Mitani JC, Rodman PS (1979). Territoriality: The relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. Behavioural Ecology and Sociobiology 5:241-251.

Mohr CO (1947). A table of equivalent populations of North American small mammals. The American Midland Naturalist 37:223-249.

Møller AP, Jennions MD (2001). How important are direct fitness benefits of sexual selection? Naturwissenschaften 88:401-415.

Mondain-Monval M, Smith AJ, Simon P, Møller OM, Scholler R, McNeilly AS (1988). Effect of melatonin implantation on the seasonal variation of FSH secretion in the male blue fox (*Alopex lagopus*). Journal of Reproduction and Fertility 83:345-354.

Monfort SL, Brown JL, Wood TC, Wemmer C, Vargas A, Williamson LR, Wildt DE (1993a). Seasonal patterns of basal and GnRH-induced LH, FSH and testosterone secretion in Eld`s deer stags (*Cervus eldi thamin*). Journal of Reproduction and Fertility 98:481-488.

Monfort SL, Brown JL, Bush M, Wood TC, Wemmer C, Vargas A, Williamson LR, Montali RJ, Wildt DE (1993b). Circannual inter-relationships among reproductive hormones, gross morphometry, behaviour, ejaculate characteristics and testicular histology in Eld´s deer stags (*Cervus eldi thamin*). Journal of Reproduction and Fertility 98:471-480.

Monfort SL, Wasser SK, Mashburne KL, Burke M, Brewer BA, Creel SR (1997). Steroid metabolism and validation of noninvasive endocrine monitoring in the African wild dog (*Lycaon pictus*). Zoo Biology 16:533-548.

Mueller UG, Wolfenbarger LL (1999). AFLP genotyping and fingerprinting. Trends in Ecology and Evolution 14.

National Academy of Science (1989). Nutrient requirements of horses. 5th ed. National Academy Press, Washington, D.C.

Nefdt RJC (1995). Disruptions of matings, harassment and lek-breeding in Kafue lechwe antelope. Animal Behaviour 49:419-429.

Nelson L, Fowler ME (1986). Rhinocerotidae. In: Fowler ME (ed) Zoo and Wild Animal Medicine. WB Saunders Company, Philadelphia, pp 934-938.

Nelson RJ (1995). An introduction to behavioural endocrinology, Sinauer Associates, Inc., Massachusetts.

Newsome AE (1980). Differences in the diets of male and female red kangaroos in central Australia. African Journal of Ecology 18:27-31.

Owen-Smith RN (1971). Territoriality in the white rhinoceros (*Ceratotherium simum*) Burchell. Nature 231:294-296.

Owen-Smith RN (1973). The behavioural ecology of the white rhinoceros. PhD thesis. University of Wisconsin.

Owen-Smith RN (1975). The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817). Zeitschrift für Tierpsychologie 38:337-384.

Owen-Smith RN (1977). On territoriality in ungulates and an evolutionary model. The Quaterly Review of Biology 52:1-38.

Owen-Smith RN (1983). Dispersal and the dynamics of large herbivores in enclosed areas: Implications for management. In: Owen-Smith RN (ed) Management of large mammals in African conservation areas. HAUM Educational Publishers, Pretoria, pp 127-143.

Owen-Smith, RN (1988). Megaherbivores: The influence of very large body size on ecology. Cambridge University Press, Cambridge.

Owen-Smith N (1998). Reproductive behaviour of white rhinoceros in the wild in Umfolozi Game Reserve, South Africa. Paper presented at workshop on problems associated with the low rate of reproduction among captive-born female southern white rhinoceros, 29-31 October, San Diego.

Parker PG, Waite TA (1997). Mating systems, effective population size, and conservation of natural populations. In: Clemmons JR, Buchholz R (eds), Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, pp 243-261.

Partridge L, Halliday T (1984). Mating patterns and mate choice. In: Krebs JR, Davies NB (eds), Behavioural ecology an evolutionary approach, Vol. 2, Blackwell Scientific Publications, Oxford, pp 222-250.

Partridge L (1983). Non-random mating and offspring fitness. In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge, pp 227-252.

Patton ML, Swaisgood RR, Czekala NM, White AM, Fetter GA, Montagne JP, Rieches RG, Lance VA (1999). Reproductive cycle length and pregnancy in the southern white rhinoceros (*Ceratotherium simum simum*) as determined by faecal pregnane analysis and observations of mating behaviour. *Zoo Biology*, 18: 111-127.

Penny M (1987). Rhinos: an endangered species. Helm, Bromley,U.K.

Peréz-Barbería FJ, Gordon IJ (1999). Body size dimorphism and sexual segregation in polygynous ungulates: an experimental test with Soay sheep. Oecologia 120:258-267.

Pienaar DJ, Hall-Martin AJ (1991). Radio transmitter implants in the horns of both the white and the black rhinoceros in the Kruger National Park. Koedoe 34:89-96.

Pienaar DJ, Hall-Martin AJ, Hitchins PM (1991). Horn growth rates of free-ranging white and black rhinoceros. Koedoe 34:97-105.

Pienaar DJ, Bothma JduP, Theron GK (1993a). Landscape preference of the white rhinoceros in the central and northern Kruger National Park. Koedoe 36:79-85.

Pienaar DJ, Bothma JduP, Theron GK (1993b). White rhinoceros range size in the south-western Kruger National Park. Journal of Zoology, London 229:641-649.

Pienaar DJ (1994). Habitat preference of the white rhino in the Kruger National Park. In: Penzhorn BL, Kriek NPJ (eds) Rhinos as game ranch animals. South African Veterinary Association, Onderstepoort, South Africa, pp 59-64.

Pienaar UDeV (1970). The recolonisation history of the square-lipped (white) rhinoceros *Ceratotherium simum simum* Burchell in the Kruger National Park (October 1961-November 1969). Koedoe 13:157-169.

Place NJ, Kenagy GJ (2000). Seasonal changes in plasma testosterone and glucocorticosteroids in free-living male yellow-pine chipmunks and the response to capture and handling. Journal of Comparative Physiology B 170:245-251.

Player IC, Feely JM (1960). A preliminary report on the square-lipped rhinoceros *Ceratotherium simum simum*. Lammergeyer 1:3-25.

Poiani A, Goldsmith AR, Evans MR (2000). Ectoparasites of house sparrows (*Passer domesticus*): an experimental test of the immunocompetence handicap hypothesis and a new model. Behavioral Ecology and Sociobiology 47:230-242.

Price CA, Cooke GM, Sanford LM (2000). Influence of season and low-level oestradiol immunoneutralization on episodic LH and testosterone secretion and testicular steroidogenic enzymes and steroidogenic acute regulatory protein in the adult ram. Journal of Reproduction and Fertility 118:251-262.

Puschmann A (1989). Zootierhaltung, VEB Deutscher Landwirtschaftsverlag, Berlin.

Queller DC, Strassmann JE, Hughes CR (1993). Microsatellites and kinship. Trends in Ecology and Evolution, 8:285-288.

Rachlow JL, Berger J (1998). Reproduction and population density: trade-offs for the conservation of rhinos in situ. Animal Conservation 1:101-106.

Rachlow JL, Berkeley EV, Berger J (1998). Correlates of male mating strategies in white rhinos *(Ceratotherium simum*). Journal of Mammalogy 79:1317-1324.

Rachlow JL, Bowyer RT (1998). Habitat selection by Dall´s sheep (*Ovis dalli*): maternal trade-offs. Journal of Zoology, London 245:457-465.

Rachlow JL, Kie JG, Berger J (1999). Territoriality and spatial patterns of white rhinoceros in Matobo National Park, Zimbabwe. African Journal of Ecology 37:295-304.

Rasmussen LEL, Schulte BA (1998). Chemical signals in the reproduction of Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants. Animal Reproduction Science 53, 19-34.

Rieches R (1998). Concerns with breeding F1 white rhinoceros in zoological institutions. Paper presented at workshop on problems associated with the low rate of reproduction among captive-born female southern white rhinoceros, 29-31 October, San Diego.

Robbins CT (1983). Wildlife feeding and nutrition. Academic Press, New York.

Robinson JA, Scheffler G, Eisele SG, Goy RW (1975). Effects of age and season on sexual behaviour and plasma testosterone and dihydrotestosterone concentrations of laboratory-housed male rhesus monkeys (*Macaca mulatta*). Biology of Reproduction 13:203-210.

Rookmaaker K (2000). The alleged population reduction of the southern white rhinoceros (*Ceratotherium simum simum*) and the successful recovery. Säugetierkundliche Mitteilungen 45: 55-70.

Rose RM, Gordon TP, Bernstein IS (1972). Plasma testosterone levels in the male rhesus: influences of sexual and social stimuli. Science 178:643-645.

Rose RM, Holaday JW, Bernstein IS (1971). Plasma testosterone, dominance rank and aggressive behaviour in male rhesus monkeys. Nature 231:366-368.

Roth T, Patton L, Brown J, Czekala N, Swaisgood R, Lance V (1998). The north American experience: female hormonal cycles in southern white rhinoceros. Paper presented at workshop on problems associated with the low rate of reproduction among captive-borne female southern white rhinoceros (*Ceratotherium simum simum*), 29-31 October, San Diego.

Roth TL, O´Brien JK, McRae MA, Bellem AC, Romo SJ, Kroll JL, Brown JL (2001). Ultrasound and endocrine evaluation of the ovarian cycle and early pregnancy in the Sumatran rhinoceros, *Dicerorhinus sumatrensis*. Reproduction 121:139-149.

Rubenstein DI (1986). Ecology and sociality in horses and zebras. In: Rubenstein DI, Wrangham RW (eds) Ecological aspects of social evolution in birds and mammals. Princeton University Press, Princeton New Yersey, pp 282-302.

Ruiz-de-la-Torre JL, Manteca X (1999). Effects of testosterone on aggressive behaviour after social mixing in male lambs. Physiology & Behavior 68:109-113.

Sanford LM, Palmer WM, Howland BE (1974). Influence of sexual activity on serum levels of LH and testosterone in the ram. Canadian Journal of Animal Science 54:579-585.

Sapolsky RM (1993). The physiology of dominance in stable versus unstable social hierarchies. In: Mason WA, Mendoza SP (eds) Primate social conflict, State University Press, New York, pp 171-204.

Schaffer N, Bryant W, Agnew D, Meehan T, Beehler B (1998). UItrasonographic monitoring of artificially stimulated ejaculation in three rhinoceros species (*Ceratotherium simum, Diceros bicornis, Rhinoceros unicornus*). Journal of Zoo and Wildlife Medicine 29:386-393.

Schenkel R (1966). Zum Problem der Territorialität und des Markierens bei Säugern- am Beispiel des schwarzen Nashorns und des Löwens. Zeitschrift für Tierpsychology 23:593-626.

Schmidt C (1995). Verhaltensbiologische Untersuchungen an Breitmaulnashör*nern (Ceratotherium simum simum* Burchell, 1817) im Allwetterzoo Münster. Diplom thesis Westfälische Wilhelms-Universität Münster.

Schreiber A, Kolter L, Kaumanns W (1995). Conserving patterns of genetic diversity in endangered mammals by captive breeding. In: Gansloßer U, Hodges JK, Kaumanns W (eds) Research and captive propagation. Filander Verlag, Fürth, pp 10-23.

Schwartz CC, Renecker LA (1998). Nutrition and energetics. In: Franzmann AW, Schwartz CC (eds) Ecology and management of the North American moose. Smithsonian Institution Press, Washington, pp 441-478.

Schwarzenberger F, Francke R, Göltenboth R (1993). Concentrations of faecal immunoreactive progestagen metabolites during the oestrus cycle and pregnancy in the black rhinoceros (*Diceros bicornis*). Journal of Reproduction and Fertility 98:285-291.

Schwarzenberger F, Tomášová K, Holečková D, Matern B, Möstl E (1996). Measurement of faecal steroids in the black rhinoceros (*Diceros bicornis*) using group-specific enzyme immunoassays for 20-oxo-pregnanes. Zoo Biology 15:159-171.

Schwarzenberger F, Walzer C, Tomášová K, Vahala J, Meister J, Goodrowe KL, Zima J, Strauß G, Lynch M (1998). Faecal progesterone metabolite analysis for non-invasive monitoring of reproductive function in the white rhinoceros (*Ceratotherium simum*). Animal Reprodution Science 53:173-190.

Schwarzenberger F, Walzer C, Tomášová K, Zima J, Göritz F, Hermes R, Hildebrandt TB (1999). Can the problems associated with low reproductive rate in captive white rhinoceroses (*Ceratotherium simum*) be solved within the next 5 years? Verhandlungsberichte zu Erkrankungen der Zootiere 39:283-289.

Schwarzenberger F, Walzer C, Weiss R, Pucher HE, Leus K, Bircher P, Moran JF (2000a). Faecal cortisol metabolites in response to management practices and disturbance in different herbivores and carnivores (*Ceratotherium simum, Diceros bicornis, Elephas maximus, Loxodonta africana, Okapia johnstoni, Rupicapra rupicapra and Lutra lutra*. European Association of Zoo and Wildlife Veterinarians, 3rd scientific meeting, Paris, France.

Schwarzenberger F, Rietschel W, Vahala J, Holeckova D, Thomas P, Maltzan J, Baumgartner K, Schaftenaar W (2000b). Faecal progesterone, oestrogen, and androgen metabolites for noninvasive monitoring of reproductive function in the female Indian rhinoceros. General and Comparative Endocrinology 119:300-307.

Searcy WA, Yasukawa K (1983). Sexual selection and red-winged black-birds. American Scientist 71:166-174.

Sneddon LU, Huntingford FA, Taylor AC (1997). Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). Behavioral Ecology and Sociobiology 41:237-242.

Sneddon JC, Argenzio RA (1998). Feeding strategy and water homeostasis in equids: The role of the hind gut. Journal of Arid Environments 38:493-509.

Spinks AC, Van der Horst G, Bennett NC (1997). Influence of breeding season and reproductive status on male reproductive characteristics in the common mole-rat*, Cryptomys hottentotus hottentotus*. Journal of Reproduction and Fertility 109:79-86.

Tainton NM (1988). Veld and pasture management in South Africa. Shuter & Shooter, Pietermaritzburg.

Thompson KV, Monfort SL (1999). Synchronisation of oestrous cycles in sable antelope. Animal Reproduction Science 57:185-197.

Tinbergen N (1973). Ethologie. In: Das Tier in seiner Welt. Piper, München.

Todd IA (1993). Wildtrak. Non-parametric home range analysis for the Macintosh. User guide. ISIS Innovation Ltd, Oxford, UK.

Torre I, Bosch M (1999). Effects of sex and breeding status on habitat selection by feral house mice (*Mus musculus*) on a small Mediterranean island. Zeitschrift für Säugetierkunde 64:176-186.

Trivers RL (1972). Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man. Aldine-Atherton, Chicago, pp 136-179.

Trollope WSW, Potgieter ALF, Zambatis N (1989). Assessing veld condition in the Kruger National Park using key grass species. Koedoe 32:67-93.

Underwood R (1982). Vigilance behaviour in grazing African antelopes. Behaviour 79:81-107.

Valdimarsson SK, Metcalfe NB (2001). Is the level of aggression and dispersion in territorial fish dependent on light intensity? Animal Behaviour 61:1143-1149.

van Ballenberghe V, Ballard WB (1998). Population dynamics. In: Franzmann AW, Schwartz CC (eds) Ecology and management of the North American moose. Smithsonian Institution Press, Washington, pp 223-245.

van Coeverden de Groot P, D`Avila Garcia J, Kellner K, Boag P. (2001). Investigation into the power of microsatellites to assign parentage in the white rhino (*Ceratotherium simum*)- A case study with 10 loci. Paper presented at the 8th International Theriological Conference, Sun City.

Van Horne B (1983). Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

van Oudtshoorn F (1992). Guide to grasses of South Africa. Briza Publikasies Cc, Cape Town.

van Rooyen N, Theron GK (1996). Habitat evaluation. In: Bothma JduP (ed) Game ranch management. 3rd ed. JL van Schaik Publishers, Pretoria, pp 74-77.

van Rooyen N, Bredenkamp GJ, Theron GK (1996). Veld management. In: Bothma JduP (ed) Game ranch management. 3rd ed. JL van Schaik Publishers, Pretoria, pp 539-572.

Van Soest PJ (1996). Allometry and ecology of feeding behaviour and digestive capacity in herbivores: A review. Zoo Biology 15:455-479.

van Wyk P (1994). Field guide to trees of the Kruger National Park. 3rd ed. Struik Publishers (Pty) Ltd, Cape Town.

van Wyk B, van Wyk P (1997). Field guide to trees of southern Africa. Struik Publishers (Pty) Ltd, Cape Town.

Velloso AL, Wasser SK, Monfort SL, Dietz JM (1998). Longitudinal faecal steroid excretion in maned wolves (*Chrysocyon brachyurus*). General and Comperative Endocrinology 112: 96-107.

von Holst D (1998). The concept of stress and its relevance for animal behaviour. In: Møller AP, Milinski M, Slater PJB (eds) Stress and behavior. Academic Press, San Diego, pp 1-131.

Vos P, Hogers R, Bleeker M, Reijans M, van de Lee T, Hornes M, Frijters A, Pot J, Peleman J, Kuiper M, Zabeau M (1995). AFLP: A new technique for DNA fingerprinting. Nucleic Acids Research 23:4407-4414.

Wada M, Shimizu T, Kobayashi S, Yatani A, Sandaiji Y, Ishikawa T, Takemure E (1999). Behavioural and hormonal basis of polygynous breeding in male bush warblers (*Cettia diphone*). General and Comparitive Endocrinology 116:422-432.

Wasser SK, Waterhouse ML (1983). The establishment and maintenance of sex biases. In: Wasser SK (ed) Social behavior of female vertebrates. Academic Press, New York, pp 19-35.

Wasser SK, Thomas R, Nair PP, Guidry C, Southers J, Lucas J, Wildt DE, Monfort SL (1993). Effects of dietary fibre on faecal steroid measurements in baboons *(Papio cynocephalus cynocephalus*). Journal of Reproduction and Fertility 97:569-574.

Wasser SK, Hunt KE, Brown JL, Cooper K, Crockett CM, Bechert U, Millspaugh JJ, Larson S, Monfort SL (2000). A generalised faecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. General and Comparative Endocrinology 120:260-275.

Watson DM, Dawson TJ (1993). The effects of age, sex, reproductive status and temporal factors on time-use of free-ranging red kangaroos (*Macropus rufus*) in western New South Wales. Wildlife Research 20:785-801.

White GC, Garrott RA (1990). Analysis of wildlife radio-tracking data. Academic Press Inc, New York.

Wildt DE (1996). Male reproduction: assessment, management, and control of fertility. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S (eds) Wild mammals in captivity. The University of Chicago Press, Chicago, pp 429-450.

Wingfield JC (1984). Androgens and mating systems: testosterone-induced polygyny in normally monogamous birds. Auk 101:665-671.

Wingfield JC, Hegner RE, Dufty AM, Ball G (1990). The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. American Naturalist 136: 829-846.

Wofford H, Holechek JL, Galyean ML, Wallace JD, Cardenas M (1985). Evaluation of faecal indices to predict cattle diet quality. Journal of Range Management 38:450-454.

Wörner M, Siepert H-P (1997). Stickstoff-/Proteinbestimmung in Futtermitteln. Labor Praxis 11:1-3.

Zar JH (1996). Biostatistical analysis. 3rd ed. Precentice Hall, New Jersey.

Ziegler T, Hodges K, Winkler P, Heistermann M (2000). Reproductive seasonality in wild female hanuman langurs (*Presbytis entellus*). American Journal of Primatology 51:119-134.

Zimmerman I (1980). Predicting diet quality from measurement of nitrogen and moisture in cattle dung. South African Journal of Wildlife Research 10:56-60.

CURRICULUM VITAE OF PETRA KRETZSCHMAR

Date of birth:	January 21, 1969
Place of birth:	Berlin
Nationality:	German

Education

June 1988:
Graduation from High School in Berlin (Abitur)

University

Basic studies	October 1988 - April 1989: Studies at the „Technische Universität Berlin“ Subjects: biology and chemistry (teaching profession)
	April 1989 - October 1991: Basic studies at the „Freie Universität Berlin“ Subject: biology (diploma)
Intermediate exams (Vordiplom)	October 1991 Average mark: 1.0 (highest possible rank)
	October 1991 – July 1994 Main studies at the „Freie Universität Berlin“ Main subjects: behaviour and ecology
Diplom thesis:	October 1994 - March 1995 Field research at the Department of Zoology, Melbourne University, Australia
	Subject of the thesis: „Home range, habitat selection and group size of female eastern grey kangaroos, *Macropus giganteus* Shaw“
Final exams (Diplom)	December 1995 Average mark: 1.0 (highest possible rank)
	Subject of exams: animal physiology and behaviour, ecology, morphology of plants

Petra Kretzschmar, Keltererweg 42, 13595 Berlin
Tel: 030/3623402, Fax: 030/3615278, email: petra.kretzschmar@gmx.de

PhD thesis	March 1997- March 1999 Field work on a private game farm in the Limpopo Province, South Africa Subject of the work: "Ecological, endocrinological and ethological investigations of female mate choice in free-ranging white rhinoceros (*Ceratotherium simum simum*)"
Sponsorship:	- „Deutscher Akademischer Austauschdienst“ (DAAD) -„Fazit Stiftung, gemeinnützige Verlagsgesellschaft mbH“
Cooperating partners:	- Institute for Zoo Biology and Wildlife Research Berlin: Dr. M. Dehnhard, Dr. M. Lechner-Doll - Ludwig Maximilian Universität München: Dr. K. Kellner and Dr. B. Kiefer

Extra-curricular education

March - April 1992
Practical training in zoo-keeping at the Zoological Garden, Berlin

July - August 1992
Telemetric analysis of home range and habitat use of Lesser Spotted Eagles at the field station for nature conservation Teterow, Mecklenburg-Vorpommern, Germany.

March - April 1993
Field study in Equador sponsored by the DAAD analysing the songs and their relation to habitats of tropical birds at the biological field station Jatun Sacha, Ecuador

November 1999
Practical training in analysing faecal samples using enzyme-immunoassays at the Institute for Zoo Biology and Wildlife Research Berlin

June - July 2002
Identification and establishment of a data file for individual white rhinos at Manketti Game Reserve, Elisras

Ongoing projects:

- Project conducted in co-operation with Prof. K. Hodges, German Primate Institute, Göttingen:
Establishment of a non-invasive endocrine monitoring technique to assess stress hormone levels in the faeces and monitoring of stress and testosterone levels of two different rhino

populations: one group of males living without females, one group living together with females.

- Project conducted in co-operation with Dr. J. Fickel, Institute for Zoo Biology and Wildlife Research Berlin: Assessing the genetic variability of white rhinoceros living today and at the change of the 19th century.

Languages

German: native speaker
English: good, written and spoken
Afrikaans: basic knowledge

Computer skills

very good

Publications and conference proceedings

KRETZSCHMAR P (1996): Wird die Gruppengröße von Östlichen Grauen Riesenkänguruhs (*Macropus giganteus* Shaw) an die Umwelt angepaßt? In: Deutsche Gesellschaft für Säugetierkunde (ed), Sonderheft der Zeitschrift für Säugetierkunde, 70. Jahrestagung Kiel. Gustav Fischer Verlag, Jena: 30-31.

KRETZSCHMAR P, GUMBERT A & GANSLOßER U (1997): Influence of habitat transparency on grouping in eastern grey kangaroos (*Macropus giganteus*). In: Taborsky M & Taborsky B (eds.) Advances in Ethology 32 (Ethology Suppl.); Contributions to the 25. International Ethological Conference, Vienna: 267.

KRETZSCHMAR P (1998): Rhinofarming. In: Gerhardt-Dircksen A, Jungbauer W, Rottländer E, Scharf K-H (eds) Praxis der Naturwissenschaften, Biologie. Aulis Verlag Deubner & Co KG, Köln: 17.

KRETZSCHMAR, P (2000): Territoriales Verhalten von männlichen Breitmaulnashörnern (*Ceratotherium simum simum*) unter Bedingungen geringer Populationsdichte. In: Deutsche Gesellschaft für Säugetierkunde (ed), Sonderheft der Zeitschrift für Säugetierkunde, 74. Jahrestagung Groningen.

KRETZSCHMAR P, GANSLOßER U, JEWGENOW K, DEHNHARD M (2000) : Non-invasive measurement of faecal testosterone metabolites revealed seasonality in free-living male white rhinoceros, *Ceratotherium simum simum*. In: Lechner-Doll M & Hofer H (eds) Advances in Ethology 35 (Ethology Suppl.); Contributions to the 3. International Symposium on Physiology and Ethology of Wild and Zoo Animals. Blackwell Science: 92.

KRETZSCHMAR P, GANSLOßER U, DEHNHARD M (2001): Androgen analysis as a possible measure to increase breeding success in white rhinoceros. Paper presented at the 8. International Theriological Congress, Sun City, South Africa.

KRETZSCHMAR P (2002): Population growth, sex ratio and reproduction of a natural living population of white rhinoceros.In: Schwammer HM, Foose TJ, Fouraker M, Olson D (eds). A research update on

elephants and rhinos. Proceedings of the International elephant and rhino research symposium, Vienna, June 7 – 11, 2001. Schüling Verlag, Münster: 196-201.

KRETZSCHMAR P, GANSLOßER U, GOLDSCHMID A, ABERHAM A (2002): Stimulation of teritorial and mating behavior by fecal samples. A comparitive study on behavior of captive and free-living white rhinoceros. In: Schwammer HM, Foose TJ, Fouraker M, Olson D (eds). A research update on elephants and rhinos. Proceedings of the International elephant and rhino research symposium, Vienna, June 7 – 11, 2001. Schüling Verlag, Münster: 299-302.

KRETZSCHMAR P, GANSLOßER U, DEHNHARD M (subm.): Relationship between Androgens, Environmental Factors and Reproductive Behavior in Male White Rhinoceros (Ceratotherium simum simum).

KRETZSCHMAR P, DEHNHARD M, GANSLOßER U, KELLNER K, LECHNER-DOLL M (2002): Ecological and endocrinological investigations of female mate choice in free ranging white rhinoceros (*Ceratotherium simum simum*). In: Dehnhard M, Hofer H (eds.) 4th International Symposium on physiology and ethology of wild and zoo animals. Blackwell Verlag, Berlin: 48.

KELLNER K, KRETZSCHMAR P, FÖRSTER M (2002): AFLP as an economical method to correct field observations for genetic wildlife management in rhinoceros. In: Schwammer HM, Foose TJ, Fouraker M, Olson D (eds). A research update on elephants and rhinos. Proceedings of the International elephant and rhino research symposium, Vienna, June 7 – 11, 2001. Schüling Verlag, Münster: 183-189.

KIEFER B, WICHERT B, GANSLOßER U, KRETZSCHMAR P, KIENZLE E (2002): Digestibility trials in the zoo compared to field studies of white rhinoceros. In: Schwammer HM, Foose TJ, Fouraker M, Olson D (eds). A research update on elephants and rhinos. Proceedings of the International elephant and rhino research symposium, Vienna, June 7 – 11, 2001. Schüling Verlag, Münster: 190-195.

KIEFER B, GANSLOßER U, KRETZSCHMAR P, KIENZLE E (in press): Food quality of free-ranging and captive male white rhinoceros (*Ceratotherium simum simum*) with special emphasize on food selection. In: Fidgett A (ed), European Zoo Nutrition II. Filander Verlag, Fürth.

KOLAR D, KRETZSCHMAR P, GANSLOßER U (2002) Do urinary scent marks influence behaviour of male and female white rhinoceros (*Ceratotherium simum simum*)? In: Dehnhard M, Hofer H (eds.) 4th International Symposium on physiology and ethology of wild and zoo animals. Blackwell Verlag, Berlin: 46.

Hiermit erkläre ich, daß diese Arbeit bisher von mir weder an der Mathematisch-Naturwissenschaftlichen Fakultät der Ernst-Moritz-Arndt-Universität Greifswald noch einer anderen wissenschaftlichen Einrichtung zum Zwecke der Promotion eingereicht wurde.
Ferner erkläre ich, daß ich diese Arbeit selbständig verfaßt und keine anderen als die darin angegebenen Hilfsmittel benutzt habe.

Petra Kretzschmar