GARAÏ, MARION ELIZABETH

The development of social behaviour in translocated juvenile African elephants *Loxodonta africana* (Blumenbach)

PhD UP 1997

The development of social behaviour in translocated juvenile African elephants *Loxodonta africana* (Blumenbach)

by

Marion Elizabeth Garaï

Submitted in partial fulfillment of the requirements
for the degree of Philosophiae Doctor

in the faculty of Biological and Agricultural Sciences
University of Pretoria
Pretoria

1997

To the most wonderful creatures, the elephants,
but especially to those in this study
that shared a part of their private lives with me.

"If I learned anything from my time among the elephants, it is the extent to which we are kin. The warmth of their families makes me feel warm. Their capacity for delight gives me joy. Their ability to learn and understand things is a continuing revelation for me. If a person can't see these qualities when looking at elephants, it can only be because he or she doesn't want to."

Douglas H. Chadwick THE FATE OF THE ELEPHANTS 1992

ABSTRACT

The development of social behaviour in translocated juvenile African elephants *Loxodonta africana* (Blumenbach)

by
M. E. Garaï

Supervisors: Prof. A. S. van Jaarsveld and
Dr P. R. K. Richardson

Department of Zoology & Entomology
University of Pretoria
Pretoria

Groups of translocated orphaned juvenile African elephants were studied in holding pens and following their release to assess how they re-organize and restructure socially by adopting roles, and if they show behavioural signs of stress. An adult female adopted a young individual. In all groups allomothering was observed to some degree. One 5 year old female prematurely assumed the role of leader and this role appears to be learned. Most groups established a linear dominance hierarchy.

Placing the trunk tip into a partner's mouth correlated with play-fighting and aggression. This behaviour is suggested to be one of appeasement to reduce aggressive motivation and prevent escalation thereof, and that the behaviour is ritualised. Four possible evolutionary steps are presented.

Nearest Neighbour analyses illustrated the changing social positions of some juveniles relative to other individuals. Tight grouping was assumed to indicate insecurity. There was a marked difference in behaviour pattern during resting times. Groups without adults were within touching distance of one another whilst resting. In a group containing an adult female some juveniles dispersed more and some juveniles formed a subgroup. It appears that dominance hierarchies, individual social relationships and caretaking of young were important factors which affected group cohesion and could influence a more central position within a group.

Certain behaviour patterns were defined as being stress related and compared among the groups. There was a significant decrease in arousal behaviour after the introduction of an adult female. Aggressive behaviour was the most frequent behaviour in four groups whilst penned and following their release. Play behaviour was absent in three penned groups, and tended to gradually increase following the release. Temporal gland secretion occurred during excitement, anticipation and nervousness. Secretion occurred in all age and sex classes. Females tend to secrete more frequently than males and older individuals more than younger ones.

Frustrated or stressed animals vocalized more frequently than relaxed ones, as did calves below 2 years of age who tended to use louder calls, than older juveniles. Acoustical analyses of four vocalizations are presented. Very young individuals appear to vocalize using marginally higher frequencies.

ACKNOWLEDGEMENTS

Many people in Switzerland and South Africa provided moral support, financial assistance, friendship and a home and without them this study could not have been conducted.

Above all I would like to thank my husband Hans Schatzmann for his unerring moral support in all these years. He never complained once although he had to live without me for five years.

My deep-felt gratitude to my mother, who 'sacrificed' her daughter to the elephants, but always encouraged and supported me in my endeavours, and to the rest of my family and friends in Switzerland, especially Monika Schiess-Meier who provided me with software and literature from Switzerland. Professor Hans Kummer tought me the analytical and critical ways of ethological thinking and I am very grateful for the solid background he supplied.

In South Africa I would sincerely like to thank and acknowledge the following people and institutions:

My supervisor Professor Albert van Jaarsveld for his tremendous support and helpful comments on the manuscript and my co-supervisor Dr PRK Richardson for his help and for making the radio collars and providing the tracking equipment. Clive Walker and Dr Anthony Hall-Martin for their invaluable help, trust and for their support when the study seemed destined to be grounded.

Mashatu Game Reserve for providing free accommodation and a vehicle and petrol. Thornybush Game Lodge and Rhinoland Safaris, for providing free accommodation and allowing me to study their elephants. Touchstone Game Ranch for providing a home during part of the study period and the permission to study the elephants. Venetia Limpopo Nature Reserve for providing three wonderful years in the bush and help with petrol. I would like to thank the National Parks Board for permission to study the elephants at Skukuza, for accommodation in the research camp and for allowing me to observe the culling operations, Kaia Ingwe and Knysna Forestry Department for the permission to study their elephants for a few days. A special thank you to Mokolo River Nature Reserve for permission to study the elephants and for giving me a wonderful home not only during the observation period, but also throughout the entire time of writing this thesis.

The Rhino & Elephant Foundation for providing the much needed vehicle as well as the running costs for 5 years, a Macintosh laser printer and other financial assistance throughout the study. The David Shepherd Foundation UK and RSA for donation of the professional DAT recording equipment.

The Mammal Research Institute for the camping equipment. The Department of Communication Pathology for the use of the speech laboratory. ISM South Africa for donating an IBM Laptop and printer. IFAW for donating a Macintosh Power PC. "Rettet die Elefanten Afrika's e.V." in Hamburg for financial assistance. TOTAL South Africa for financial assistance. The Office of the President of Botswana for permission to study the elephants at Mashatu.

Johan Theron of Timbre Audio Systems for his valuable help with the recording equipment. Melanie Shepherd for her tremendous input in the UK to locate and purchase the recorder and microphone. Sue Downy and Lucky Mavrandonis for their enthusiastic help and financial support in obtaining the recording equipment. Dr Emily Groenewald for her invaluable help and input with the many hours of analyses of the tapes on the Sonograph. Belinda Reyers for her help with the PCA. Dr Richard Burroughs for his sensitive approach during darting and collaring of the elephants. Dr Cobus Raath for inviting me to the Kruger cull, his help with accommodation and permission to collect data at the Skukuza bomas.

Many people helped me find a new home in South Africa and provided friendship and moral support during the study. My warmest thanks go out to all but in particular to: Heide Bär, Nicholeen Briers, Heather Cowie, Merry and Nigel Fairhead, David Methven, and Pete le Roux.

Many friends helped with accommodation during my stays in Pretoria and Johannesburg, provided friendship and generally made me feel at home in South Africa, I am grateful to all, especially to Karina and Hans Becker, the late Rowena and Dan Bregman, Athalie Brett, Audrey and Dr Hym Ebedes, Amanda and Anthony Irving, Peggy and Harry Parham, the late Tanno Schild, the late Gerald Tracy and Bets Wappenaar.

TABLE OF CONTENTS

Content **Page**

CHAPTER 1

INTRODUCTION

African elephants have highly advanced, intricate social systems (Wilson 1975). They live in stable family units which are led by the eldest female (Douglas Hamilton 1972; Moss & Poole 1983; Moss 1976,1988). The social structure of this unit is matriarchal and young males leave the family unit during puberty between 9 and 15 years and form loose bachelor herds (Hanks 1979; Short, Mann & Hay 1967; Douglas-Hamilton 1972). The females remain in their family units and form life-long bonds. Strong ties are also found between various family units (Moss 1981, 1988; Moss & Poole 1983). Bonding ensures co-operation, which is necessary for group defence (Sikes, 1971; Douglas-Hamilton and Douglas-Hamilton 1975), leadership, locating food resources (Laws, Parker & Johnstone 1975; Hanks 1979) and raising calves (Lee 1987).

The matriarchs have the longest environmental and social knowledge which they pass on to their offspring during the long periods of development and socialisation. The matriarchs also carry a heavy responsibility towards the family unit; they make all the decisions concerning daily and seasonal movements, lead and defend the group. Being a long-lived species with long gestation and intercalving periods and only a single young being produced, elephants have to invest heavily in the offspring. Therefore, females with calves tend to stay together and co-operate in raising their young. When there is more than one female to look after the young their survival chances are increased (Lee 1987). These females are frequently older siblings of the calf (Lee 1987). Caretaking of young by females other than the mother is well known among social mammals (Riedman 1982; Gittleman 1985) and has been termed allomothering behaviour (Lee 1987; Nicholson 1987).

Since the eighties and particularly during the first half of the nineties, juvenile elephants ranging from about 2 - 12 years of age, were captured during the annual culling operations in the Kruger National Park and sold in groups of similarly aged conspecifics, which were probably unrelated. These juveniles spent some time in holding pens (boma) in the Kruger National Park and were then translocated onto various private or other state reserves. Here they again spent some time in a boma in order to acclimatise and calm down, after which they were released onto the reserve. The confinement period also served to help them form social relationships within a group.

Rowell (1972 in Van Schaik & Van Hooff 1983) made the distinction between: *social organization* and *social structure.* The former 'consists of the process of social interaction and their patterns of distribution among group members' (i.e. the social relationships), and the latter 'is the composition of the group and the spatial patterns of individuals' (group cohesion and group size). The social organization is the instrument used by individuals to achieve the social structure in which the three primary interests are best served, namely feeding, predation avoidance and reproduction (Van Schaik & Van Hooff 1983).

The principle aims of the present study were to assess how these juveniles would organize themselves and how they would build a social structure. Would the juveniles show any form of bonding by forming special relationships among two individuals (Garaï 1989, 1992), adhere to rules of a dominance hierarchy and adopt specific roles (Bernstein & Sharpe 1966). Had the juveniles already acquired the social instrumentation and the structural basis necessary for all subsequent behavioural development (Mason 1979), to form a functional cohesive group that would optimise feeding and antipredation strategies in order to eventually reproduce and maximise their fitness. Given the long period of childhood and adolescence found in elephants one would assume that much has to be learned during this period. A greater genetical scope for learning implies greater behavioural plasticity and through this increased adaptability (Mason 1979), which brings with it a loss of phylogenetic 'wisdom'. This means there is greater demand on individuals to construct their own history through learning and experience (Mason 1979). Each society is made up of a specific set of roles which have to be learned. However, not only individual dispositions and personal histories, but also disposition and history of other group members will influence these roles. For example, a leader is a leader not only because of its own intrinsic properties, but because others follow (Hinde 1969).

The results of a principal component analysis (PCA) conducted after the study revealed that it was not feasible to adopt an experimental approach towards the analyses. Therefore general factors involved in the development of behaviour of the different study groups could not be assessed using methods other than a fundamental descriptive approach.

An additional aim of the present study was to investigate whether translocated juveniles suffered undue stress. Predictability and controllability of the social environment and social events is an important feature of an individual's coping strategy (Tennessen 1989; Sachser & Lick 1991). Loss of these two psychological instruments can lead to acute or chronic stress. All social mammals can discriminate between familiar and alien conspecifics and in early childhood familiar conspecifics become objects of attachment and loosing such objects causes distress (Bischof 1975). As has been shown in infant monkeys, separation from the maternal group induces a physiological stress response and the formation of a new social group affects the immune and pituitary-adreno-cortical systems (Gordon *et al.* 1992 and Gust *et al.* 1991 in Gust, Gordon & Hambright 1993). The physiological stress response prepares the organism for reaction and enables it to retain a homeostatic balance by releasing the appropriate hormones such as adrenaline or glucocorticoids. The stress response can be triggered by a stressor (physical e.g. aggression from a partner), or by the mere expectation of it (psychological e.g. expecting aggression from the partner) (Sapolsky 1990). It has been suggested that social insecurity may be associated with higher stress levels and that social skilfulness (i.e. the ability to cope with a situation) improves with age (de Villiers, van Jaarsveld, Meltzer & Richardson 1996). It appears that the emotional manner in which an individual copes with stress is of great importance (Sapolsky 1990) and that this is frequently learned and developed with age and experience.

Familiarity with an environment can enhance coping strategies (Haemisch 1990). Thus, it follows from the above that any unfamiliar environment or enclosure (e.g. a boma) where events are unpredictable, will enhance stress.

Within a few minutes of capture these young juvenile elephants lost all familiar conspecifics, including the objects of greatest attachment, their mothers. They were placed into confinement together with unknown elephants, and social interactions and outcomes in the enclosure become largely unpredictable and uncontrollable. Moreover, social skilfulness of young juveniles is likely not to be as well developed as in older juveniles. It therefore seems trivial to suggest that these animals were experiencing extreme stress, fear and/or frustration.

Measurements of stress through hormonal assays can show that cortisol levels are elevated in stressed animals. However, recognising stress using behavioural elements and patterns is not quite as easy and has been largely avoided therefore. In the present study an attempt was made to define certain behaviour patterns that could be related to stress, and the author is fully aware of the dangers associated with allocating psychological requisites to elephants. However, there is today sufficient evidence that these are present in animals (Masson & McCarthy 1994; Arzt & Birmelin 1993) and scientific studies of emotions in chimpanzees and dolphins have been conducted (Buirski, Plutchik & Kellerman 1978).

In hormonal terms, any event or situation which induces the release of so-called stress hormones (adrenaline, glucocorticoids) is a stressor. Stress has however, not been defined explicitly in behavioural terms, except where visible physical signs can be associated with it (e.g. decreased physical condition, self afflicted injuries in caged animals). Aggression, fear, insecurity, unfamiliar surroundings, loss of family could induce a stress response from an animal. It has been shown that stress will lead to a reduction in variability and complexity of exploratory behaviour (Alados, Escos & Emlen 1996), because of an increase in metabolic rate and energy consumption. It seems reasonable to assume that there will also be a change in the complexity of the entire behavioural repertoire and that behaviour patterns not directly related to energy consumption or coping strategies, such as play, will be absent. It also logically follows that behaviours related to coping strategies such as ' the flight or fight syndrome', should be increased (e.g. signs and signals of fear, frustration and aggression). The only recorded visible sign of extreme stress in elephants, based on anecdotal evidence only, is the secretion of the temporal gland (Adams, Garcia & Foote 1978; Buss, Rasmussen & Smuts 1976; Hall-Martin & van der Walt 1984). In the present study data on temporal gland secretion and the context in which it occurred were analysed, as well as changes in secretion over time, in order to assess whether it can in fact be used as sign of stress.

CHAPTER 2

STUDY GROUPS AND METHODS

1. STUDY GROUPS

The study animals are presented with details on their established history. Most of the juveniles had been captured and translocated during the annual culling operations in the Kruger National Park. With the exception of the elephants at Mokolo, who originated from the same family unit, all other individuals were most likely unrelated and originated from different family units and different areas in the park. The adult female Jane at Venetia and some of the elephants at Thornybush came from the culling operations at Hwange National Park in Zimbabwe. In each study group an individual was radio-collared to facilitate daily location. All ages provided are estimates based on the given heights after Laws (1966).

Venetia Limpopo Nature Reserve (VLNR) 1991, Boma

Observation period: 2 Nov - 21 Dec 1991 (Total recording time : 113 hrs 40 min)

Study animals: Bloukop (B), female, ca. 11 years; Skerptand (S), female, ca 10 years; Cheeky (Ch), female, ca. 10 - 11 years; Poot (P), female ca. 10 years; Reverse (R), male, ca. 9 - 10 years, Eentand (E), male, ca. 8 years.

The Boma:

Four crosswise adjacent wooden pens, 25 m X 25 m, were fitted with steel sliding gates. The wooden vertical poles were placed 50 cm apart, with concreted steel poles every five meters, reinforced with 7 horizontal cables, so that the elephants could interact in adjacent pens. There was a water trough in each pen and the centre section where the four corners met, was covered with shade cloth. Adjacent to two of the pens there was a 50 m X 300 m paddock with a mesh wire fence, 5 horizontal steel cables and three electrified wire strands. A large mudwallow was available. The elephants were free to walk into the pens whenever they wished, but they only went inside for feeding and drinking. They were fed pellets and Lucerne twice a day, as the natural browse in the boma was depleted. Data were only recorded in the outside enclosure for this group. One female (Ch) was fitted with a radio collar before their release. The elephants had already been in the boma for 4 months when observations started.

When the boma gates were opened, two of the females (Ch and P) wandered off on their own and settled in the eastern side of the reserve, where they stayed until 1994. The other four elephants stayed in the western side and joined up with the new elephants in 1992 (see further). Unfortunately the radio transmitter only had a range of 500m, making it nearly impossible to locate the two elephants in the then 20 000 ha reserve. I only found them 9 times in five months. During 1992 more elephants were acquired and I discontinued looking for the two females.

Venetia Limpopo Nature Reserve 1992 Boma

Four groups of elephant arrived and were kept in the four pens (see above for boma details). Groups A and B had alternate access to the 2 ha sized paddock.

Group A: (arrived on 21 May 1992) 4 females, aged about 6 - 7 years: Stompie (St), Lady (L), Kopseer (K), Rosy (Ro). One female? (Houdini) broke out of the truck on arrival and was later seen to have joined the two females Ch and P on the reserve. Total observation time: 56 h 40 min.

Group B: (arrived on 26 May 1992) 3 males, 5 females, aged about 4 - 5 years: Ajax(A), Sam (Sa), Goliath (G), Dumbo (D), Tertia (T), Langtand (Lt), Mouse (M), Baby (Ba).

Female D was fitted with a radio collar on 21 July 1992. Total observation time 46 h 25 min.

Group C: (arrived on 26 June 1992) 5 males aged about 2.5 - 3.5 years: Fold (F), Long-lip (Ll), Two-bumps (Tb), Bubbles (Bb), Squeak (Sq). Total observation time: 11h.

Group D: (arrived on 28 June 1992) 5 males aged about 18 months - 2 years: Tracy (T), Notch (N), Big-ears (Bg), Snare (Sn), Rumble (Ru). Total observation time: 26 h 40 min.

Sn had a snare wound on his leg on arrival and he, together with Bg as company, were sent to the Veterinary Institute at Onderstepoort for two months after the other elephants were released from the boma. The three others were resold and went to Stockley Trained Animal Consultants in Natal for further translocation. Ru did not survive the trip to Natal during which the elephants had been in the crates for too long. One male went to Randall Moore in Botswana and the other to the Pinnawela Zoo in Colombo, Sri Lanka. Bg and Sn were released from the boma at the same time as the two adult females from Zimbabwe in 1993. The two males eventually joined up with the three females on the eastern side of the reserve.

Jane: (arrival 7 July 1992) from Zimbabwe where she had been hand raised as an orphan from the Hwange culling operations. She was about 18 years old. Jane was penned with group C for one week, then together with group C and B for a month before they were released from the boma on 17 August. Group A was released on 15 July 1992. Jane and the thirteen juveniles spent three weeks near Regina dam in a small woodland of about 1 km in length and about 200 m width. After that they were found to have joined up with group A and the four elephants from the 1991 release. The group of now 22 elephants stayed in the North Western section of the reserve (Melisande, Patricia, Flora) until the northern perimeter fence was removed in 1994, which extended the reserve to 35 000 ha. In 1993 tracks indicated that they moved around during the night, extending their range into the North Eastern sections.

In November 1993 two adult females were acquired from Gonarezhou Game Reserve in Zimbabwe. They joined the group soon after their release. The youngest male (Sq) had died between December 1993 and the beginning of February 1994. On 28 March 1993 the young male F was darted and fitted with a radio collar, as the transmitter on female D's collar had ceased to function.

Venetia Limpopo Nature Reserve (VLNR) 1992-1994, free-ranging

The reserve: is situated in the northern parts of the Northern Province, near the Limpopo valley. Fourteen different vegetation types have been identified (O'Connor 1991) for the reserve. The main vegetation types are *Colophospermum mopane* woodland and *Colophospermum mopane* shrub with riverine woodland along the dry river beds. There are several dams on the reserve with water all year round.

Data were divided into four observation periods:

Period I 14 Sep - 20 Nov 1992 (Total obs time: 146 hrs 50 min)
Period II 8 Apr - 19 Jul 1993 (Total obs time: 179 hrs 25 min)
Period III 15 Jan - 21 May 1994 (Total obs time: 93 hrs 25 min)
Period IV 2 Feb - 1 May 1994 (Total obs time: 96 hrs 20 min)
Additional observation were done from 18 June - 18 August 1994 (Total obs. time: 40 hrs 25 min).

On 8 May 1994 a family unit comprising 14 elephants (12 females, two males) were acquired from the Kruger National Park. One large female and her offspring joined Jane's group, the other group stayed in close proximity and occasionally joined up with Jane's group. At about the same time the two females from 1991 (Ch and P) joined up with Jane. The remaining three elephants (H, Bg, Sn) were seen alone by the game guards, but it is likely that they eventually also joined the group. One very young individual of the new family unit died shortly after arrival. This family unit walked great distances in the beginning which may have been stressful for the juvenile. One of the females had been fitted with a radio collar during the Kruger National Park capture operations. Observations were continued but it became increasingly difficult to get near the elephants, as they had new born calves and the new adult females became very nervous and aggressive. The vegetation was dense after good rains and necessitated an approach of up to 15 - 20 m. Observations therefore had to be terminated for security reasons. In the following chapters only data up to the time when the new family group joined is presented (periods I - IV).

Touchstone Game Ranch

Study animals: 10 juveniles (4 females, 6 males) ranging between 4.5 - 7 years.
Females: Celeste (C) (probably the eldest), Kelly (K), Flora (F), Daba (D), Males: Babar (B), Arthur (A), Twiddles (T), Jason (J), Pom (P), Mickey (M).

The elephants were acquired in 1990 and had spent about 6 months in the boma before being released in December, initially into a 4000 ha section of the reserve, which was later extended to 7500 ha. They had reportedly repeatedly split into two groups but had formed one group after the first year. Despite an attempt to habituate them in 1991 this was not possible as no radio collar had been fitted. Observations only started in 1993 when female K was fitted with a radio collar in March.

The elephants had to be habituated and after 6 weeks I was able to start collecting data.

Data were divided into following observation periods:

Period I	19 Apr	- 29 Jul 1993	(Total recording time:	171 hrs 30 min)
Period II	1 Aug	- 29 Nov 1993	(Total recording time:	95 hrs 35 min)
Period III	15 Jan	- 21 May 1994	(Total recording time:	104 hrs 10 min)

The reserve is situated in the Waterberg region of the Northern Province. The vegetation is mixed sour veld (Acocks 1975). The one area where there was sweet veld at the foot of a hill (termed "amphitheatre") turned out to be a favourite area for the elephants.

Thornybush Game Lodge

7 Apr - 19 May 1992 (Total obs time: 37 hrs)

Study animals: Antenna (A), female, 15 years; Pregi (P), female, 13 - 14 years; One Tusk (O), female, 13 - 14 years; Big Boy (B), male, 13 - 14 years; Safari (S), male 4 years. The elephants had been together for many years (except the young male). Two cows and one bull originated from the Hwange National Park in Zimbabwe in 1985 (probably P, O and B), a further bull and female came from the Kruger National Park the same year (probably A and another male (R). The young male S also originated from Kruger in 1989. The second male (R) had broken into the adjacent Timbavati Reserve and was not in the group during observations. He was later killed by a bow-hunter as he had the habit of breaking into houses in search of oranges. Male S became a problem in 1996 and was sold to the Knysna Elephant Park in the Cape for training, where he died of food poisoning soon afterwards. All elephants had been habituated to humans and hand fed as young animals. It was therefore not a problem to follow them. All three females have had calves since the observations.

The reserve is located in the lowveld region near Hoedspruit and was 4500 ha at the time of the observations.

Spektakel Game Ranch

31 Aug - 16 Oct 1991 (Total obs time: 107 hrs)

Study animals: 3 females: Tara (T), Wrinkles (W), Inyani (I), 2 - 2.5 years; 3 males: Skukuza (S), Punda (P), Letaba (L), 3.5 - 4 years.

Boma: The 30 m X 50 m large pen was fenced with steel poles set 10 cm apart and contained a water trough and feeding troughs. The pen was open to a *ca.* 4.5 ha fenced in paddock, which contained a large dam where the elephants could bathe. The fence was wire mesh with three electrified wire strands. The elephants only went to the pen for feeding twice a day, where they were fed pellets. Natural browse, mainly acacia, was available in the paddock. They spent 6 months inside the paddock before being released onto the 7000 ha reserve. The reserve is in the sweet veld area of the Waterberg in the Northern Province. Observations were only done during the boma time and data were only taken from the paddock, not the pen. After a few days the elephants had habituated and I could observe them well from the outside through the fence. Male S died just prior to release, probably as a result of a snake bite.

Mokolo River Nature Reserve
Boma: 13 Jun - 24 Nov 1994 (Total obs time: 83 hrs 40 min)
Free: 20 Jan - 24 Oct 1995 (Total obs time: 249 hrs 45 min)

Study animals: The first group 2 females, Cheeky (Ch) and Baby-Reverse (B), and the male, Tiny (T), arrived in 1994 and were released after having spent six months in the boma.
The second group arrived on 12 June 1994. They originated from the same family group and were most likely related. The group consisted of two females, Raisin (R), aged about 5 years and Careful (C) aged about 4 - 5 years, and the male Peanuts (P) aged about 4 years. Female R was fitted with a radio collar in the boma. Unfortunately this collar fell off in January, shortly after the release, and the elephants had to be located by following their tracks. The first group had not been habituated to the observer and observations were carried out whenever they were encountered. As habituation could not be done on a daily basis very little data could be obtained from this group and therefore only data from the second group was used for analyses. The second group habituated to me during the boma period.

The boma consisted of a smaller and a larger paddock of about 2 ha in total, with an electrified fence. There was a stream in the smaller section and a mudwallow. The elephants were kept for a month in the smaller section, before the fence was opened to the larger section. They were also released after having spent five months in the boma on 24 November 1994.

The reserve is situated in the Waterberg with mixed vegetation. The Mogol river runs along one edge of the reserve.

Skukuza Boma
For two days in 1994 and one week in June 1995 observations were made at the Skukuza bomas in the Kruger National Park, where the juveniles were kept after being captured during the culling operations. There were several groups of juveniles and new individuals arrived daily. They were either kept in separate bomas or grouped with other juvenile elephants. The criteria for grouping was age and sometimes sex, but also depended on the orders that had been placed by buyers. Similar aged juveniles were usually penned and sold together in a group, the size of which depended on the tender specification. Some males were captured and penned together for veterinary experiments.

Each boma consisted of two 12 X 12 metre sections with a gate between the sections, which was only closed for cleaning purposes. The wall around the boma was concrete up to 50 cm high with 1.8 m high steel poles concreted into the wall every 1.5 metres. Seven horizontal cables were fixed to the poles so that the elephants could see into the neighbouring pens, but could not climb through the fence.

Kala Ingwe

11 Oct - 14 Oct 1994 (Total obs time: 19 hrs 20 min)

Two groups in separate bomas, but they could see each other through the wooden fence.
Group 1: females Malaika (M) *ca.* 2.5 years and Tandy (T) , male Shingwezi (S) both about 2 years old. (Obs time: 9 hr 45 min).
Group 2: female Balina (B) and male Wally (W), both probably under 2 years old. (Obs time: 9 hrs 10 min). One young elephant in the group had died and both B and W had also nearly died. B had a large abscess on her tooth and W had skin burn from the sun on his back. They were kept in a separate boma so the others would not bully them. Both fed very little. This group as well as the Skukuza elephants provided data on vocal recordings.

Mashatu Game Reserve (Botswana)

11 - 19 Oct and 9 - 24 Nov 1995
29 Apr - 13 May and 27 May - 9 June 1996

The elephant in this reserve are free ranging and move from Zimbabwe into Botswana. It appears that some of the families are resident for most part of the year and they have habituated to vehicles and can be easily approached. This reserve provided baseline data on behaviour of non translocated, normal family groups.

Knysna Forest, large boma

During 1994 three 8 - 10 year old female elephants were translocated to Knysna Forest in the Eastern Cape and some vocal recordings were done while they were in the boma. This consisted of a large, *ca.* 2 ha paddock with an electrified fence, situated in a clearing at the edge of the forest and recordings were made from outside the fence, but when the elephants were near the observer. There was one wild elephant in the forest and fresh footprints were seen in the vicinity of the boma during that time.

2. METHODS

a) Habituation

Each group had to be habituated to the observer. The groups that could first be habituated in the boma and the Thornybush group that was used to humans, were less problematic. The Touchstone group had been released before observations started and these young elephants were so petrified of humans that they ran to the other side of the reserve when they smelled humans. During the first few weeks game guards helped me track the elephants, which were rarely found. An attempt to habituate them to my smell by sleeping in a tree near their favourite water hole for a month failed. A few months later, after permission to radio-collar an individual had been granted, a three-steps-system of habituation was developed at Touchstone, which proved to be very successful and was ultimately applied to all other groups, even to the wild elephants at Mashatu with positive results.

Step 1: association of an unknown sound to the positive experience "no harm". During the first weeks I located the elephants by radio signal and then started to call, sing and eventually talk to them. Distance to the group was slowly shortened.

Step 2: association of the voice to the smell. By the end of a couple of weeks the elephants responded positively to my voice, even when they smelled me, by interrupting their flight when I called.

Step 3: association of the sound and smell to a specific person. When the elephants first saw me, they got a fright, but immediately refrained from running away when they heard my voice, which they had come to know well. During the subsequent daily observations I always called upon arrival and kept reassuring the elephants by frequently talking, especially when they were nervous. They always immediately calmed down when they heard my voice. This method proved successful even when adult females charged me at Venetia or Mashatu. Interestingly the elephants only responded to *my* voice, smell and sight but still ran away from other people. After six weeks I was able to walk with the Touchstone elephants, keeping about 20 m distance to them when possible. If visibility permitted, I kept a larger distance and occasionally I had to approach nearer in very thick bush.

b) Observational data

All data were collected using a small tape recorder and transferred to data sheets daily and later onto computer (see Appendix 3 for a data sheet example). A pair of Habicht binoculars 7 X 42 helped to identify individuals and monitor their interactions. The large light factor (36) of these binoculars was helpful in thick vegetation. Elephants were initially identified by ear marks, tusks, etc. and were soon known individually.

1. Interactions

All occurring dyadic interactions were recorded *ad lib.* whenever the two individuals interacting could be identified. For boma groups all individuals could be observed simultaneously. Observations in the wild were done whenever individuals were visible in the dense bush, therefore these data might be more biased towards certain individuals than the boma data. Particularly at Venetia, visibility was often poor, due to the large size of the group and the dense mopane bush (*Colophospermum mopane*). For obvious reasons it was easier to obtain balanced data on all individuals in the smaller sized groups and the boma groups. It was not possible to do focal sampling as elephants moved about too much and the observer could not follow an individual at close quarters into the group. However, as observations occurred over extended periods of time it is hoped that the sample size is adequate to rend an accurate picture of what was happening in the group.

Interaction elements were recorded as such and were then grouped according to Garaï (1989,1992). For a list of elements see Appendix 1.

Affiliative: any form of touching or smelling at a partner with the trunk tip, leaning or rubbing against a partner, standing over or walking next to a recumbent partner.
Aggressive: any form of pushing, kicking, trunk slapping, chasing a partner, including threat behaviour such as 'trunk flick', 'mock charge', 'head shake'.
Dominance: 'push away', displacing and 'push drive'.
Submissive: 'presenting' and give way'.
Investigate: investigating what a partner is doing (approaching smelling or touching an object) or feeding on (touching a partner's food or mouth while feeding).
Play-fight: sparring, pushing heads or trunks,
Play: 'trunk-over-head', trunks entwined, climbing on a recumbent partner, gentle trunk pushing.
Elements which could not be categorised with certainty were placed in a group "other".

2. Other behaviour:

All vocalizations were recorded on an *ad lib.* basis, as either a rumble, trumpet, cry or scream. If possible the animal emitting it as well as any reactions by other elephants were noted. A detailed description of vocalization methods is provided in Chapter 9.

All visible suckling bouts by the juvenile at Venetia, duration and possible interactions with other individuals were recorded.

Any unusual behaviour patterns and reactions by other elephants were recorded *ad lib.* and reactions to noises or other game and people, i.e. running away, cluster formation, vocalization, interactions.

When the elephants walked 'in single file', the leader and the last individual, and where possible the whole formation was noted.

'Initiating' a group movement was noted as such whenever an individual set off in a certain direction and the other group members followed; flapping and sliding of the ear pinna against the body as described by Moss (1988) and Poole (1996) for matriarchs was never seen in the juveniles. Occasionally the individual that initiated group movement emitted a rumble.

The presence or absence of temporal gland secretion, or TGS (Poole 1987) and the secretion state was noted at each first sighting of an individual. Details are described in Chapter 8 on stress. Additionally whenever TGS was seen to be fresh it was noted together with any potential cause, and the existing social situation documented.

3. Five minute scans

Every five minutes a scan of following parameters was carried out (see Appendix 3 for a data sheet example):

1. Focal animal (Fo).
2. Identification of nearest neighbour (NN)
3. Distance (DN) to nearest neighbour;
4. Distance to matriarch (DM) (where applicable).

Distance categories used:

1 = 0 - 2 m; 2 = 2 m - 10 m; 3 = 10 m - 30 m; 4 = 30 m - 50 m; 5 = 50 m - 100 m.

5. Group or subgroup spacing category (Ø):

Category 1 = No individual more than 2 m away from another (all within 'touching' distance)
Category 2 = all individuals within a diameter of 30 m
Category 3 = all individuals within a diameter of 50 m
Category 4 = all individuals within a diameter of 100 m
Category 5 = individuals dispersed further apart than a diameter of 100 m
Category 6 = group divided into separate units, location of second group not known.

6. Activity: Elephants are capable of doing two activities simultaneously, in which case both activities were recorded, the more predominant one first, e.g. resting feeding or feeding resting (see below). Activities were recorded as follows:

feeding (fe): when feeding occurred alone, either standing or moving a few steps at a time; feeding walking (fe wa): the elephants were walking at a slow but constant pace and feeding at the same time; feeding resting (fe re): during the hot hours of the day the elephants clustered under trees and rested, however during these periods they would pull down branches and slowly feed on these; sandbathing (sb): throwing or blowing sand onto any parts of the body. Sandbathing frequently occurred intermittently when the individual was feeding (fe sb) or resting (re sb); resting (re): the animals were motionless, eyes open or closed, standing or lying down; mudding (md): throwing mud onto any part of the body, or lying and wallowing in mud, including preparation of mud; drinking (dr): obvious activity; standing (st): standing could occur any time between activities, but if longer than 1 min, it was recorded as resting; walking (wa): locomotion without any other activity (e.g. feeding); social (soc): any form of social interactions. For the analyses double activities were grouped e.g. fe sb was computed with feeding and with sandbathing, only n > 5 were considered.

Additionally five habitat parameters were recorded but were not used in the following analyses and therefore are not presented here.

4. Other

At Mashatu Game Reserve the elephants were sexed and aged into the following categories: 0 = < 1 yr; 1 = 1 - 1.9 yrs; 2 = 2 - 4 yrs; 3 = 5 - 9 yrs; 4 = 10 - 14 yrs and not lactating; 5 = 15 - 19 yrs; 6 = 20 - 29 yrs; 7 = 30 - 39 yrs; 8 = 40 - 49 yrs; 9 = 50+ yrs (Data at Mashatu were collected at the end of the five year study period, by which time I relied on my experience to be able to judge the age of a juvenile to the nearest 5 years. Older categories may be more subjective than the younger categories.) At all sightings of elephant groups, sex, age group and size were noted. When possible an attempt was made to stay with one group and all interactions were noted as above as well as nearest neighbours, using the age categories for focal and neighbour.

c) Questionnaires

A total of 24 questionnaires were completed during personal interviews conducted on various reserves in South Africa. All these reserves had translocated juvenile elephants. Some of these results were used in Chapter 8.

d) Analyses of data

Nearest Neighbour

A cluster analysis was carried out for all nearest neighbours within 10 m of each other using the method described by Morgan, Simpson, Hanby & Hall-Craggs (1976). The Cluster Analysis is based on the similarity value (S).

> [Sij = Nij/ (Ni + Nj) multiplied by 1000
> where Nij = number of times i and j were nearest neighbours; Ni = number of times i was sampled; Nj = number of times j was sampled; the multiplication factor is simply for convenience].

This value has been termed an association index (Ginsberg & Young 1992; Mitchell 1994) and Jacob's association index (De Ghett 1978 in Nair 1989) where the combined number of times the 2 elements occurred (Nij) is either added (Nair) or subtracted (Mitchell) to the other figures (Ni + Nj). This will obviously increase or decrease the denominator accordingly, but in the end the sequence of highest to lowest value remains consistent. A test was done on one of the NN matrices (Touchstone period II) to verify this pattern.

A maximum spanning tree (MST) was constructed, so that every individual had at least one link to another individual. The MST gives a more graphic representation of the associations in a group than a dendrogram. The 'branching' in the MST was manipulated to illustrate proximity patterns with other individuals in the group, taking additional similarity values into consideration. The rules of a MST exclude the formation of closed 'loops', however this rule was modified in the Touchstone MST to illustrate the close relationship between three individuals (see Chapter 6). Similarity values (or degrees of association) are represented in the figures, the higher the value the stronger the similarity; These neighbours were thus seen together more often.

Arousal behaviour

Group A at Venetia was very nervous during the boma stay and provided the opportunity to define what was termed 'arousal' behaviour. The behavioural elements were defined as follows: listening (ls, animal stands motionless, eyes open), ears raised (er, ear pinnas are raised above the head), ears spread and raised (es, ear pinnas are held at an angle from the body and raised above the head), head held high (hdh, the top of the head is visibly higher than the back, tusks held horizontal), tail up (tl up, the base of the tail is raised so that the proximal part or the entire tail is near to horizontal), walking around (wa ar, walking around or in a circle for no apparent reason and not object orientated), running (rn, running away from a stimulus or running around), clustering (cl, all animals huddle in a close unit), loud vocalizing (trumpeting, screaming), diarrhoea (only if this occurs immediately after a stimulus), temporal gland secretion (tgs, visible secreting from the temporal gland) aggression (agg, aggressive behaviour towards a partner or person). Sampling of arousal behaviour was carried out using the One-Zero method (Altmann1974) for 30 sec intervals.

Interactions

Significance of certain behavioural differences were tested using a *chi*-square test. Sample size and type of sample was frequently not independent and did not warrant tests for normality or homoscedasticity, therefore non-parametric tests were chosen. Other tests used include: McNemar, Binomial, Spearman's rank correlation, Kendall's coefficient of concordance, linearity tests, Wilcoxon (Siegel 1987).

Acoustic analyses

Occurrence, type of vocalization and where possible individual and situation and reactions of other elephants were noted *ad lib*. Digital tape recordings of some of the vocalizations were made and later analysed on a sonograph. The exact methods are described in Chapter 9 on vocalizations.

CHAPTER 3

SOCIAL ORGANIZATION IN TRANSLOCATED JUVENILE AFRICAN ELEPHANTS:

THE ACQUISITION OF ROLES

INTRODUCTION

When observing a group of elephants one will perceive certain behaviour patterns that are repetitive and predictable (Bramblett 1973). These behaviour patterns reflect the structure of the group and the complexity of the social organization (Bernstein & Sharpe 1966). Thus specific signals and response patterns are integrated into a functional context. These behaviours have been described as roles. Roles are phylogenetic adaptations with a genetically acquired basis (Bramblett 1973). Elephants are extremely adaptable and occur in a variety of habitats. A prerequisite of adaptability is behavioural plasticity which brings with it a loss of phylogenetic 'wisdom' (Mason 1979). This demands from the individual that it creates its own history (Mason 1979) and makes the appropriate decisions through learning and experience. One can therefore assume that elephants need the relatively lengthy period of physical maturation in order to acquire social skills and to learn about their future roles in order to maximise their fitness.

Various groups of juvenile African elephants, captured during the annual culling operations at the Kruger National Park and sold to private owners or other reserves in the country, were studied and compared in order to determine how they adapt without adults and how they reorganize themselves socially. Following the break down of the family unit through translocation, the question arises whether the juveniles prematurely behave according to their specific future roles or whether certain aspects of these roles have to be learned through experience.

In the following the term 'group' is used rather than 'herd' or 'family unit', as the juveniles generally do not originate from the same family unit and therefore represent artificial groups.

ROLES

Leadership / Matriarch:

Normally the oldest female in a family or herd adopts the role of matriarch (Moss & Poole 1983; Moss 1988). Matriarchs have the longest environmental and social knowledge which they acquired partly through learning from their mothers and matriarchs, and partly through experience (Douglas-Hamilton 1975; Leuthold 1977). The role of matriarch implies a significant responsibility as she leads and defends the group, takes up the nearest and most vulnerable position towards danger (Dublin 1983), or decides when to flee, makes decisions as to daily and seasonal movements, feeding and drinking places, social contacts etc. According to Moss (1988) a group that loses its matriarch becomes totally disorientated and disintegrates. The question was, would and could a young juvenile take over this responsible role and what were the criteria for evaluating its success. As the term 'matriarch' is generally applied to an adult female, in the following the term 'leader' is used for a juvenile that would take on this role.

Maternal care:

Elephant births in zoos have demonstrated that primiparous mothers are often helpless with a new-born calf and keepers frequently have to intervene and rescue it from the mother's aggressive behaviour. This implies that certain maternal behaviour patterns have to be learned either by observing other mothers, or by having an experienced cow in the group to assist. Important maternal behaviour patterns, apart from providing nutrition through suckling, is providing protection, security and comfort (Lee 1986), help and opportunity for socialisation. To answer the question whether a young translocated female will be a successful mother requires a long term study, however the maternal behaviour of a young adult female, who had been hand raised as an orphan, revealed some interesting observations.

Allomothering:

Elephants are typical K-selected species producing a single young in which they must invest heavily, with a long intercalving period (Kerr 1978; Laws *et al.* 1975; Moss 1994). This means that parental skills are vital and it is of advantage if these can be 'practised' (Lancaster 1971; Hrdy 1976; Riedman 1982). Therefore aunting (Hrdy 1976; 1977; Wilson 1975) or allomothering (Lee 1987; Nicholson 1987; Rapaport & Haight 1987) behaviour can be expected in elephants. Care of alien young by females is frequently observed in mammalian groups whose members are related by matrilinear descent (Riedman 1982; Gittleman 1985) and this provides an ideal opportunity to learn maternal behaviour. Calf survival rate depends on how many allomothers a calf has, in other words the more females in the group the better the chances of successfully raising the calves (Lee 1987), and females help each other, which makes sense in the light of maximising their inclusive fitness (Hamilton 1964). Allomothering behaviour is exceptionally pronounced in Asian and African elephants (Lee 1987; Riedman 1982; Rapaport & Haight 1987). Particularly the young juvenile females show great interest in caring for younger siblings (Lee 1987).

Helpers:

Females in a family unit will form strong bonds (Moss 1988; Moss & Poole 1983) which ensures the cooperation necessary for group defence (Sikes 1971; Douglas-Hamilton and Douglas-Hamilton 1975), leadership, locating food resources (Laws *et al.* 1975; Hanks 1979) and raising calves (Lee 1987). Helping, aside from allomothering, will be of mutual benefit as the helper will ensure its inclusive fitness (Hamilton 1964), be able to expect reciprocity (Trivers 1971) and possibly gain improved access to resources (Dublin 1983). Bonding between unrelated Asian elephant females has been described and termed a "special relationship" (Garaï 1989,1992).

A distinction between allomothers and helpers is made in this study insofar as allomothers are in general young nulliparous females (Lee 1987), most likely an older sister of the calf, and therefore not yet capable of defending the group or making decisions about group movements. Whereas an adult daughter (probably with her own offspring), or sister of the matriarch, would qualify as helper and be capable of assisting with group defence and initiate movements.

Juveniles:

Behavioural interaction patterns of young male elephants differ from those of young females. Males become increasingly independent from their mothers (Lee 1987) and develop social relationships with peers. Independence increases and males gradually leave the group at puberty (9 - 15 years)(Hanks 1979; Short *et al.* 1967) and disperse (Douglas-Hamilton 1972) until older males become solitary and only visit female groups for mating (Poole 1987). Females stay in the group and take on the roles of helpers, allomothers, mothers and possibly matriarch. One can therefore expect that juvenile males will tend to seek the company of other young males and venture away from their mothers earlier than females, and that juvenile females will tend to stay near adult females and, eventually, seek the company of younger individuals. Elephants are generally physically mature between the age of 11 - 13, with a range between 9 - 16 (extreme values 7 - 33) depending on ecological factors (Buss & Smith 1966; Laws 1969; Kerr 1978; Moss 1994; Williamson 1976; Whyte 1996).

STUDY GROUPS AND METHODS

1. Study groups

Data of the following groups were used in this chapter (see Methods, Chapter 2 for details).

Venetia Limpopo Nature Reserve (VLNR) 1991, Boma

Six juveniles: two males, four females aged between 8 - 11 yrs.

Venetia Limpopo Nature Reserve (VLNR) 1992 - 1994

21 juveniles (10 males, 11 females; between 2.5 and 12 years
one adult female, Jane (*ca.* 18 yrs)
Data were divided into following observation periods:

Period I	14 Sep	-	20 Nov 1992	(Total obs time: 146 hrs 50 min)
Period II	8 Apr	-	19 Jul 1993	(Total obs time: 179 hrs 25 min)
Period III	15 Jan	-	21 May 1994	(Total obs time: 93 hrs 25 min)

Touchstone Game Ranch

10 juveniles (4 females, 6 males) ranging between 4.5 - 7 years.
Data were divided into following observation periods:

Period I	19 Apr	-	29 Jul 1993	(Total recording time: 171 hrs 30 min)
Period II	1 Aug	-	29 Nov 1993	(Total recording time: 95 hrs 35 min)
Period III	15 Jan	-	21 May 1994	(Total recording time: 104 hrs 10 min)

Thornybush Game Lodge

Females: A: *ca.* 15 yrs, P *ca.* 13 yrs, O ca. 13 yrs; males: B *ca.* 13 yrs, S, juvenile 4 yrs.

Spektakel Game Ranch

Six juveniles: 3 females 2 - 2.5 yrs, 3 males 3.5 - 4 yrs.

Mokolo River Nature Reserve

Three juveniles 4 - 5 years; one male, two females.

Mashatu Game Reserve (Botswana)

Free ranging elephants in normal family groups, not translocated.

2. Observational data

The following parameters were used from the 5 min scan sheets for analyses: Focal animal and nearest neighbour, distance of neighbour and distance to matriarch (were applicable) as follows: 1 = 0 - 2 m; 2 = < 10 m; 3 = < 30 m; 4 = < 50 m; 5 = < 100 m.

The following interaction categories were used in this chapter (details in Chapter 2 and Appendix 1): Affiliative; Aggressive; Dominance; Submissive. All vocalizations were recorded as either rumble, trumpeting, cry, scream, and if possible the animal emitting it noted as well as any reactions by other elephants. For Venetia all visible suckling bouts of the juvenile, duration and possible interactions by others were noted. Alertness and threat behaviour were recorded.

At Mashatu Game Reserve the elephants were sexed and aged in the following categories: 0 = < 1 yr; 1 = 1 - 1.9 yrs; 2 = 2 - 4 yrs; 3 = 5 - 9 yrs; 4 = 10 - 14 yrs and not lactating; 5 = 15 - 19 yrs; 6 = 20 - 29 yrs; 7 = 30 - 39 yrs; 8 = 40 - 49 yrs; 9 = 50+ yrs. For simplification the results of nearest neighbour choice in Table 1 were pooled (categories: f5 - f9 and juveniles 0 - 3).

3. Analyses:

Significance was tested with a *chi*-square test for expected and observed values. Correlations were tested with the Spearman's rank correlation. Nearest neighbour data, for all nearest neighbours within 10 m of each other, were analysed by means of a cluster analysis following Morgan *et al.* (1976). For the analysis the data for the adult females at Mashatu (category 5 and above) were pooled as the age of a mother was irrelevant. The choice of an adult or another juvenile by the juveniles (0 - 2) was tested using a Binomial test. In order to compare the data for Venetia with that of Mashatu (section on Juveniles) the nearest neighbour data of the known individuals were grouped in the same categories used for Mashatu. Data from Periods I and III were taken, which comprised one year. The nearest neighbour results for each category were divided by the number of individuals per category to obtain equal possibilities of choice. A *chi*-square test was used to test for significance ($p < 0.001$, df = 1).

RESULTS

1. THE MATERNAL ROLE

VLNR 1992 - 1994

The approximately 18 year old female "Jane" was introduced to some of the juveniles while they were still in the enclosure (or "boma") where they were kept for a 5 month period prior to release into the reserve. She was penned with a young group of 5 males (Group C), about 2.5 - 3.5 years old, for one week, then a group of eight (Group B; 3 males, 5 females) roughly 4 - 5 year old juveniles were allowed to join them. These individuals stayed in the enclosure together until they were released one month later. Although Jane was not a biological mother her behaviour in adopting the maternal role towards a young male justifies this being termed 'maternal' behaviour and not 'allomothering'.

Spacing:

Based on a cluster analysis of similarity values for nearest neighbours Jane's nearest neighbour in the "boma" was the youngest male (Sq). Results from the first period after the release continued to show by far the highest nearest neighbour values for the young male Sq and Jane. After three weeks the other previously released juveniles joined Jane's group and she was now with 21 juveniles ranging from about 2.5 - 12 years. Throughout period II and III Sq and Jane remained nearest neighbours (see Chapter 6). Even on those occasions when he was not her nearest neighbour he spent most time at distance 2 (2 m - 10 m) from her (35.6% in period I; 44% in period II) and rarely moved further than distance 3 (10 m - 30 m) from Jane. In period III, one year after the release, he started to venture further from her and, when not her nearest neighbour, he spent most time at distance 3 (55.6%) or 2 (33.3%). At the beginning of period IV Sq had died of an unknown cause.

Interactions:

Soon after the release Sq started to suckle from Jane, which he continued to do until he died. Jane's mammary glands developed and she stood for Sq whenever he demanded to suckle. Although he appeared to be obtaining milk this remained unsubstantiated. It was also uncertain whether he was receiving adequate quantities, although the suckling bouts averaged 2.7 min in the first three weeks and 1.3 min in period I (range: 30 sec to 4 min). In the following observation periods it was not possible to monitor suckling time due to thick summer vegetation and the close-knit grouping behaviour of the elephants. During the first period 122 suckling bouts by Sq and 13 attempts to suckle were recorded. During periods II and III only 40 and 23 suckling bouts respectively were recorded, as the visibility was impaired. Sq vocalized (rumbles and growls) significantly more than any other juvenile ($x^2 = 1168$; $p < 0.0001$) especially in connection with suckling behaviour and frequently cried out or screamed when Jane moved her leg while he suckled. In period I 137 screams or cries out of 221 were recorded for Sq. This was significantly high ($x^2 = 1302$; $p < 0.0001$) compared with the other juveniles. In period II he was again the individual that screamed most ($x^2 = 44$; $p < 0.001$). Many screams appeared to be cries of frustration, which raises the question whether he was receiving sufficient milk.

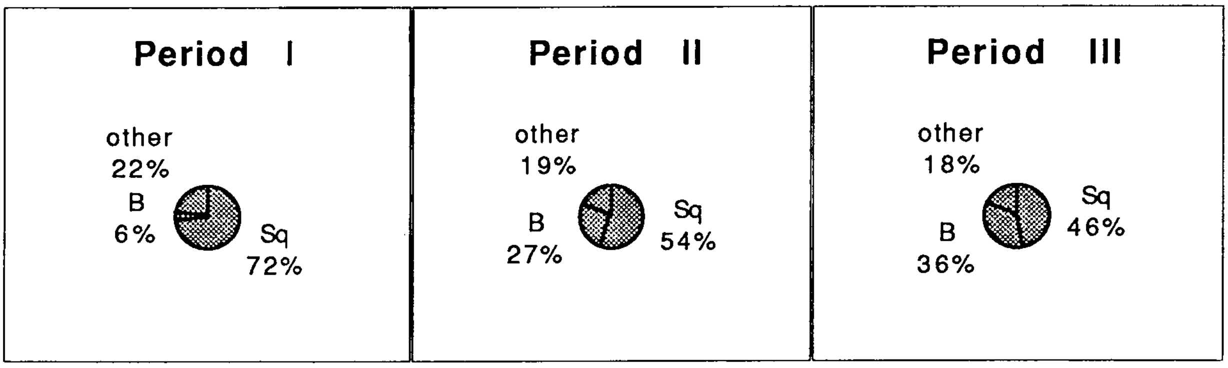


Figure 1. VLNR. The distribution of Jane's affiliative behaviour to the juveniles expressed in percentage of the number of affiliative interactions observed in each observation period. B and Sq are two individuals, "others" comprises 19 other juveniles.

Jane directed most of her affiliative behaviour (72%) to this young male during period I ($x^2 = 520$; $p < 0.001$) (Fig. 1). Of this 33.7% occurred during suckling bouts, when she repeatedly touched him on the lip or on the face or ears with her trunk tip. Sq very rarely interacted with other elephants and 88.9% of his total interactions other than suckling or suckling attempts were directed towards Jane. During period II she still directed most of her affiliative behaviour towards Sq (54%; $x^2 = 160$; $p < 0.001$) although less than before. This decline in affiliative interactions to Sq continued in period III (Fig. 1), but he still remained the individual who received most attention from Jane. During this second period Sq directed 67.6% of his total interactions besides suckling towards Jane. These interactions were either affiliative contacts or investigating what she was feeding on.

Sq always rested standing or lying down next to Jane. She would sometimes wait for him if he was slow to follow and frequently ran to him if he screamed. On one occasion, after a sleeping bout, she started to walk away while he was still lying down sleeping. After a few minutes she came running back, obviously upset, looking for him and touched him on the lip and rumbled when she found him. She never displayed this behaviour towards any other juveniles. Sq always ran to Jane when he was upset or nervous and he was allowed to feed next to her, which was not true for many other juveniles, who were kept at a distance by Jane.
Jane had taken on the maternal role to such a degree, that a casual observer would have assumed that she was the biological mother of Sq.

2. THE ROLE OF MATRIARCH OR LEADER

Data from Mashatu showed that in all observed 'walking in single file' conformations an adult female (category f6 and above) was leading (92%) or in second place (8%). It was therefore assumed that a leader would initiate most group movements, lead a single file formation, face danger and defend the group. It was tested whether the leader would be the most alert and the one to show most threat behaviour, and whether aggressive and dominance behaviours (see methods) were correlated to leading behaviour. In a normal family unit, where dominance is defined by age (Moss 1988), the matriarch would be the most dominant.

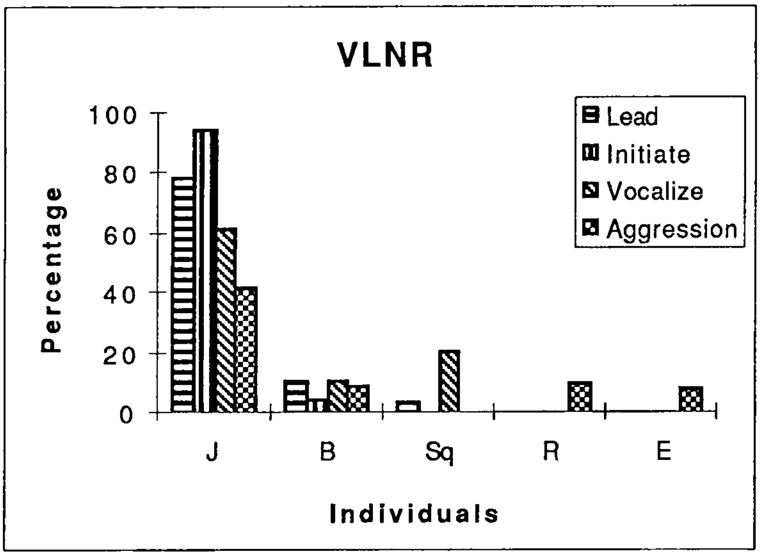


Figure 2. VLNR. Behaviours of a leader
Lead: leading a walking formation
Initiate: initiating group movements
Vocalize: rumbling
Aggression: any aggressive behaviour

VLNR 1992 - 1994

The adult Jane showed significantly higher values for initiating (94.5%; $x^2 = 453$; $p < 0.001$) and leading (78.6%; $x^2 = 48$; $p < 0.001$) than any other individual (Fig. 2). She also vocalized (rumbling) significantly more than any other elephant in the group (61.2%; $x^2 = 8093$; $p < 0.001$). Jane showed very little dominance behaviour, presumably it was not necessary for her to establish her dominance as she was the only adult and as such dominant over the juveniles. Significantly more aggressive behaviour was displayed by Jane (41.8%; $x^2 = 873$; $p < 0.001$) compared to other individuals during all three periods (Fig. 2). Due to the large group size and thick vegetation it was not possible to discern who was most alert. When there was nervousness in the group Jane always investigated, unless she knew it was me (I would call and she recognised my voice). Jane never displayed any threat behaviour towards me, but juveniles did. From the very beginning, Jane took over the role of matriarch and the juveniles followed her immediately.

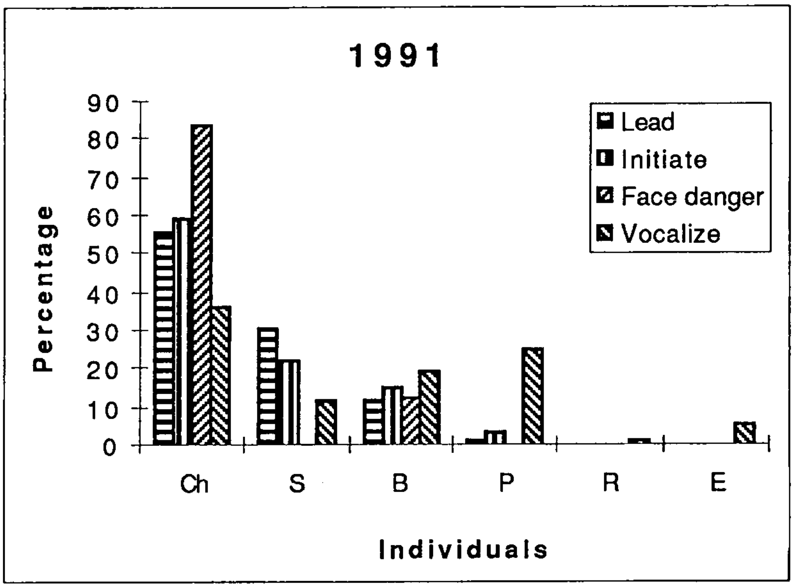


Figure 3. VLNR. Behaviours of a leader
Lead: leading a walking formation
Initiate: initiating group movements
Face danger: face a danger and approach it
Vocalize: rumbling

VLNR 1991

One of the females (Ch, Cheeky) showed significantly higher tendencies for leading ($x^2 = 54.9$), initiating ($x^2 = 100.1$), facing danger ($x^2 = 32$) and vocalizing ($x^2 = 127.9$; all $p < 0.001$) (Fig. 3). She was also the individual to walk most frequently between the group and danger (7/ 8 times), this was termed 'shielding behaviour'. One other female (P) also had significantly higher vocalizing frequencies and the female S showed a tendency to lead the group ($x^2 = 6.86$; $p < 0.01$). Only the two males (R and E) never initiated group movements and never led. Ch (Cheeky) would frequently stand on her own at the bottom of the boma and look out. She showed the least play behaviour and in general interacted with others the least of all six elephants. However, she intervened most when female B and male R were play-fighting. She displayed significantly most affiliative behaviour (53.4%; $x^2 = 49.1$; $p < 0.001$) towards female P who frequently stood next to her. Ch was the only one never to show any submissive behaviour but also showed the second least dominance behaviour. It appeared that she was not attempting to ascertain dominance or leadership, but that the others followed her when she walked and ran to her in danger. It was very interesting and surprising that Ch, together with P, walked out of the boma alone when they were released, and only joined up with the other elephants three years later (see Chapter 6).

Aggressive behaviour was shown most by female B (Blou) and mainly towards male R, with whom she had most play-fighting bouts (67.9% of her play bouts). She also showed the most dominance behaviour, mainly to male R (81.3% of her total dominance behaviour).

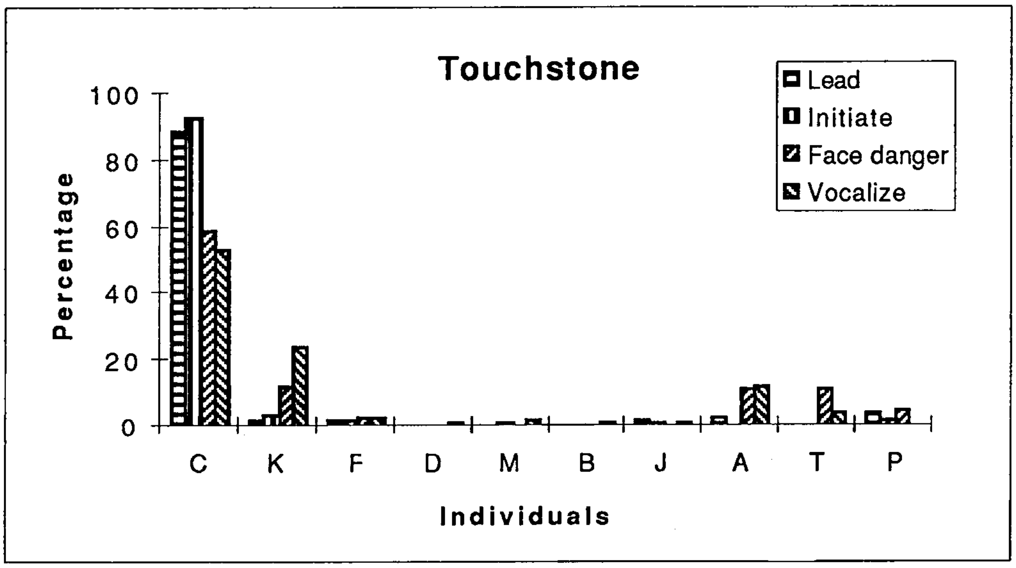


Figure 4. Touchstone. Behaviours of a leader
Lead: leading a walking formation
Initiate: initiating group movements
Face danger: face a danger and approach it
Vocalize: rumbling

Touchstone

The female C (Celeste), probably the oldest in the group, showed a significant propensity for leading ($x^2 = 440$; $p < 0.001$), initiating ($x^2 = 1057$; $p < 0.001$), facing danger ($x^2 = 233$; $p < 0.001$) and vocalizing ($x^2 = 525$; $p < 0.001$)(Fig. 4). Females C (Celeste) and K (Kelly) and male B displayed dominance behaviour more frequently and only male B displayed aggressive behaviour more regularly ($x^2 = 24$; $p < 0.001$). Figure 5 shows the relationship between being 'alert' and 'threat' behaviour. Both female C and male A had the highest values for both these behaviours. Although during period I C was the most alert (possibly because of the observer).

If Jane's behaviour at VLNR can be taken to represent normal leading behaviour, Celeste would emerge as the leader of the Touchstone group. Alertness and threat behaviour need not necessarily be reserved for the leader or matriarch. It also appears that aggression and dominance behaviours are not necessarily attributes of a leader, but may serve to establish a hierarchy among the remaining group members (see Chapter 4).

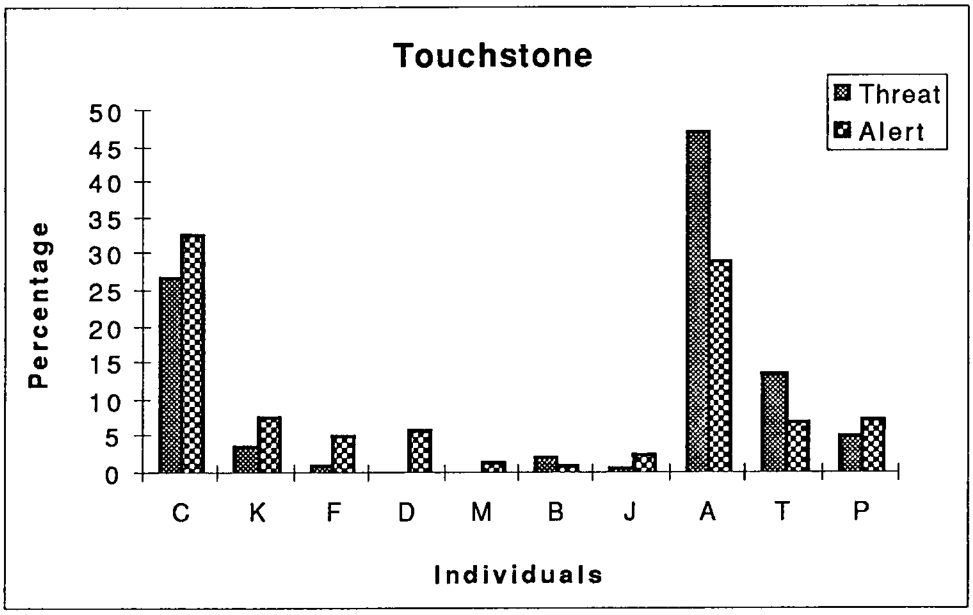


Figure 5. Touchstone. Relationship between being alert and showing threat behaviour

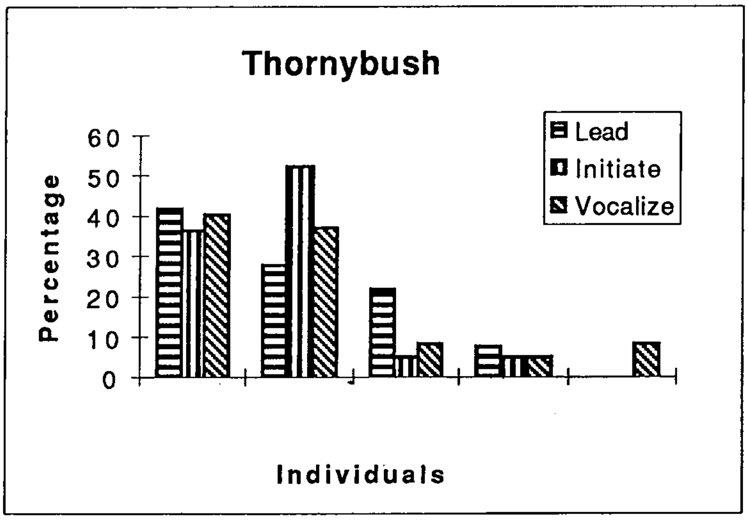


Figure 6. Thornybush. Behaviours of a leader.
Lead: leading a walking formation
Initiate: initiating group movements
Vocalize: rumbling

Thornybush

The oldest female A showed a significant tendency ($x^2 = 12.1$; $p < 0.001$) to lead. Both females A and the pregnant female P vocalized more (A: $x^2 = 31.4$; $p < 0.001$; P: $x^2 = 22$; $p < 0.001$) (Fig. 6) and both females initiated movements (P slightly more). Female A and male B displayed significantly more (A: $x^2 = 8.56$; $p < 0.005$; B: $x^2 = 14.25$; $p < 0.001$) aggressive behaviour, but only male B showed dominance behaviour more frequently($x^2 = 36.5$; $p < 0.001$). (There seemed to be no clear matriarch, although female A was the oldest. The question arises whether the pregnant, but younger female P was challenging for leadership status, or whether A and P were leading the group together. P displayed some aggression towards A, but A never reciprocated.)

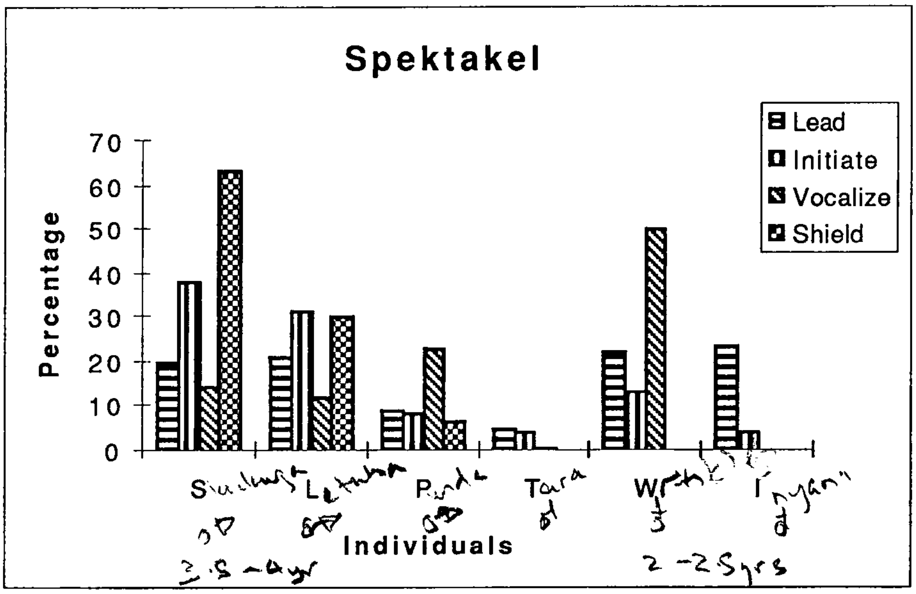


Figure 7. Spektakel. Behaviours of a leader
Lead: leading a walking formation
Initiate: initiating group movements
Vocalize: rumbling
Shield: Walking between the group and danger

Spektakel

The two males S and L, the oldest individuals, initiated movements frequently (S: $x^2 = 25.23$, $p < 0.001$; L: $x^2 = 12.19$; $p < 0.001$). In addition, S would walk significantly more ($x^2 = 39.2$; $p < 0.001$) between the group and potential danger (the observer). However, any individual would lead the walking formation (Fig. 7). Female W was the one to emit significantly more vocalizations ($x^2 = 78.4$; $p < 0.001$). Males S and P both displayed significantly more aggressive behaviour (S: $x^2 = 616.4$; P: $x^2 = 50$; $p < 0.001$) and dominance behaviour (S: $x^2 = 255$; P: $x^2 = 301$; $p < 0.001$). (Thus, there was no clear leader for this group, but the very young females followed the older males. There was strong cohesion within the group.)

Mokolo

Boma:

Female R, the oldest of the juveniles, initiated movement and led the group more often($x^2 = 16.49$, $p < 0.001$ and $x^2 = 16.00$, $p < 0.001$ respectively). She also vocalised (rumbling) most frequently ($x^2 = 48.3$, $p < 0.001$, $n = 144$). All three showed threat behaviour towards the observer. Female R displayed most aggressive ($x^2 = 77$, $p < 0.001$) and dominance behaviour ($x^2 = 65$, $p < 0.001$). It appeared as if she was likely to take over the leading position.

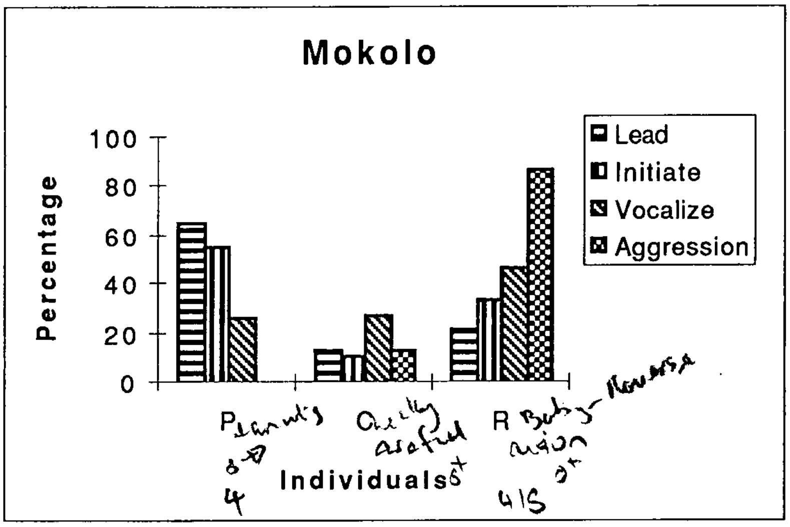


Figure 8. Mokolo. Behaviours of a leader
Lead: leading a walking formation
Initiate: initiating group movements
Vocalize: rumbling
Aggression: any aggressive behaviour

Free:

Male P, the youngest of the group, significantly led and initiated movement most often ($x^2 = 14$; $p < 0.001$; $x^2 = 10.97$; $p < 0.001$), but female R still vocalized more frequently ($x^2 = 10.08$; $p < 0.005$) (Fig. 8). Female R also still displayed more aggressive ($x^2 = 39.7$; $p < 0.001$) and dominance behaviour ($x^2 = 57.2$; $p < 0.001$). Judging by dominance and aggression one would have predicted her to become the leader of the group. However, she was obviously not in a position to do so, and it was the younger male P who took the initiative once they had left the boma. All three always stayed in close proximity of one another. It was rather surprising that these three did not join up with the other group, which contained a female of about 7 years of age.

3. THE ROLES OF ALLOMOTHER AND HELPER

VLNR 1991

Female P was a sociable elephant displaying the second most affiliative behaviour. She directed most affiliative and significantly most play behaviour ($x^2 = 202.6$; $p < 0.001$) towards female S. No nearest neighbour analysis was conducted for the boma, but female P and Ch were frequently together and investigated each other's food most frequently. It seemed as if these two females had formed a special relationship (Garaï 1989,1992), an assumption which was confirmed when they left the boma together on their own.

VLNR 1992 - 1994

The second youngest male Bb, together with three other young males (Ll, F, A), had been marginalised from the social unit. The results for the cluster analysis for nearest neighbour during period I showed a very weak association with F. Whereas the other three males eventually joined up with two older males to form a subgroup (see Chapter 5), Bb was frequently alone. During period II he attempted to get closer to Jane and the cluster analysis shows a very weak association with her. In period III he showed a weak nearest neighbour association with Sq (who was Jane's nearest neighbour). This indicates that he was still attempting to associate with Jane and Sq. During all three periods there was hardly any interactions between Jane and Bb and she displayed no interest in him when he lagged behind or even when he went missing for two days. After Sq died the cluster analysis shows that Bb and Jane were nearest neighbours. By now he was approximately 4 years old, so he showed no suckling behaviour, but was allowed to feed and rest near Jane. She now waited for him when he lagged behind. Jane clearly displayed allomothering behaviour towards Bb, who had taken over Sq's position near Jane.

The oldest juvenile female B (Blou, from the 1991 group), who at the beginning of the study was about 11-12 years old, had joined up with the group after Jane and the 13 juveniles had been released. During periods I and II she directed significantly more affiliate behaviour to Sq ($x^2 = 98.5$; $p < 0.001$; 37.8% of her total affiliative behaviour) than towards any other elephant. Jane displayed second most affiliative behaviour ($x^2 = 26.8$; $p < 0.001$) towards Blou in period II (Sq: 52.3%; B: 25.6%) and in period III ($x^2 = 17.6$; $p < 0.001$; Sq: 46.2; B: 35.8%) (Fig. 1).

The cluster analysis showed that Blou had Sq as nearest neighbour in period I, Jane as nearest neighbour in periods II and III. In 81.8% of the observations, when another female stood on the other side of Sq while he suckled, it was Blou. She would frequently wait for Sq when Jane moved on. As is shown in Figure 2 she displayed some leading and initiating behaviour and the second most aggressive behaviour of all females. Jane and Blou would run together in a danger situation, touch each other and rumble. When Jane lay down to rest during the day Blou always stood next to her. Blou was also the only partner with which Jane played. There appeared to be a 'special relationship' between the two females and Blou would assist Jane in defending the group and looking after Jane's adopted "offspring". Blou showed similar allomothering and helping behaviour, akin to that usually expected from an older daughter (Lee 1987).

Touchstone

Interactions

Celeste displayed significantly more affiliative behaviour towards the youngest male M (x^2 = 85.6; $p < 0.001$; 41.3%) than to any other individual for all three observation periods. The second individual to receive most affiliative behaviour from C was female K (Kelly) (20.2%). Kelly directed most affiliative behaviour towards male M (x^2 = 141; $p < 0.001$; 46.1%) and directed second most affiliative behaviour towards Celeste (21.8%). M himself showed most affiliative behaviour towards Celeste (x^2 = 17.28; $p < 0.001$; 30.2%) (Fig. 9). Celeste never showed any aggressive behaviour towards Kelly, who herself showed no aggression towards Celeste or to male M.

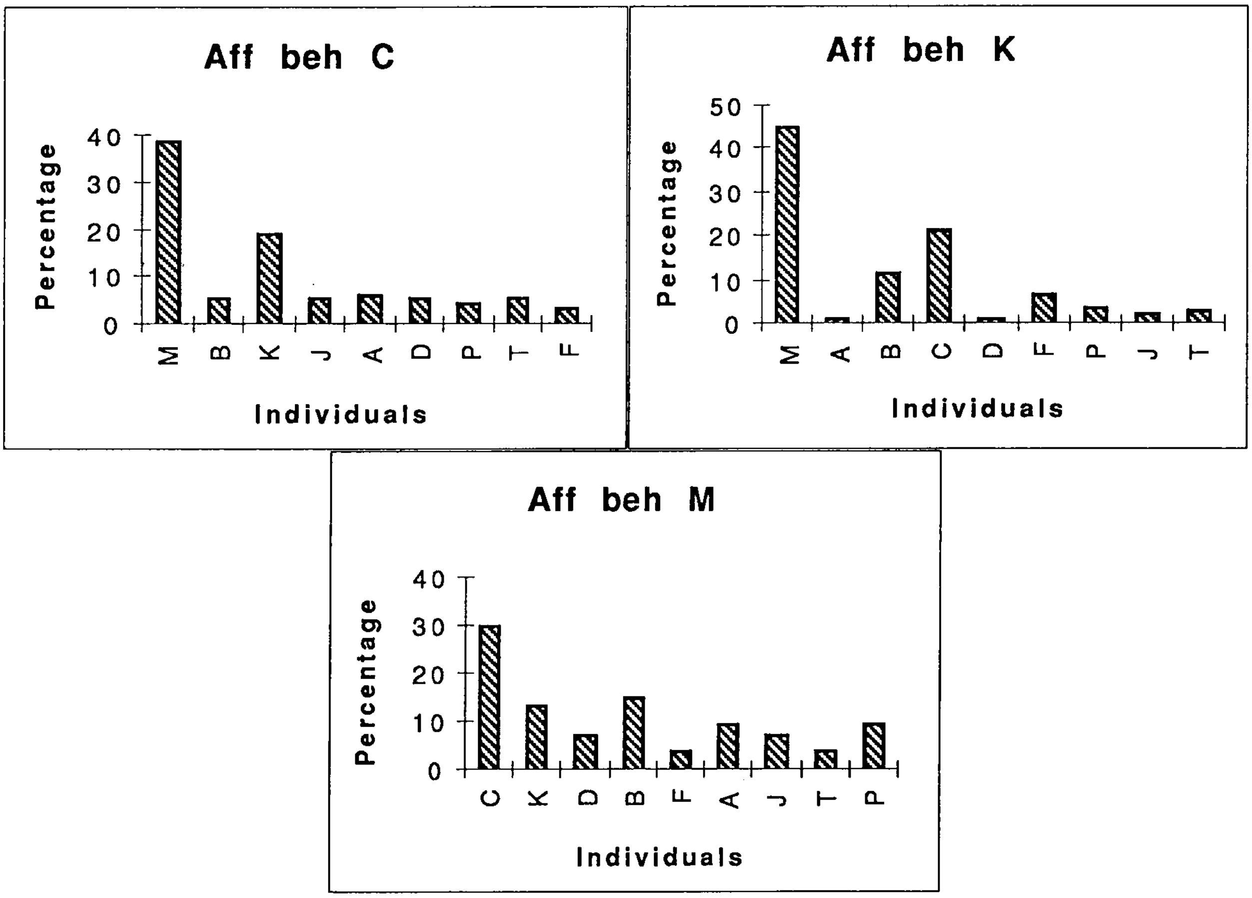


Figure 9. Touchstone. Distribution of affiliative behaviour expressed as a percentage of the number of affiliative interactions observed for the three individuals: female C, female K and male M respectively.

Spacing

The nearest neighbour analysis showed the closest association between Celeste and male M, and Kelly and male M in period I. In period II and III the values were still highest for Celeste and male M, and Kelly and male M, but also high for Celeste and Kelly. These three individuals spent most of their time together. Both females would stand together facing danger and rumble. In period III Kelly occasionally faced danger alone. The similarity in behaviour pattern to VLNR suggests that Celeste had not only adopted the role of leader in the group, but also that of allomother to the male M, whereas Kelly had adopted the role of helper and formed a 'special relationship' with Celeste.

Thornybush

Two of the females, A and O, displayed most of their affiliative behaviour towards the young male S (Fig. 10; A: 81.8%; O: 60.8%). Female A was the one to react most (80% of reactions) to S when he was in potential danger, running to him and even physically pulling him away, (electric fence, vehicles, people, rough play by male B) or when he vocalized. Occasionally female O would also react to his calls. Female A pushed him up steep banks and waited for him. S frequently ran to female A when in trouble and directed 71.7% of his affiliative behaviour to her. When walking in single file S walked in the middle of the group, but in 81.8% of the observations directly in front or behind female A.

Female A had adopted the role of allomother to S and females O and P helped to look after the group, however, there did not appear to be a special relationship between any two females at that stage.

Spektakel

One of the two males P and S, that had displayed most aggressive and dominance behaviour, also displayed the most affiliative behaviour (P: $x^2 = 18.33$; $p < 0.001$). Male S was the recipient of the most affiliative behaviour ($x^2 = 17.27$; $p < 0.001$), mainly from the two females T and I. No individual reacted towards another in a danger situation. There appeared to be no special relationship in this group, however all individuals kept in close contact.

Mokolo

Both females C and R directed most of their affiliative behaviour towards the male P (C: $x^2 = 42.37$; $p < 0.001$; R: $x^2 = 6.06$; $p < 0.025$; 92.4% and 66.4% respectively). Both females would walk up to and stand next to P when he lay down to rest, a behaviour P never displayed towards the females. The females displayed some aspects of 'allomothering' behaviour towards P.

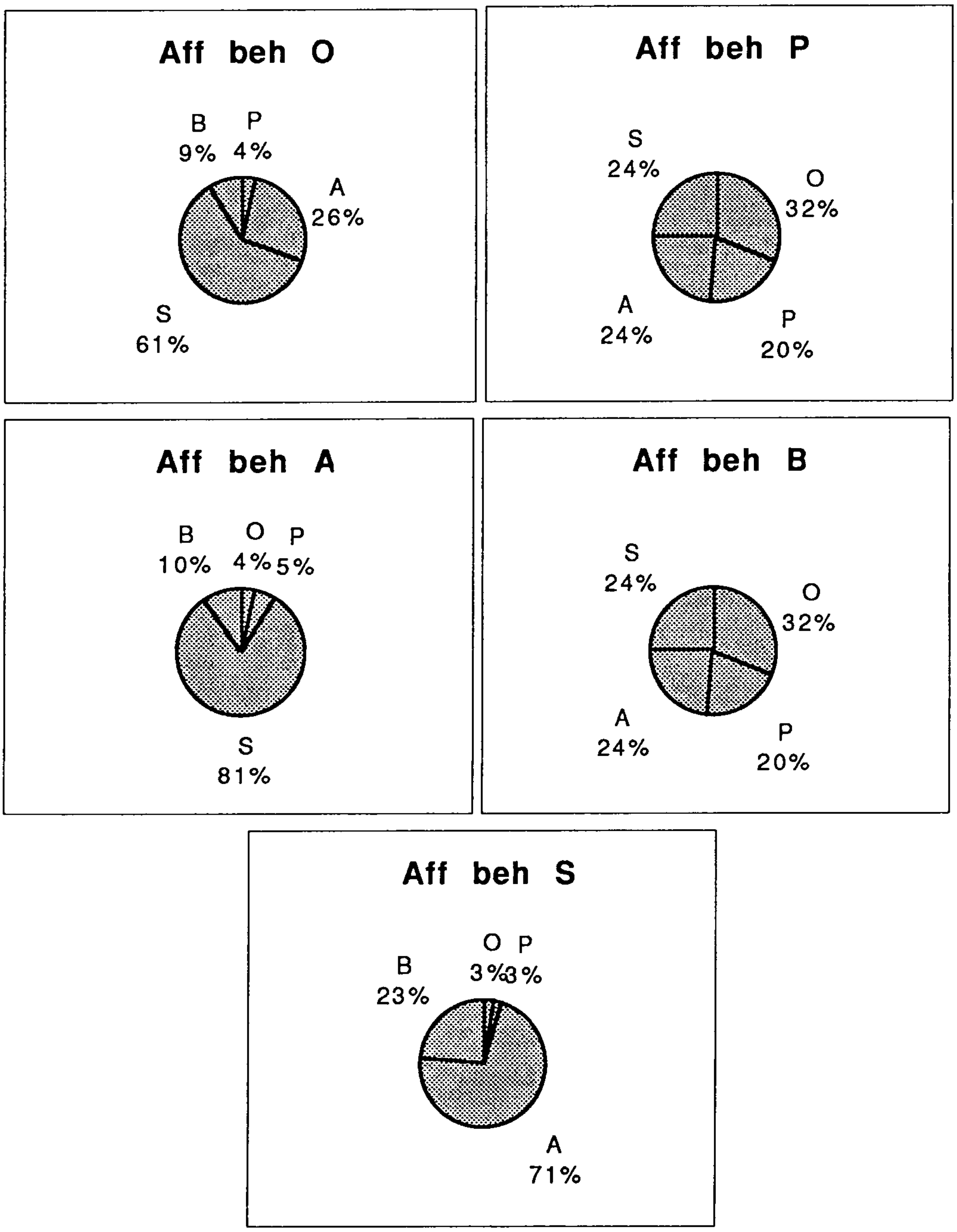


Figure 10. Thornybush. Distribution of affiliative behaviour expressed as a percentage of the number of affiliative interactions observed for the females: O, P, A; and the males: B, S.

4. THE JUVENILE ROLES

Mashatu Game Reserve

Table 1. shows the similarity values for nearest neighbours for each age/sex group for all observation periods. The highest value for each group demonstrates the preferred nearest neighbour.

Table 1. Similarity values of nearest neighbours for each age/sex category

	f0	f1	f2	f3	f4	f5	f6	f7	f89	m0	m1	m2	m3	m4	m5	m6
f0	6															
f1	25	22														
f2	18	31	30													
f3	16	33	59	17												
f4	26	20	43	55	26											
f5	48	34	73	49	34	16										
f6	12	43	91	58	38	19	12									
f7	17	36	119	62	46	36	19	23								
f89	4	34	63	40	26	27	13	18	20							
m0	36	17	15	24	7	9	24	44	32							
m1	0	23	12	3	16	3	18	39	12	0	16					
m2	11	20	27	24	21	48	79	93	74	8	20	9				
m3	11	25	31	26	20	40	47	45	33	0	8	38	32			
m4	15	7	11	38	10	16	29	26	6	6	5	24	50	46		
m5	13	0	10	11	8	21	20	14	15	6	7	5	25	61	39	
m6	0	0	0	3	5	7	6	0	5	0	0	6	9	7	60	43

Table 2 shows the choice made by each sex/age category for either an adult female or a juvenile as nearest neighbour, based on Table 1. Adult females (f5 - f9) have been grouped. Juveniles (0 - 3) have also been grouped. Females in categories 0 - 3 and males in categories 0 - 2 prefer an adult female as nearest neighbour. Females from the age of about 10 years (category f4) start associating more with younger individuals. Males from about the age of 5 years (category m3) start to seek the company of older males.

Table 2. Choice of preferred nearest neighbour (NN) by each sex / age category, based on similarity values

Adult females (categories 5 - 9) and juveniles (categories 0 - 3) have been grouped.
Focal: focal age/sex group; NN: preferred choice of nearest neighbour

Focal NN	f0	f1	f2	f3	f4	f5	f6	f7	f89	m0	m1	m2	m3	m4	m5
adult f	x	x	x	x						x	x	x			
juvenile					x	x	x	x					m4	m5	m4

Analysis of the second most frequent nearest neighbour showed that females in category 4 (> 10 years) will choose an older adult female, whereas females in category 5 (> 15 years) will choose a young juvenile (categories 2 - 3). The second most frequent nearest neighbour of males in category 3 (> 5 years) will be an adult female, whereas males from category 4 (> 10 years) and higher will be near other males.

Juveniles in categories 0 - 2 chose an adult female as nearest neighbour in 79% of the observations (binomial, $z = -25.22$; $p < 0.0001$, $n = 1892$), whereas adult females selected a juvenile (48.2%) or another adult female (51.8%) with equal frequency ($z = -0.5417$; $p = 0.29$, $n = 276$). Categories 3 and 4 were left out of this analysis as there is an apparent sex difference (Table 1). When the data for juveniles only was analysed by sex (categories 0 - 3), the results showed that females preferred the company of other juvenile females over that of juvenile males ($z = -7.228$, $p < 0.0001$, $n = 207$). Young males did not seem to have a sex preference before reaching age category 4 ($z = 0.7396$, $p = 0.23$, $n = 117$).

Venetia Limpopo Nature Reserve

Nearest neighbour data were grouped according to the age categories used at Mashatu for comparison. During Period I the categories m2 ($x^2 = 574.6$), f2 ($x^2 = 104.7$), f3 ($x^2 = 17.5$) and f4 ($x^2 = 47.85$; all $p < 0.001$) significantly chose to be near the adult female Jane, however, the two females in category f4 also significantly chose one another's proximity ($x^2 = 25.17$; $p < 0.001$). The adult Jane significantly chose the proximity of a young m2 male ($x^2 = 27.88$) (there was no f2). The category 3 and 4 males significantly chose one another's proximity ($x^2 = 59.9$; $x^2 = 23.23$; $p < 0.001$). In period III, one year later, the adult female Jane significantly chose the proximity of a female in category 4 ($x^2 = 15.9$; $p < 0.001$). Juveniles in categories m2, f3 and f4 significantly chose Jane's proximity ($x^2 = 156.1$; $x^2 = 33.4$; $x^2 = 81.4$; all $p < 0.001$). The two males in category 4 significantly chose one another's proximity ($x^2 = 58.4$). Category m3 now consisted of juveniles that had been m2 the previous year. This category chose to be associated with the adult Jane ($x^2 = 6.4$; $p < 0.025$).

DISCUSSION

Adoption of an orphaned calf is known to occur among elephants. It was nevertheless surprising to see to what extent Jane fulfilled this maternal role. Even her mammary glands developed, probably in response to frequent suckling. Seen against the lack of any experience in this regard, and as she had not had any offspring herself, and had grown up a hand-reared orphan, this was quite extraordinary. Suckling of an orphaned calf in has also been documented in Kenya, but in that instance the female did not develop mammary glands (McKnight 1995). Jane obviously recognised which was the youngest and therefore most vulnerable juvenile, and went so far as to choose the next in line after Sq died. Although it was not possible to establish their ages, unequivocally Sq and Bb were most likely a few months younger than the other two small males, and Bb was not the only one that attempted to approach Jane. Some other juvenile males had been in closer proximity to Jane than Bb, but were not selected after Sq died. From an evolutionary perspective it seems difficult to explain why a female would adopt a nonkin calf. However, adoption occurs in elephants, and most likely evolved through kin selection as orphaned calves are likely to be within the family unit.

Role of leader

Jane adopted the role of leader, whether willingly or reluctantly cannot be answered. It appeared that she had no choice, as from the first moment Jane was introduced to the juveniles these immediately followed her, often so close that she could hardly move, and she had a calming effect on them (Garaï 1993, 1994). Jane was unquestionably the adopted matriarch.

Assuming that Jane's behaviour and the behaviour shown by matriarchs in the wild population at Mashatu represent a baseline pattern, the criteria "leading of group formation", "initiating movements" "face and approach danger" and "vocalization" were used to define the role of a "leader". The last criterion "vocalization" only includes low frequency rumbles (Poole *et al.* 1988), which are used by elephants to initiate group movements, give warning and contact calls (Poole 1996), and initiate resting periods (present study). Here it is not implied that this criterion is normal for a group of wild elephants. But the relationship between the amount of vocalization and the three other criteria for a "leader" found in this study, suggests that it may be used as indicative criterion together with the other leading type behaviours in a group of juvenile elephants.

Cheeky (Venetia boma 1991) qualified in terms of the above criteria, however, her behaviour and the reactions of the others upon their release, showed that she was not a strong enough group leader to keep the group together. It would appear that individual disposition is important. She was an elephant that often stood on her own and seemed to adapt to the captivity of the boma least well of all elephants. Celeste at Touchstone qualified in terms of all four criteria. This is possibly the most surprising outcome of the study, considering that this elephant was not more than 5 years old when the group was released. At Thornybush there seemed to be no clear leader of the group, although by age, female A should have qualified. Both females A and P showed leadership qualities and it was unclear whether the younger but pregnant female P was helping A to lead the group, or whether she was in the process of challenging for leadership.

At Spektakel the three older juveniles were males and as such probably more aggressive. Young males are known to play-fight more frequently and establish a dominance hierarchy (Lee 1986; Poole 1987). Being older, the males S and L showed more initiative with regard to group movements. The behaviour of male S to frequently walk between the group and the observer could reflect a certain responsibility towards the group. The group was very cohesive and there was much play behaviour. At Mokolo one would have predicted the older female R, who was most aggressive and dominant, to lead the group, as she did while they were in the boma. However, after their release leading and initiating movements were carried out by the young male P. During their stay in the boma the two females pushed him in front when they were nervous. This supports the statement in Drews (1993) that dominance does not imply leadership. The three were very relaxed and chose to remain separate from the older group, with which they joined occasionally and seasonally, and the 6 - 7 year old female in the older group did not appear to be capable of holding the two groups together. She was never observed to display leadership behaviour.

Roles of allomother and helper

Both Jane and Blou's behaviour towards the young males and towards each other showed allomothering and helping behaviour. It is interesting that none of the other juvenile females between five and ten years of age showed allomothering behaviour. The same behaviour patterns as seen at Venetia were observed at Touchstone between Celeste and male M and between Celeste and Kelly. The two young females adopted the roles of allomother and helper. At Thornybush female A took over the role of allomother to male S. Female O would also react to S when he called.

The forming of special relationships was observed from as early as 6 - 7 years of age (Kelly). The Venetia and Touchstone results showed that unrelated elephants will take on different roles in a newly established group. These roles, or parts of them, may even be taken on prematurely, which suggests that to some degree these behaviours may be genetically determined. This is especially true for allomothering behaviour, which were observed in all groups where an older female was present. However, the fact that the other older females at Venetia did not allomother young males raises some questions. Is allomothering behaviour only directed to a young which has a mother (real or adopted) and from whom a certain degree of co-operation can be expected at the time and/or also reciprocity expected in the future? Were the females at Venetia too insecure and their social structure so disturbed that they did not show the behaviour ?

There was a large discrepancy in leading ability between similarly aged females, such as Celeste and the female at Mokolo. It would appear that the role of matriarch has to be learned. However, group composition, age and sex distribution as well as individual disposition could play a part in forming and influencing leadership abilities. It is also possible that the status of the mother could have an influence, for instance if Celeste was the offspring of a matriarch, she may have learned, albeit at a very early age, what leadership entails.

Aggression

In most groups aggression and dominance behaviour did not correlate with leading ability, only at Venetia Jane was the most aggressive individual. However, this aggression towards the young juveniles probably served to maintain order. She only allowed certain individuals near her, others, even very young ones, were always peripheral to the group. Jane acted typically for a *K*-selected species, she invested all her energy, helped by Blou, in one juvenile. To achieve this she needed to keep others at bay, so that she could secure the best feeding opportunity and shade for "her" juvenile, and protect him. The results from the other groups suggest that aggression is related to the dominance hierarchy which needs to be established in a group of juveniles and not to the role of leader (see Chapter 5).

Roles of juveniles

The results from Mashatu Game Reserve showed that females up to the age of about 9 - 10 years will tend to stay near an adult female, whereas males choose other male company by the age of five years. This supports findings made by Lee (1987) that males tend to increase their proximity to their mothers more than females do. The results that young females prefer each others company to that of a young male, may reflect an early indication of the future female roles within the family unit.

At the Venetia Limpopo Nature Reserve the choice of an adult as nearest neighbour by the juveniles f2, f3 and m2, and the choice of m3 and m4 for other juvenile males, reflect the similar choices made in the Mashatu group. Only the females in category f4 differ. In Period I they kept in close proximity to each other, probably because they had spent six months in the boma together. One of these females eventually formed a bond with Jane and helped her look after the youngest individual. Therefore these two females showed closest proximity values. Non of the older females (category 3) showed any tendency to keep near to the young individuals, as no other female had shown any signs of allomothering. This contrasts with the findings in a normal group, where females will stay in close proximity to calves (Lee 1987). This may suggest that the loss of their mothers and the stability of a family had an impact on these juveniles. Even the older juveniles appeared to prefer the proximity of an adult, which could reflect a certain degree of insecurity.

Each group was unique in the way they addressed their social organization. Only time will tell whether the lack of adults affects the socialisation process and whether problems will arise in future. Some incidents in game reserves with translocated elephants that have now reached maturity tend to suggest that such problems may be encountered.

CONCLUSIONS

Allomothering behaviour appears to be genetically determined in female elephants. Care and adoption of alien young will be allotted to the youngest and to one young at a time in a group. In general, it seems that leading behaviour has to be learned, and in most cases will only be adequately performed by an adult female, but that a young 5 - 6 year old female is capable of taking on this role. However, individual disposition, early learning and possibly the social status of the individual could influence her capabilities in this regard. The forming of special relationships among females, helping defend the group and looking after the young, will occur from an age as early as 6 years. Groups of juveniles will form a cohesive group, organize themselves socially, and the roles may be divided between males and females. However, only long term monitoring will elucidate, whether these emergent social structures are adequate for normal social development.

CHAPTER 4

SOCIAL ORGANIZATION IN TRANSLOCATED JUVENILE AFRICAN ELEPHANTS:

THE DOMINANCE HIERARCHY

INTRODUCTION

The different categories and definitions of dominance in animal behaviour have been discussed by Drews (1993) who concludes that despite the great variation of definitions it is generally agreed that dominance refers to agonistic behaviour. Dominance is based on the definition by Schjelderupp- Ebbe (1922 in Drews), where dominance is an attribute of the pattern of repeated, agonistic interactions between a dyad, characterised by a consistent outcome in favour of one individual and a default yielding response by the other. However, Drews also describes some non-agonistic dominance definitions. Dominance hierarchies allows animals in a group to adhere to a set of rules in order to avoid escalation of aggressive behaviour (Cords 1988) and forms an important part of the social structure. Should aggressive behaviour nevertheless erupt, then animals may use appeasement or submissive behaviour to relieve the intensity of the conflict. In the following a difference between these two behaviour patterns in elephants is suggested.

Male elephants form dominance hierarchies (Poole 1987), which they attain through agonistic encounters and maintain through visual, acoustic and olfactory signals (Poole & Moss 1981; Poole 1987, 1989). Female elephants rarely fight but can display aggressive behaviour. Dominance in a normal family group seems to be attained by other mechanisms: age (Moss 1988), individual disposition, social status e.g. lactating mother and allomother to dominant's calf (Dublin 1983). However, Dublin (1983) showed that there is significantly more aggression towards subordinate females by dominant ones during the breeding season and that they can be denied access to scarce resources.

The manner in which translocated juvenile elephants form a dominance hierarchy is as yet undetermined. Whether a dominance hierarchy in juvenile groups could be measured by the direction and frequencies of aggressive and submissive behaviour as has been shown for captive Asian elephants (Garaï 1989,1992) was evaluated. Dominance is frequently transitive in animal groups (Appelby 1983), but need not necessarily be so. Certain bonds, such as between adult and juvenile, or special relationships between two female elephants could influence the linearity. The behaviour "trunk-over-back" ("tob"; i.e. placing the trunk along the back of another individual) is a behaviour known from courtship and mating behaviour (Poole 1996). This behaviour can also be shown by females and the relationship between this behaviour and the dominance hierarchy was investigated.

STUDY GROUPS AND METHODS

1. Study groups

see Methods, Chapter 2 for details. Data of the following groups were used for analyses.

Venetia Limpopo Nature Reserve (VLNR) 1991, Boma

Six juveniles (2 males and 4 females) ranging between 8-11 years.

Venetia Limpopo Nature Reserve (VLNR) 1992 Boma and Free

Boma:
Group A: 4 females, aged about 6-7 years old.
Group B: 3 males, 5 females, aged about 4-5 years
Group C: 5 males aged about 2.5 - 3.5 years
Group D: 5 males aged about 18 months - 2 years.
Free: The adult female Jane and 21 juveniles (Data from all three periods were pooled)

Touchstone Game Ranch, Free

10 juveniles (4 females, 6 males) ranging between 4.5 - 7 years. They had been released together for two years. (Data from all three periods were pooled).

Thornybush Game Lodge, Free

Three females aged 13-15 years, one male ca. 13 years and a juvenile male, 4 years old.

Spektakel Game Ranch, Boma

Six juvenile: 3 females 2 - 2.5 years, 3 males 3.5 - 4 years.

Mokolo River Nature Reserve, Free

Two females and a male aged about 4-5 years.

Kala Ingwe, Boma

1. 2 females, 1 male aged ca. 2.5 yrs, 2 yrs and < 2 yrs respectively (obs time: 9 hrs 45 min)
2. 1 female, 1 male aged < 2 yrs (obs time: 9 hrs 10 min)

2. Observational methods

Data from the behaviour categories Aggression and Submission were used in the following analyses (see Methods, Chapter 2, and Appendix 1 for details).

Aggressive behaviour: any form of pushing, hitting with the trunk, kicking and chasing.

Submissive behaviour: was measured by the two elements, "give-way" (moving out of the way of another individual that approaches or shows aggressive intentions i.e. threat behaviour) and "presenting" which is derived from the sexual behaviour of presenting the rear end by a female to a male, and is used as appeasement or submissive behaviour by a lower ranking individual in primates (Walters & Seyfarth 1987; Kummer 1975). Both 'give-way" and "presenting" have been shown to serve as submissive behaviours in Asian elephants (Garaï 1989,1992).

Significance was tested using a *chi*-square test , df =1 applies in all cases (Sokal & Rohlf 1981), and rank correlations on frequencies of occurrence were conducted using a Spearman's rank (r_s) correlation (Siegel 1987). Linearity of hierarchies was tested in groups with $N > 6$ individuals using the test proposed by Appelby (1983), where circular triads are calculated by the coefficient *d*, and significance is tested by Kendall's coefficient *K*, which is very similar to Landau's index (1951 in Appelby). Appelby gives values for significance up to N = 10. Where N > 10, *chi*-square is calculated by the formula:

$$x^2 = 8 / N\text{-}4\ [N(N-1)(N-2) / 24 - d + 0.5] + df, \text{ where } df = N(N-1)(N-2) / (N-4)^2$$

RESULTS

VLNR 1991, Boma

Table 1 summarises the results of rank correlations for all groups. In the Venetia boma group (1991) there were no significant correlations in ranks of frequencies of aggressive and submissive behaviour. However, the linearity test showed a significant linear dominance hierarchy with no reversals ($d = 0$, $K = 1$, $p = 0.022$). Table 2. shows the outcome of the linearity test, where the dominant of a dyad is the individual that showed higher frequencies of aggression than the partner and where the individuals have been placed to form a hierarchy. A linearity test for submissive behaviour showed no significant linearity ($d = 1.875$, $K = 0.786$, $p = 0.12$), but this could be due to too little data. All individuals showed submissive behaviour to Ch. Both Ch and B received significantly more submissive behaviour than the others ($x^2 = 28.9$; $x^2 = 33.6$; $p < 0.001$), but whereas Ch received submissive behaviour from all, most submission received by B was from male R. Female B was the most aggressive and also showed most "trunk-over-back" behaviour. However, 81.3% of her aggressive behaviour and 77.5% of her 'tob' behaviour was directed towards male R, which whom she had frequent play-fights. Out of 530 play and play-fight elements showed by B, 89.2% were directed towards R. This male was involved in most play-fight bouts, 56.4% of which were with female B. Whereas most of the play-fighting between other individuals consisted of gentle sparring the play-fights between B and R escalated to hard fighting.

Table 1. Spearman's rank correlations (r_s) between ranks of actors and recipients of aggressive and submissive behaviour.

1	2	3	4	5	6	7
Groups	**Act - Rec Agg**	**Act - Rec Subm**	**Act agg - Rec subm**	**Act subm- Rec agg**	**Act agg - Act subm**	**Act tob**
VLNR 91 boma	rs = 0.657 n.s.	rs = 0.657 n.s.	rs = 0.6 n.s.	rs = 0.77 n.s.	rs = 0.857 n.s.	rs = 0.714 n.s.
A boma VLNR 92 4f	rs = -1 p< 0.05	rs = -1 p<0.05	rs = 1 p<0.05	rs = 1 p<0.05	rs = -1 p<0.05	tob shown by most agg (Ro) to least agg (L) only
B boma VLNR 92 3m, 5f	rs = -0.613 n.s. tendency	rs = -0.58 n.s. tendency	rs = 0.786 p<0.05	rs = 0.952 p<0.01	rs = -0.619 n.s.	rs = 0.732 p<0.05
C boma VLNR 92 5m	rs = -0.828 n.s.	very little submissive behaviour shown by the one to receive most (Ll) aggression				tob shown by the most aggressive only (F)
D boma VLNR 92 5m	p<0.05 rs = -1	very little submissive behaviour shown by the one to receive most (Ru) aggression				tob shown by one ind. only
Spektakel large boma 3m, 3f	rs = -0.371 n.s. accordance by sex	rs = -0.27 n.s. accordance by sex	rs = 0.6 n.s. accordance by sex	rs = 0.757 n.s. accordance by sex	rs = -0.671 n.s. accordance by sex	rs = 0.8 n.s. tob shown mainly by males
Touchstone free 6m, 4f	rs = -0.694 p< 0.05	rs = -0.588 n.s.	rs = 0.675 p<0.05	rs = 0.936 p<0.01	rs = -0.53 n.s.	rs = 0.573 p<0.05
Thornybush free	rs = -0.8 n.s.	rs = -0.275 n.s.	rs = 0.986 p<0.05	rs = 0.5 n.s.	rs = -0.443 n.s.	tob not seen
Mokolo free 1m, 2f	accordance	accordance	accordance	accordance	accordance	tob shown mainly by most agg f (R)
VLNR free 10m 11f 1 adult f	rs = -0.647 p<0.01	not sufficient data				tob mainly shown by two oldest males

Column 1: study groups, free ranging or in bomas
Column 2: actor and recipient of aggression
Column 3: actor and recipient of submissive behaviour
Column 4: actor of aggression and recipient of submissive behaviour
Column 5: actor of submission and recipient of aggression
Column 6: actor of aggression and recipient of submissive behaviour
Column 7: actor of aggression and actor of "trunk-over-back"(tob)
"accordance" : these groups showed similar patterning, but the size of the group precluded statistical analysis.

Although female B showed significantly high values and most aggressive behaviour (34.3% of all aggressive interactions; $x^2 = 148$, $p < 0.001$), it was female Ch who was the dominant individual by linearity, followed by female P. Female P formed a special relationship with Ch and although she was younger that B was dominant to her. P and Ch went off alone together following the release.

TABLE 2. Dominance hierarchy for the Boma group at VLNR 1991

		Subordinate					
		Ch	P	B	R	E	S
Dominant	Ch	-	10	10	31	13	8
	P	2	-	84	38	9	47
	B	2	14	-	222	13	22
	R	0	10	124	-	46	13
	E	1	0	2	16	-	12
	S	1	35	2	3	6	-

Absolute values of aggressive interactions are given. Row individuals are dominant to column individuals. No reversals. Ch, P, B, S are females; R and E males

VLNR 1992 Boma

In Group A (4 females) all aggressive and submissive behaviours were significantly correlated, two negatively three positively ($p < 0.05$)(Table 1). The most aggressive individual received least aggression, showed least submission and was the recipient of most submissive behaviour from others, and *vice versa*. The behaviour "trunk-over-back (tob) was shown by only two individuals, but mostly by the most aggressive female Ro, and mainly towards the most submissive female. Ro was significantly more aggressive than the other three individuals ($x^2 = 435$; $p < 0.001$) and very nervous. She calmed down considerably after the elephants had been released and had joined up with all the others and the matriarch.

Group B (3 males, 5 females) showed significant positive correlations between ranks of 'aggressor' and 'recipient of submissive behaviour' ($p < 0.05$) and between ranks of 'actor of submissive behaviour' and 'recipient of aggression' ($p < 0.01$)(Table 1). Female D (rank 1), who showed significantly higher values ($x^2 = 80$; $p < 0.001$) of aggression than any others in the group, showed no submissive behaviour and received nearly no aggression from others. Male A (rank 7) and female M (rank 8) received significantly (A: $x^2 = 39.19$; M: $x^2 = 89.97$; $p < 0.001$) more aggression than the others. M showed significantly more ($x^2 = 159$; $p < 0.001$) submissive behaviour than any others and displayed no aggression.

The behaviour "trunk-over-back" (tob) was displayed significantly more ($x^2 = 170$; $p < 0.001$) by female D than by any others and never by female M. There was also a positive correlation between the ranks of 'aggressor' and "tob" ($p < 0.05$). The linearity test showed significant linearity with one reversal ($d = 1$, $K = 0.952$, $p < 0.003$), shown in Table 3a. Male Sa was dominant to male G. Likewise there was significant linearity for submissive behaviour ($d = 1$, $K = 0.952$, $p < 0.003$), shown in Table 3b. Male G was submissive to male Sa. The dominance hierarchy seemed well established in this group. Female D would initiate movements out of the inner boma into the larger exercise camp and vocalized most, suggesting she was attempting to fill a leadership role (see Chapter 3).This female appeared to lose her rank after the elephants were released with the matriarch and joined up with older juveniles. D joined up with some of the males in a subgroup for a while, together with female M. There was now no aggression from her towards M and a cluster analysis of nearest neighbours showed them to have the highest association values. D eventually joined the main group again, but kept to herself, whereas M stayed with the subgroup of males, who occasionally split off from the main group (Chapter 6).

Group C consisted of five young males and in general they did not interact much with one another. There were no significant correlations between the ranks of aggressor and submissive individuals, but the most aggressive male F received least aggression and showed no submission, and the least aggressive male Ll showed no aggression, received most aggression and showed most submissive behaviour. The behaviour "trunk-over-back was shown by F only.

Group D comprised five very young males and there was a significant negative correlation between the ranks of 'aggressor' and 'recipient of aggression' ($p < 0.05$). Only the smallest male Ru showed any submissive behaviour, mainly to Bg the oldest and most aggressive individual. "Trunk-over-back" was only shown by male N to Ru, who showed aberrant behaviour and repeatedly suckled N's ear pinna (Garaï 1993, 1994 and Chapter 7).

Table 3a. Dominance hierarchy for the boma group B at VLNR 1992

		Subordinate							
		D	G	Lt	Sa	Ba	T	A	M
Dominant	D	-	20	11	23	12	17	23	16
	G	0	-	10	2	14	12	21	25
	Lt	0	1	-	12	3	2	8	13
	Sa	0	**31**	2	-	6	10	26	12
	Ba	0	2	1	5	-	9	14	8
	T	2	2	1	0	2	-	10	32
	A	0	1	0	1	1	0	-	20
	M	0	0	0	0	0	0	0	-

Absolute values of aggressive interactions are given. Row individuals are dominant to column individuals, one reversal: Sa is dominant to G (bold type).

Table 3b. Submissive hierarchy for the Boma group B at VLNR 1992

		Receiver							
		M	A	T	Ba	Sa	Lt	G	D
Submissive	M	-	8	13	7	5	12	13	11
	A	0	-	6	2	9	2	5	1
	T	0	0	-	6	5	3	5	1
	Ba	0	0	1	-	1	1	2	1
	Sa	0	1	0	0	-	4	0	3
	Lt	0	0	0	0	0	-	3	3
	G	0	0	0	0	**5**	0	-	5
	D	0	0	0	0	0	0	0	-

Absolute values of submissive behaviour are give. Row individuals are submissive to column individuals. One reversal: G is submissive to Sa (bold type).

Spektakel, Boma

There were no significant aggressive or submissive relationships evident for this group (Table 1 and Figure 1a), however, the most aggressive male S showed no submission and female I showed no aggression but was significantly more submissive than any others ($x^2 = 42.7$; $p < 0.001$). Although group size precluded statistical analysis, the patterns observed in this group when investigated separately for each sex, followed the patterns observed in the other larger groups (Fig. 1b and 1c). The linearity test of dominance showed significance with male S being the dominant, followed by male L ($d = 0$, $K = 1$, $p = 0.22$). Data with 4 unknown relationships were insufficient to estimate the linearity in submission.

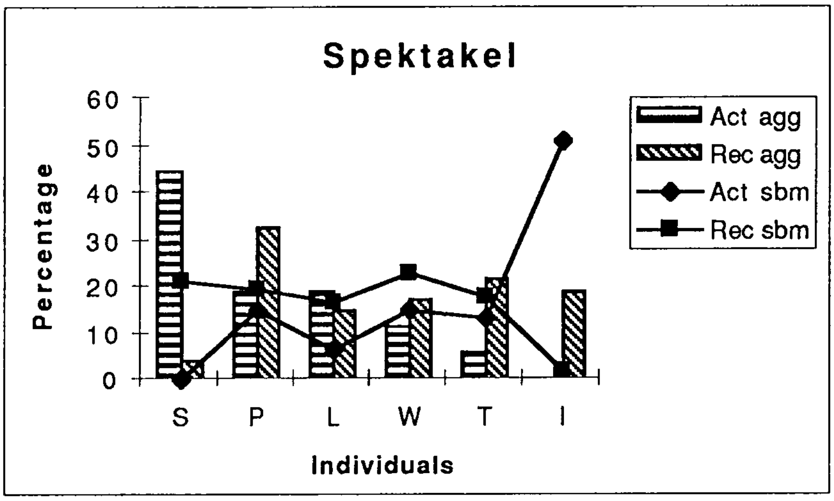


Figure 1a. Relationship between aggressive and submissive behaviour for all six animals.
Act agg: actor of aggression; Rec agg: recipient of aggression
Act sbm: actor of submission; Rec sbm: recipient of submission

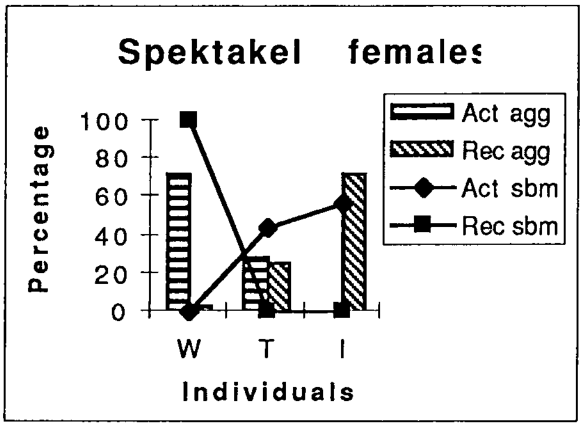


Figure 1b. Relationship between aggressive and submissive behaviour for the females only.

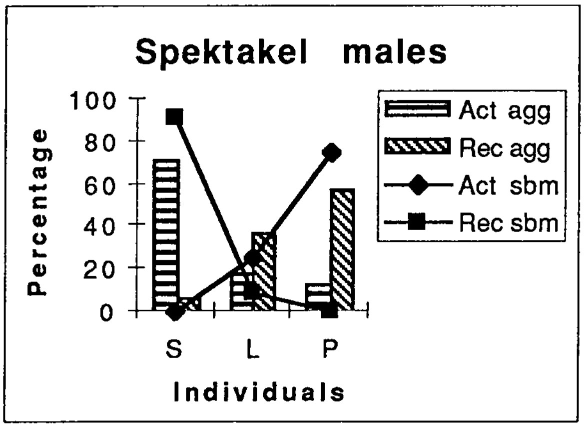


Figure 1c. Relationship between aggressive and submissive behaviour for the males only.

"Trunk-over-back" (tob) behaviour was frequently observed in this group, which also displayed much play-fighting and in general a lot of play behaviour. The behaviour "tob" was shown mainly by the males and significantly more so by P and S (P: $x^2 = 226$; S: $x^2 = 116$; $p < 0.001$). Female I, the youngest individual never displayed "tob".

Touchstone

There was a significant negative correlation between ranks of 'aggressor' and 'recipient of aggression' ($p < 0.05$)(Table 1), a significant positive correlation between ranks of ' aggressor' and 'recipient of submission' ($p < 0.05$) as well as between ranks of 'actor of submission' and 'receiver of aggression' ($p < 0.01$). Female C, the leader of the group never displayed any submission. "Trunk-over-back" correlated significantly and positively with rank of 'aggressor' ($p < 0.05$) and was shown mainly by the oldest male and females C (the leader) and K, who helped C defend the group and look after the youngest male M (see Chapter 3 on Roles). Most "tob" was received by the males P and A. Both these males walked at the rear of the group more than any other individuals (P: 39.2% of observations; A: 22.9%). The behaviour "tob" was also shown towards the youngest male M by females C and K. These two females were looking after M and it seems that the behaviour "tob" can be seen in different contexts. In this case it could have been affiliative. The linearity test showed significance ($d = 3$, $K = 0.925$, $p < 0.001$) with one reversal and identified female K as the most dominant, even though C was the leader. Interestingly the youngest male M was dominant to the oldest male B. Male M was allomothered by the leading female (Chapter 3). Data were insufficient for a submission linearity test, but the rank correlations suggest that linearity probably was present.

Thornybush

In this group the only significant positive correlation (Table 1) was between the ranks of 'aggressor' and 'recipient of submission' ($p < 0.05$). Play-fights occurred between the oldest female A (ca. 15 years) and the male (12 - 13 years). Most aggression was shown by male B especially towards female A. It would seem that the dominance hierarchy was not clear. "Trunk-over-back" was not seen in this group. There was a large age difference in this group (range = 4 - 15 years).

Mokolo

No statistical analyses could be carried out on this small group, however, the patters observed were similar to patterns found in larger groups. "Trunk-over-back" was displayed by both females, but mainly by the most aggressive individual towards the young male P. This could also have been an affiliative behaviour pattern, as they both directed most of their affiliative behaviour towards him.

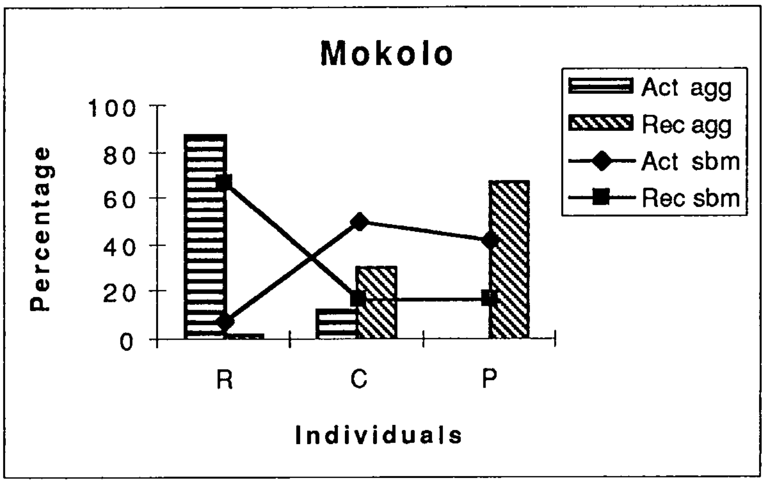


Figure 2. Mokolo. Relationship between aggressive and submissive behaviour
R and C are females, M is a male.

VLNR, Free

Following the release of the various boma groups, all elephants joined up with the adult female Jane to form one large group of 22 elephants. Jane was significantly ($x^2 = 1265$; $p < 0.001$) more aggressive than any other individual and received significantly ($x^2 = 206$; $p < 0.001$) more submissive behaviours. A rank correlation for the juveniles shows a significant negative correlation between the ranks of 'aggressor' and 'recipient of aggression' ($p < 0.01$). The youngest male Sq did not fit into this correlation, he had been adopted by Jane (Chapter 3) and therefore received no aggression other than from Jane herself. In general, insufficient submissive behaviour was observed among the juveniles for statistical analyses, but after Jane, the oldest juvenile female B received most submissive behaviours. "Trunk-over-back" was shown mainly by the two oldest males.

A linearity test displayed significant linearity ($d = 249.5$, $x^2 = 88.5$, $p < 0.001$). There were at least 5 reversals. Because of the numerous empty cells in the matrix, the linearity of the hierarchy has to be viewed with caution, nevertheless there is a tendency for the hierarchy to reflect the ages of individuals. As mentioned previously, Sq did not fit into this linearity.

Kala Ingwe

These elephants were only observed for a few days and were not included in Table 1.
It was interesting to note that in group 1 the oldest female M (ca 2.5 years) was the most aggressive (76.3% of the total) and displayed 'tob' to the youngest individual, a male (< 2 years), who was also the recipient of most aggressive behaviour (65.8%). Female M received no aggression from the other two, but the male was submissive to her, frequently 'presenting'.

DISCUSSION

In two boma groups and two free-ranging groups there was a significant negative correlation between the ranks of 'aggressor' and 'recipient of aggression'. In addition, the Mokolo group showed a similar pattern, as did the Spektakel group when analysed by sex. In two boma groups and three free ranging groups there was a positive correlation between the ranks of aggressor and 'recipient of submission' and at Spektakel and Mokolo a similar pattern was evident.

Linearity in dominance hierarchies was shown for all groups where tests could be carried out. Linearity for submissive behaviour was shown in two of these groups. In the other groups data were insufficient to conduct statistical tests. It was not always the most aggressive individual that was the dominant one. Submissive behaviour was shown by all others towards the dominant and/or most aggressive individuals. In the wild, subordinate animals can avoid dominant ones, for instance at a feeding spot, this is possibly why submissive behaviour is seen relatively rarely. Alternatively in an established hierarchy it is not necessary to display subordinate signals if the subordinate animal has clearly demonstrated that he accepts the dominance of the other (De Waal 1987). The results of the free ranging Venetia group, although not comprehensive, show that the dominance hierarchy tends to be maintained by age, with a few possible exceptions when same age individuals are present in the same group. Attainment of dominance through age has been established for elephants (Moss 1988) as well as for several ungulate species (see Thompson 1993). Linearity was observed even in a group of similar aged juveniles. This is rather surprising and raises the question whether there are factors other than age that influences the linearity of hierarchies. An interesting point is that at Venetia, Touchstone and Thornybush, where the youngest individual was allomothered by the oldest female, these specific juveniles did not seem to adhere strictly to the rules of dominance hierarchy and even showed aggressive behaviour towards older individuals. This would suggest that having a mother or an allomother guarantees a certain amount of protection from aggression from other group members. It would be interesting to find out whether the position of the mother or allomother influences the position of the juvenile, as has been shown for primates (Kawai 1958; Cheney 1977; Gouzoules *et al.* 1987) and how long this influence lasts in the absence of the dominant matriarch. At Venetia 1991 female P had formed a special relationship with the most dominant female Ch and was dominant to the older female B. It is possible that the relationship to a dominant female enhances the status of an individual.

The unisex groups in the bomas (groups A and D at Venetia) showed that both females and males will establish a dominance hierarchy. In the Venetia group (1991) the dominant individual was not the most aggressive. She appeared to adjust least well to the captive situation and left the boma with one other individual, only to join the others three years later. It would appear that being dominant requires not only acceptance from other group members but also the disposition to accept this position by the individual. Dominance may involve higher costs to the individual, as has been shown for some mammals (Moore 1996) and the individual must be prepared to accept these costs. At Thorny-bush it appeared that the dominance hierarchy was not established and was either still in the formation stages, or the dominance relationship had been established between certain indivi-duals, which therefore did not have to display aggression. At Spektakel the hierarchy was also not yet established, although these individuals had been together for several months. These elephants were very young and playful and the fact that the males were older may have influenced the dominance hierarchy. However, the absence of older females may in part adversely effect male socialisation.

The correlations in some groups and the general trend in all groups for an individual being more likely to receive aggression if he/she is not aggressive himself/herself, and also that an individual is more likely to show submission if he/she is not aggressive, collectively support the notion that a dominance hierarchy can be measured by the direction of aggressive and submissive behaviours (defined by "presenting" and "give-way") in a group of juvenile African elephants. A similar pattern was also suggested for captive Asian elephants (Garaï 1989;1992).

In any group of animals strategies for harmonising the social organisation have to be found to ensure group cohesion and co-operation. In the end, this is crucial for the security of each individual. A dominance hierarchy is one such strategy. Advantages associated with dominance were clearly seen during feeding time in the bomas when some individuals were denied access to the feeding troughs. Even in the wild, low ranking individuals were pushed away from shady spots, rare food resources and towards the more vulnerable positions on the periphery of the group.

The behaviour "trunk-over-back" correlated with the ranks of aggression in two groups and was displayed more by males or by the most dominant female in all groups investigated. This behaviour can frequently be seen during play, in which case it is not always possible to discern whether it is a play element or a dominance behaviour, this is as play behaviour will include all behaviour categories and behavioural sequences may be reversed during play sequences (Millar 1987). It appears that "tob" can be observed in different contexts such as play behaviour and friendly interactions. In the latter case it possibly has an affiliative connotation, although dominance behaviour in this context cannot be excluded. The behaviour of the females C and K at Touchstone serve to illustrate this. They both showed "tob" most frequently to the youngest male M, towards whom they both displayed allomothering behaviour (Chapter 3).

It is interesting that the behaviours 'trunk-over-back' and 'presenting' were shown by the very young individuals at Kaia Ingwe. Observations of captive Asian elephants (Garaï, unpublished data) revealed that a calf 'presented' for the first time when it was introduced to its father at the age of a few weeks, without apparently having to learn the behaviour from experience.

CHAPTER 5

SOCIAL ORGANIZATION IN TRANLSLOCATED JUVENILE AFRICAN ELEPHANTS:

TRUNK - MOUTH - CONTACT: AN INTRIGUING BEHAVIOUR

INTRODUCTION

The behaviour of placing the trunk tip into a partner's mouth has various connotations. When an individual is feeding or apparently chewing on something a second individual may place its trunk tip into the mouth of the first as means of gaining information on what the other is eating (Adams & Berg 1980). This behaviour was termed 'mouth inspect' in the present study. However, two individuals that are not feeding may place the trunk tip into each other's mouths, and this can occur within various contexts: when elephant families or groups meet each other they perform a so called 'greeting ceremony' (Moss & Poole 1983) during which they place the tips of their trunks into a partner's mouth. The behaviour can also be seen when elephants play or any time during the day when two individuals meet, or in between other activities, either performed one after the other or simultaneously, often involving complicated twisting of the trunks, but can also be shown by one individual only. This behaviour (termed trunk-mouth-contact -tmc-, Garaï 1989,1992) has also been described as a 'reward' from mother to offspring and feeding of partners (Kurt 1986), and as a gesture of recognition and friendship and a behaviour of reassurance (Adams & Berg 1980), however the latter authors did not differentiate between placing the trunk tip into the mouth of a partner and touching a partner's lip with the trunk tip. This latter behaviour (termed trunk-lip-contact - tli-) has been shown to be an affiliative behaviour in Asian elephants (Garaï 1989 1992).

In a study on captive Asian elephants (Garaï *op. cit.*) there was a positive correlation between the amount of aggressive behaviour between dyads and trunk-mouth-contact (tmc). This behaviour was seen mostly between the more aggressive individuals and during sparring bouts, and was seen less between partners which had a special relationship with one another. The question was raised whether it is a behaviour of appeasement to prevent aggressive behaviour from escalating (Hammerstein 1981; Maynard Smith & Parker 1976) and whether a higher ranking individual will perform tmc more than others. In the present study further and more detailed observations on this interesting behaviour were made.

METHODS

1. Study Groups

(see Methods Chapter 2, for details) Data of following study groups were used for analyses:

Venetia Limpopo Nature Reserve 1991, Boma
Spektakel Game Ranch, Boma
Thornybush Game Lodge

Play-fighting bouts of sufficiently long duration could be observed in the above groups only. Additionally, observations in a boma were more likely to be unbiased as all individuals could be observed all the time.

2. Observational data

Data of tmc was taken from the *ad lib.* sheets and put into two way matrices for each study group. Similarity tests (see Chapter 2, Methods) were conducted per dyad so that the behaviour could be analysed in relation to the frequencies that individuals performed the behaviour in total. A Spearmans' rank correlation was subsequently used to test for significance. The same was done with frequencies of play-fighting bouts. Elements of play-fighting sequences were analysed for patterning of the behaviour (described in the Results). Linearity tests were conducted and compared with dominance, affiliative and aggressive behaviours observed in each group. For the analyses of behaviour between sexes a Binomial test was used.

RESULTS

Venetia Limpopo Nature Reserve 1991, boma

Figure 1 shows the results of a comparison of tmc (n = 164) and play bouts (n = 309) per dyad for the Venetia 1991 boma group. In the 9 dyads that showed both behaviours there was a significant correlation ($r_s = 0.967$, $p < 0.01$), the other 6 dyads displayed either no play bouts and/or tmc or data were too few for analyses. As discussed in Chapter 7 on stress, (section 2), female B and male R was the only dyad where play fighting escalated to higher levels. Ranked in terms of aggressive behaviour female B was the most aggressive (but not the most dominant, (see Chapter 4), followed by R and then P. These three individuals also had highest values for tmc.

When analysed within context, tmc occurred 67.1% during play or play-fighting. Analyses of entire sequences showed that of two preceding and two following single elements, in 85.7% tmc was preceded and/or followed by an aggressive element (e.g. push-trunks, see Appendix 1 for definitions), in 52.4 % tmc was preceded or followed by the play element trunk-over-head (toh), in 4.8% by a dominant element and in 3.6 % by an affiliative element (trunk-lip-contact).

Out of 46 sequences of play-fighting in 67.4% tmc occurred within the first three elements of the sequence and in further 4 sequences within the first third of the sequence. In long play-fight sequences tmc could occur several times. There did not appear to be any pattern as to which individual performed tmc. There was also no linearity (linearity test) and tmc does not seem to be a behaviour of dominance or submissiveness. Female P performed most tmc, followed by male R and female B, whereas R was the recipient of most tmc, followed by P and B.

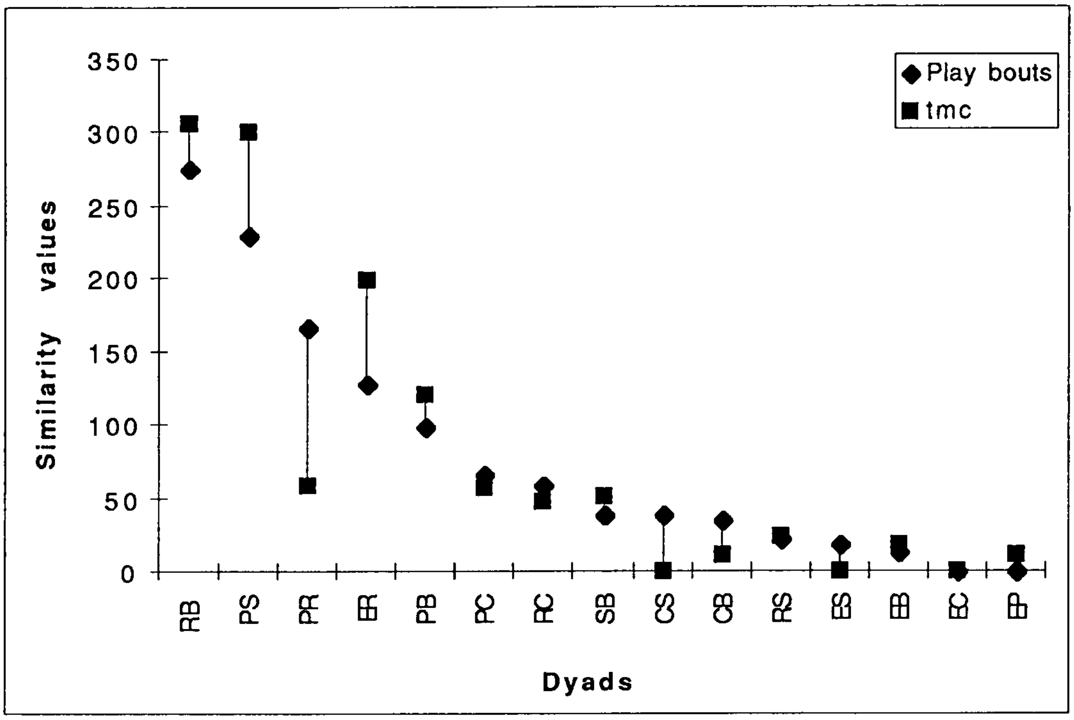


Figure 1. Comparison of play fighting bouts and the amount of trunk-mouth-contact (tmc) per dyad for the Venetia 1991 boma group based on similarity values. (Individuals: R and E are males B, P, C, S are females).

Spektakel Game Ranch

Figure 2 shows the results for this group (tmc: n = 138). Female I never played, female W played very little and female T played slightly more frequently. In the dyad SI, female I performed tmc once to male S. It was mainly the three males (S, P, L) that had play fighting-bouts and these individuals also showed most tmc. It is interesting that the males showed much tmc to the females, but not *vice versa*, although the males were more aggressive and more dominant. Male S was the most aggressive and the most dominant as per linearity test (Chapter 4), and he was the recipient of most tmc, followed equally by P and L, whereas P performed the behaviour most, followed by L and then S. Eighty three percent (82.6%) of the recorded tmc occurred during play or play-fighting.

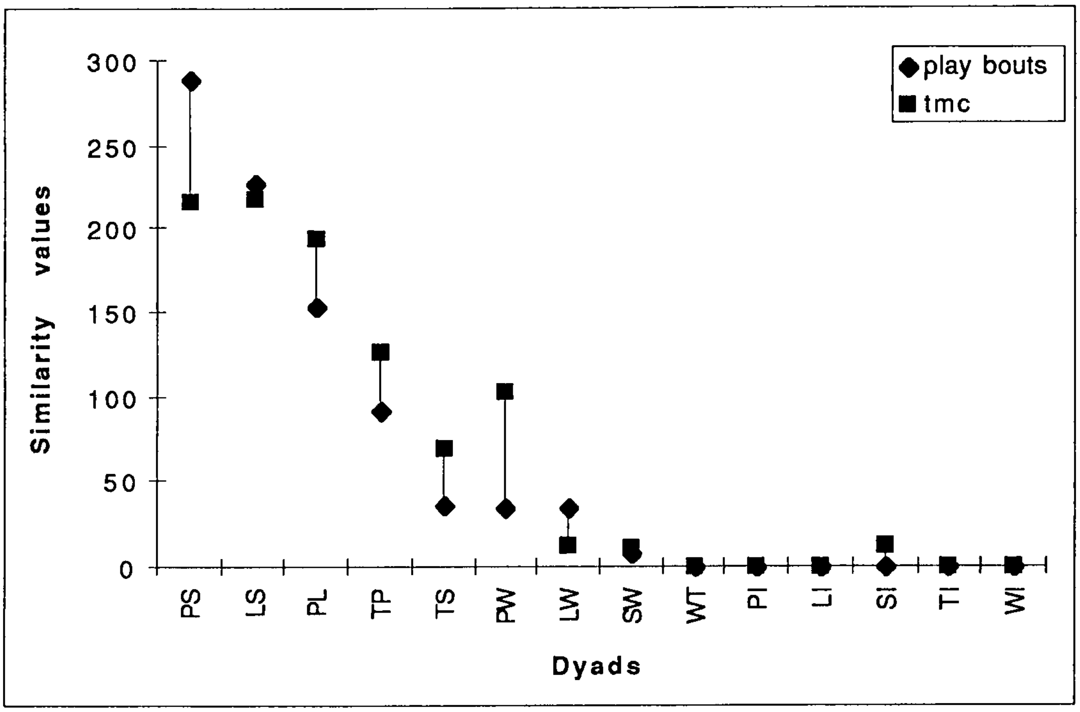


Figure 2. Comparison of play fighting bouts and the amount of trunk-mouth-contact (tmc) per dyad for the Spektakel group based on similarity values. (Individuals: S, L, P are males T, W, I are females).

During most of the play sequences between two individuals a third or fourth individual would join in, which made further analyses of a sequence impossible, however, nearly every time a new individual joined a play session he would perform tmc with one of the other two partners.

Thornybush Game Lodge

Due to the rather short observation period of this group not many tmc elements were recorded (n = 17). However in this group play-fighting occurred between female A and male B and six sequences were recorded, in addition three play sequences between male B and the juvenile S were recorded. In all sequences tmc occurred and was preceded or followed by an aggressive element or a play element (within 2 preceding or 2 following elements), such as trunk-pushing. Gentle play occurred between male B and the juvenile S. Male B, the most aggressive individual performed tmc most. Female A and the juvenile received most tmc. Of all recorded tmc 64.7% occurred during play or play-fighting.

Investigatory, aggressive and affiliative behaviour and trunk-mouth-contact

In order to assess whether there was any association between tmc, investigating what a partner was feeding (see Appendix 1 for details), aggressive and affiliative behaviour, the data of these behaviours for Spektakel and Venetia 1991 were compared. There were no correlations between the ranks of any of these behaviour categories. There was also no correlation between ranks of investigating and tmc. At Spektakel the most aggressive individual, male S, was the recipient of most tmc and investigatory behaviour, but this did not apply at Venetia. At Spektakel investigating occurred significantly more frequently between the males than between the females (Binomial test, $z = 3.87$, $p < 0.00007$), and significantly more from females to males than *vice versa* (Binomial test, $z = 3.48$, $p < 0.0003$). At Venetia 1991 females B and S were the recipients of most investigatory behaviour. Investigating had no linearity at either reserve. It appears that investigating is done to the individual that happens to be nearby and not to a specific individual.

DISCUSSION

The behaviour trunk-mouth-contact (tmc) was seen mainly in the context of play or play-fighting and was generally preceded or followed by an aggressive or play behaviour element (within two preceding and two following elements). If tmc were a behaviour reserved for dominant individuals one would expect a linearity, which was not the case. If tmc were a behaviour of submission one would expect the individuals lower in the hierarchy to perform it more than the dominant ones, this was also clearly not the case in the present study. Those individuals that diplayed most play-fighting and were most aggressive also showed most tmc. The above results strongly suggest that tmc is a behaviour of appeasement used to reduce aggressive motivation. Serious fighting between two animals can escalate to harmful levels, it is therefore for the benefit of both individuals involved to assure that these levels are not reached. Allowing a partner to place his trunk tip into one's mouth, shows non-harmful intent (the trunk tip could easily be bitten), on the other hand placing the trunk tip into a partner's mouth shows trust and possibly indicates acceptance of the rules of non-harmful play-fighting. The transition between gentle play and play-fighting is gradual and it is therefore necessary to have rules to prevent play from escalating. It would be interesting to see whether seriously fighting bulls, which allow fighting to escalate, still perform tmc. Showing non-aggressive intentions would be necessary at each encounter, which would explain the mutual tmc of family members when two groups meet (Moss & Poole 1983), or when two individuals meet.)

The behaviour is possibly ritualised and the original function has been changed. Four possible evolutionary steps are suggested:

1. Kurt (1986) suggested that tmc could be derived from the behaviour of placing food into a partner's mouth, a behaviour seen by him in wild Asian elephants. This would represent a friendly gesture.

2. Feeding of another partner was never seen in the present study nor in the study on captive Asian elephants (Garaï 1989,1992), but occasionally an individual might take food out of another's mouth, e.g. a calf from an adult. Allowing another individual to take food is probably a sign of affiliation and therefore tmc could be ritualised from this behaviour pattern.

3. The behaviour could be a ritualisation of the mouth inspecting by calves when they place their trunk tips into their mother's mouth to investigate what she is eating and thus learn what is edible and what isn't.

4. Mothers will inspect the mouths of their calves to assess what these are chewing on. This friendly behaviour (showing concern) could also be felt as a 'reward' by the calf (as suggested by Kurt, 1986) which would be another possible evolutionary origin of the ritualised tmc.

All four suggested of the above scenarios originate from affiliative intentions, supporting the suggestion that tmc is likely to be a behaviour of appeasement.

CHAPTER 6

SOCIAL STRUCTURE IN TRANSLOCATED JUVENILE AFRICAN ELEPHANTS:

GROUPING BEHAVIOUR

INTRODUCTION

Elephants live in permanent matriarchal family groups with long lasting bonds between the members. Some family units have consistent associations with each other in extended herds (Moss & Poole 1983). The main function of elephant families is to ensure maximum protection and increase the survival chance of calves. Females in a family unit cooperate in protecting calves and defending the group. The role of matriarch is essential to the cohesion of the group. East African studies have shown that members of a family unit which has lost its matriarch will fragment (Moss 1988). However, elephants which have experienced heavy poaching, such as in Uganda, will congregate into larger herds (Abe 1994). Translocated juveniles that have lost their families are frequently grouped with same aged peers as older juveniles can be aggressive towards younger individuals. It is uncertain how these juveniles will react: maintain close-knit groups or fragment into subgroups. In the former case an understanding of the strategies employed to maintain group cohesion is required, and in the latter, how subgroups form from artificially constituted groups.

METHODS

1. Study groups

Data for the following groups were used for analyses. See Chapter 2 for details.

Venetia Limpopo Nature Reserve (VLNR)
Touchstone Game Ranch, Free
Mokolo River Nature Reserve, Free
Mashatu Game Reserve

Additional information on grouping behaviour was obtained through a questionnaire and interviews with 24 private owners of juvenile elephants in South Africa.

The original VLNR boma groups are as follows: Group A: four females aged 6 - 7 years, St, L, K, Ro. Group B: three males Sa, G, A, and five females D, Lt, T, Ba, M all aged 3.5 - 4.5 years. Group C five males aged 2 - 3.5 years Ll, Bb, Sq, F, Tb. (Estimated ages are given for 1992).

2. Observational sampling

Spacing categories of the group and nearest neighbours were noted at 5 min intervals. Focal animals and their nearest neighbours were not sampled more than twice in a 30 minute period.

Spacing categories were as follows:
Category 1 = No individual more than 2 m apart (all within 'touching' distance)
Category 2 = all individuals within 30 m
Category 3 = all individuals within 50 m
Category 4 = all individuals within 100 m
Category 5 = some individuals over 100 m apart
Category 6 = group divided into separate units, location of second group unknown.

Nearest neighbour patterns was depicted using a Cluster Analysis (Morgan *et al.* 1976) based on the similarity value (S). (See Chapter 2). A maximum spanning tree (MST) was constructed, so that every individual in the group had at least one link to another individual. The rules of a MST generally exclude the formation of closed 'loops', however this rule was modified in the Touchstone MST to illustrate the close relationship between three individuals (C, K and M). Similarity values are provided in the figures. The higher the similarity value the more frequently these neighbours were seen together.

RESULTS

Spacing of individuals

<u>Venetia Limpopo Nature Reserve (VLNR)</u>

In 1991 the first six elephants (8 - 11 years old) were acquired. After having spent six months in the boma they split into subgroups of two (2f) and four (2f, 2m) following their release and remained in totally different areas of the 20 000 ha reserve. The two females that walked off on their own had formed a special relationship (Chapter 3) in the boma. In 1992 another 17 (2.5 - 7 years old) juveniles and the eighteen year old female Jane, who was not related to any of the juveniles, were acquired. Soon after Jane and 13 juveniles were released together the four from the 1991 release and the four females (group A), which had been released a month earlier, joined up with Jane. In 1993 two additional adult females were acquired who also joined up with Jane. The other two females from 1991 were joined in 1992 by a female that had escaped during the offloading of group A (see page 7), and in 1993 by two very small males (the only two remaining from group D, details on page 7). This little group remained separate until 1994. In this same year a family unit of 14 elephants including adults was acquired.

Figures 1, 2 and 3 show the spacing of nearest neighbours for Jane and the 21 juveniles for periods I, II and III respectively. The strongest association during all three periods is between Jane and her adopted juvenile male Sq, who was the youngest individual (Chapter 3). The affiliative behaviour from Jane to Blou (B) increased with each successive period (Chapter 3), and Blou eventually formed a special relationship with Jane, helped her defend the group and look after Sq. These three elephants remained in close proximity to one another throughout the observation period.

The original groups A, B and C from the boma can still be seen in period I, with a few exceptions. Male Tb from group C attempted to associate with Jane. The most dominant female D, the most submissive female M (Chapter 4) and male A from group B, associated with the young males from group C. The two females D and M were pushed to the periphery of the group during period II. Female M remained in the subgroup throughout the entire observation time, whereas female D joined Jane's group again in period III. R and E the oldest males (8 - 10 years old in 1991) were pushed to the periphery of the group and eventually joined up with the smaller males F, A, Ll and the females M and D to form a subgroup.

Towards the end of period III two adult females were acquired and they joined the main group. It was at about the same time that the subgroup started to split off, for one or two days at a time; this may however, have been coincidental. The subgroup had no definite leader. R and E would take turns to lead. The two young males Ll and F were always in close proximity of one another, but Ll chose the oldest male R as his nearest neighbour. There were very few interactions between the elephants of the subgroup but they appeared very relaxed.

The two males Ll and Bb, the youngest males in the group (about 3 years old at the time), went off on their own for two - three days. Bb had been peripheral to the group in period I but attempted to get nearer to Jane in the following year. However, she seemed to ignore him until after Sq's death, when he took over the desired place next to Jane (Chapter 3). The other young male Tb followed Jane and never ventured far from her, but she never showed any allomothering behaviour towards him.

In period II and III female St attempted to get closer to Sq. This may represent an attempt to increase her affiliation with Jane *via* Sq and thus gain better access to scarce resources and protection, a strategy sometimes used by female elephants (Dublin 1983). She occasionally showed threat behaviour towards the observer and stood together with Jane and Blou to face danger.

When the family group arrived in 1994 one of the new females and her calf joined Jane's group. The new group was always in the same area as Jane's group and occasionally joined up with them. It was at this same time that the five other elephants, which had remained separate (two since 1991), joined up with Jane's group.

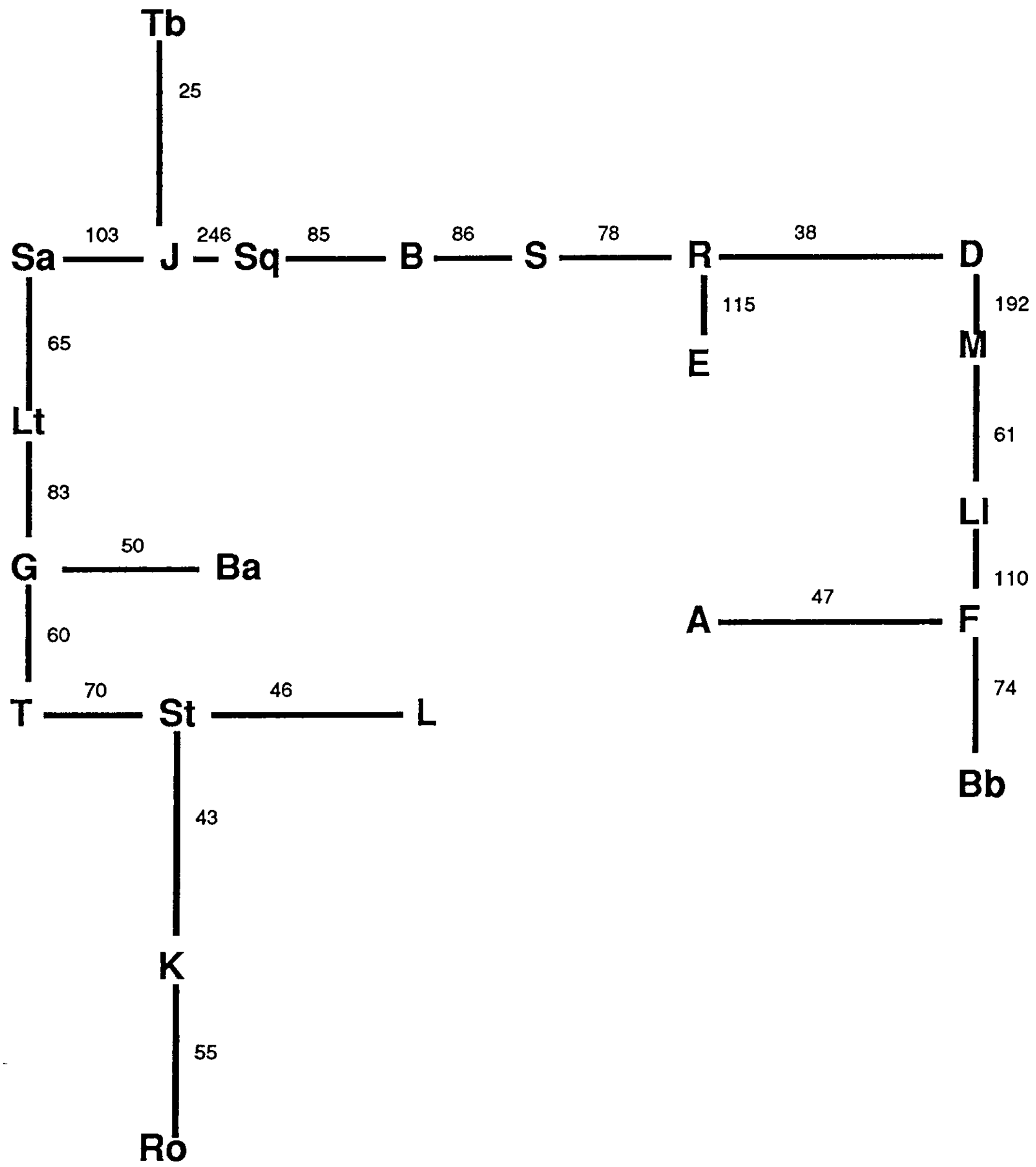


Figure 1. Nearest Neighbour Analysis for Jane and 21 juveniles.
Period I, VLNR. Figures are similarity values, the higher the value the closer the association.

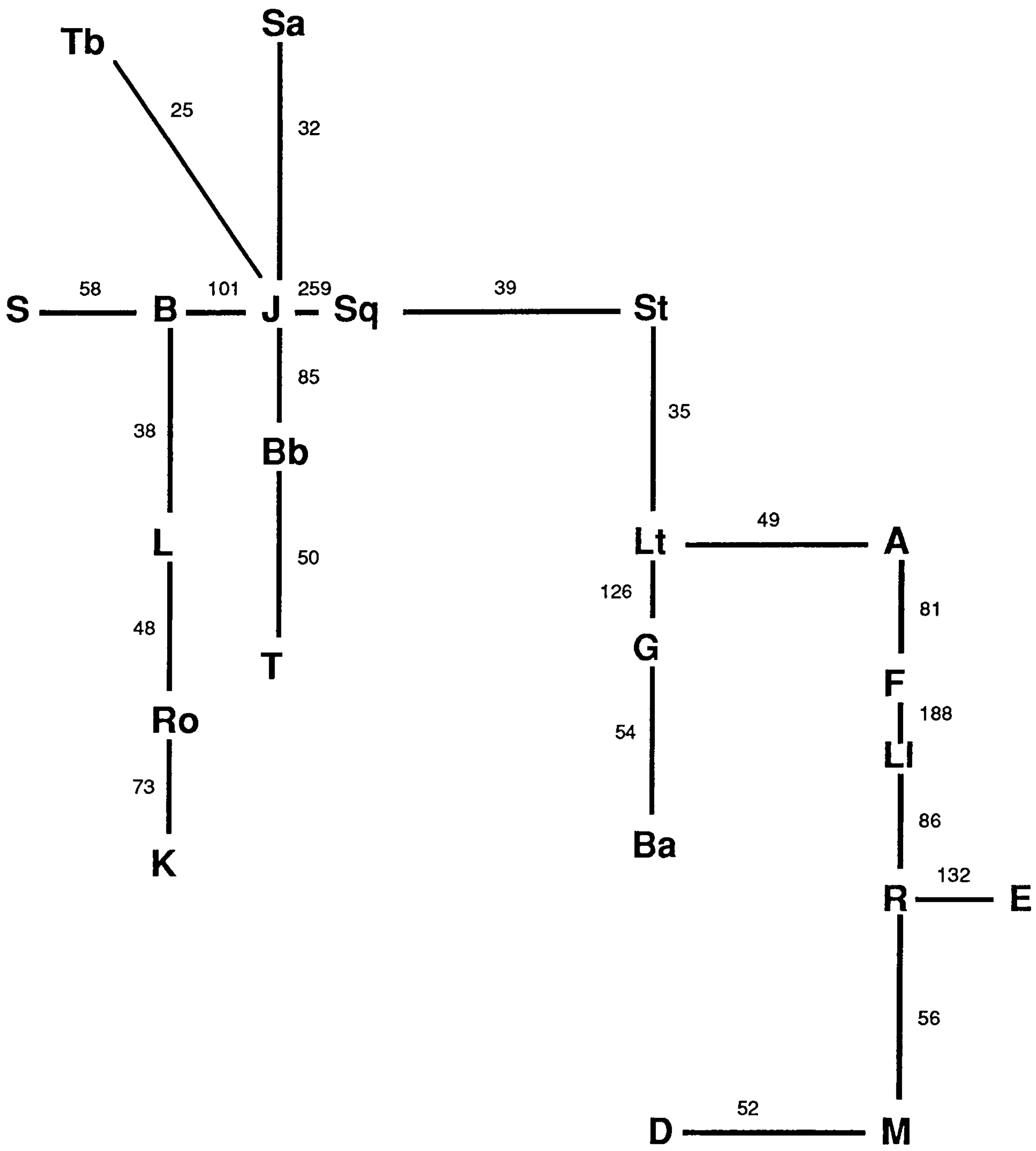


Figure 2. Nearest Neighbour Analysis for Jane and 21 juveniles. Period II, VLNR. Figures are similarity values, the higher the value the closer the association.

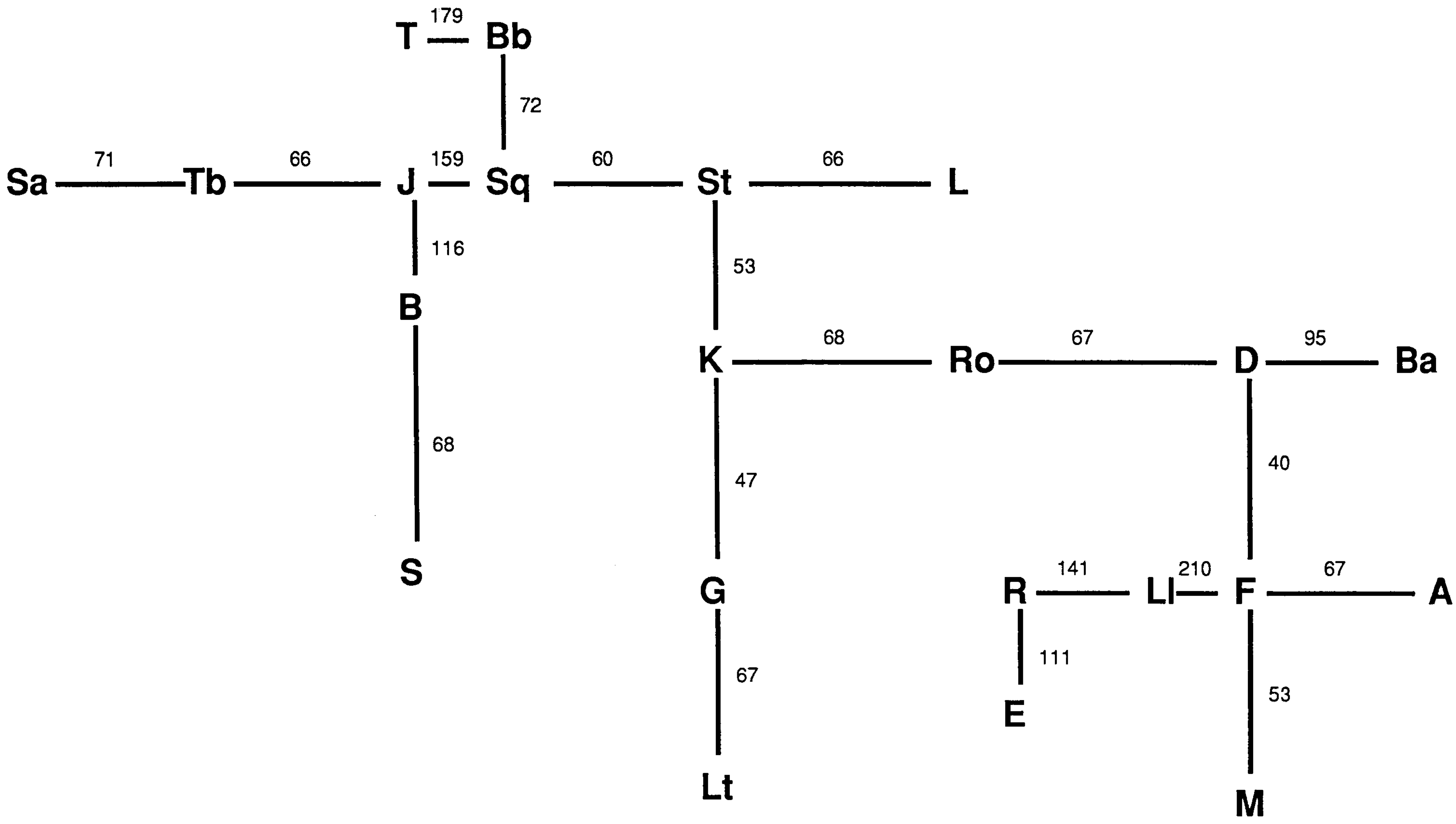


Figure 3. Nearest Neighbour Cluster Analysis for Jane and 21 Juveniles . Period III, VLNR. Figures represent similarity values, the higher the value the closer the association.

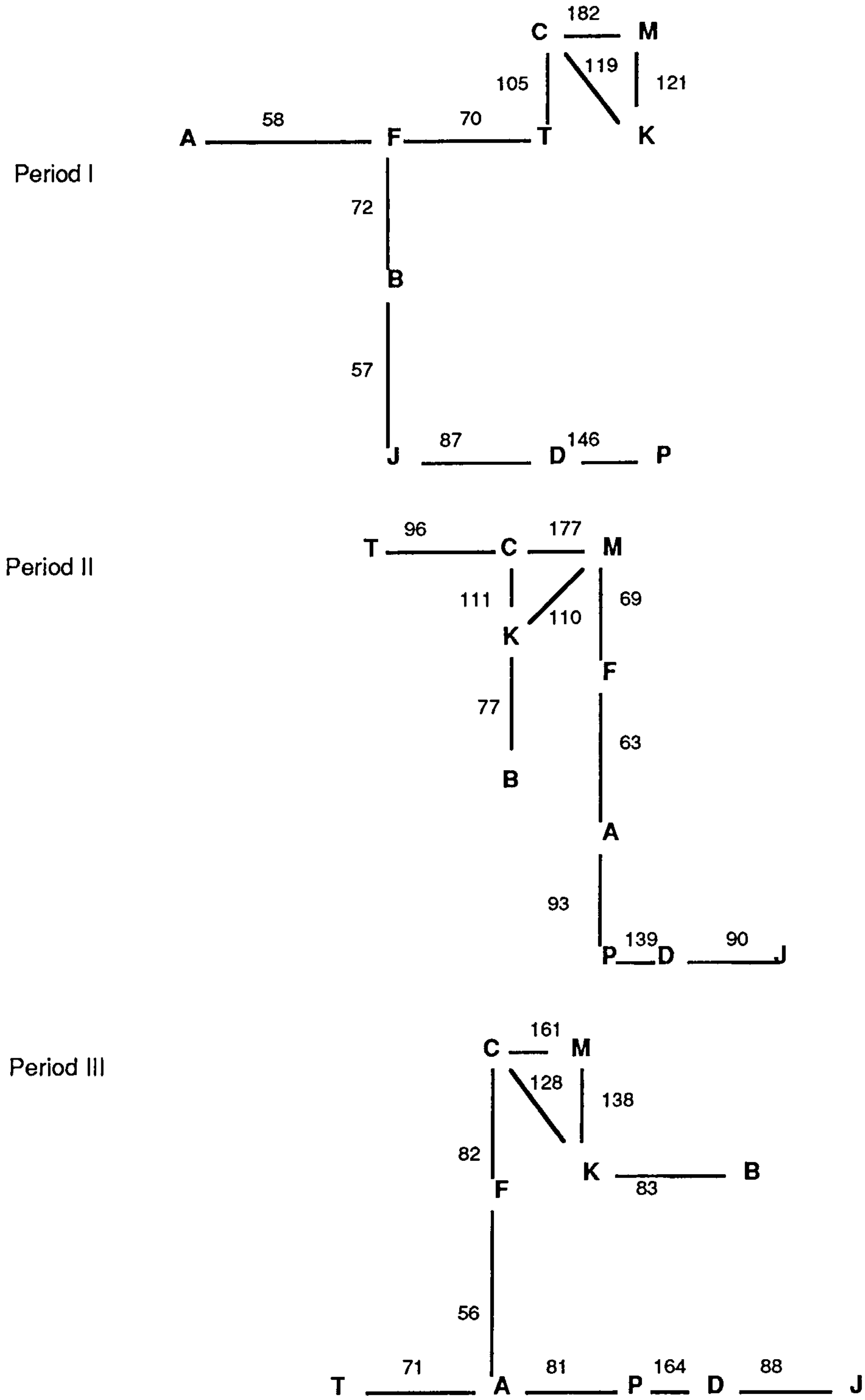


Figure 4. Nearest Neighbour Cluster Analysis for Touchstone Game Ranch Periods I, II and III. Figures represent similarity values, the higher the value the closer the association.

Touchstone Game Ranch

The ten juveniles on this reserve were about 5 - 7 years old at the beginning of the study. The oldest female was the leader and took on the roles of group leader and allomother for the youngest individual, a male (Chapter 3). A nearest neighbour analysis (Fig. 4) showed that the leading female C, the youngest individual M and another female K formed a close-knit unit. This second female formed a special relationship with the leader and helped her look after the young male. In all three periods the triad C, K and M were closely associated. Two other males (A, P) were at the bottom of the dominance hierarchy and were frequently seen to walk at a greater distance from the main group than other individuals. Notably, one of them (P) walked mostly at the rear of the group. By period III there was a tendency for the young males T, A, P, J and the youngest female D to keep at a distance of the central triad. The other older female F and the oldest male B kept nearer to the triad. Except for the oldest male B, there is a lot of similarity between the social organization of this group and the Venetia group.

Spacing Patterns

Venetia Limpopo Nature Reserve (VLNR)

Figure 5 shows the spacing patterns for the periods I, II, III and after the two adult females had joined in November 1993. In period II, there is a shift to a tighter group formation. I can provide no other explanation for this than the fact that lion activity increased greatly in the reserve during this period. In period III and especially in the time after the two females arrived there was a shift to a looser formation. This was when the subgroup started to split off.

Touchstone Game Ranch

Figure 6 shows the spacing pattern for this group of 10 juveniles. In all observation periods they mostly remained within 2 m of one another (Category 1) and hardly ever more than within 30 m of each other (Category 2). This behaviour contrasts with Venetia. Although there were considerably less individuals and therefore a smaller spacing diameter would be expected. This study was carried out two years after the Touchstone elephants had been released. Reportedly they had split into groups of eight and two during the first six months following their release. Two young individuals had been kept in a separate boma where they could see the others, as one of them had been repeatedly harassed and prevented from feeding. One can assume that these two walked off together, as they left the bomas after the main group.

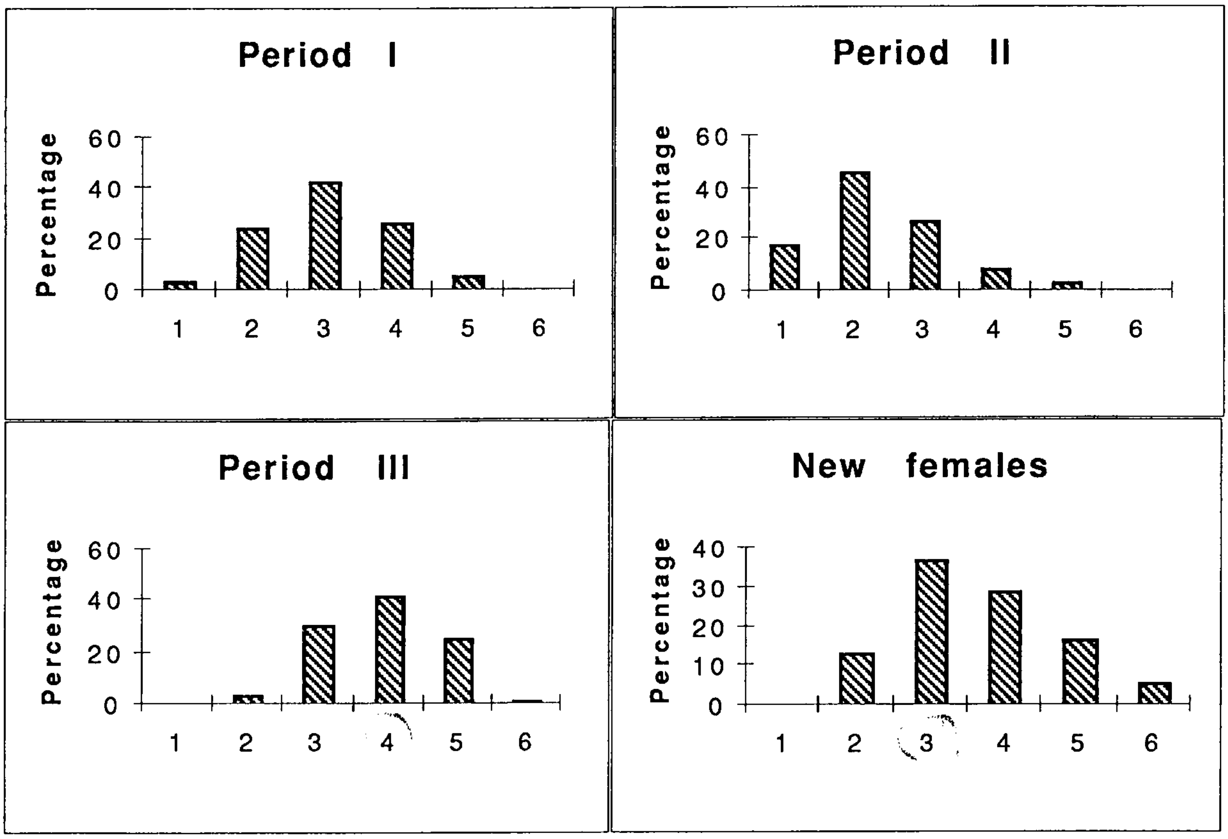


Figure 5. VLNR. Distribution of spacing categories for four periods.
1 = No individual more than 2 m apart; 2 = all individuals within 30 m; 3 = all individuals within 50 m; 4 = all individuals within 100 m; 5 = some individuals over 100 m; 6 = group divided into separate units.

Mokolo River Game Reserve

Two groups comprising two females and one male each were obtained in two consecutive years. Each group was kept in a large boma for nearly 6 months and then released. The older group was about 6 - 7.5 years of age, the second group about 4 - 5 years old at the beginning of the study. One may have predicted that the two groups would join up and that the oldest female (7 - 8 years) would lead them. However, this was not the case. Although the two groups joined occasionally and even frequented the same areas, they remained two distinct units. During the summer months they remained on a peninsular surrounded by a high hill on one side and the perimeter fence on the others, but still in two groups. In the dry season they chose a different area and were seldom seen together. Possibly the dry vegetation forced them to spilt into smaller units due to feeding competition (Jarman 1974; Western *et al.* 1984). Similar behaviour was noted by Moss (1988) at Amboseli. After two years the groups are frequently seen together, but they still wander off in separate directions and both groups appear relaxed.

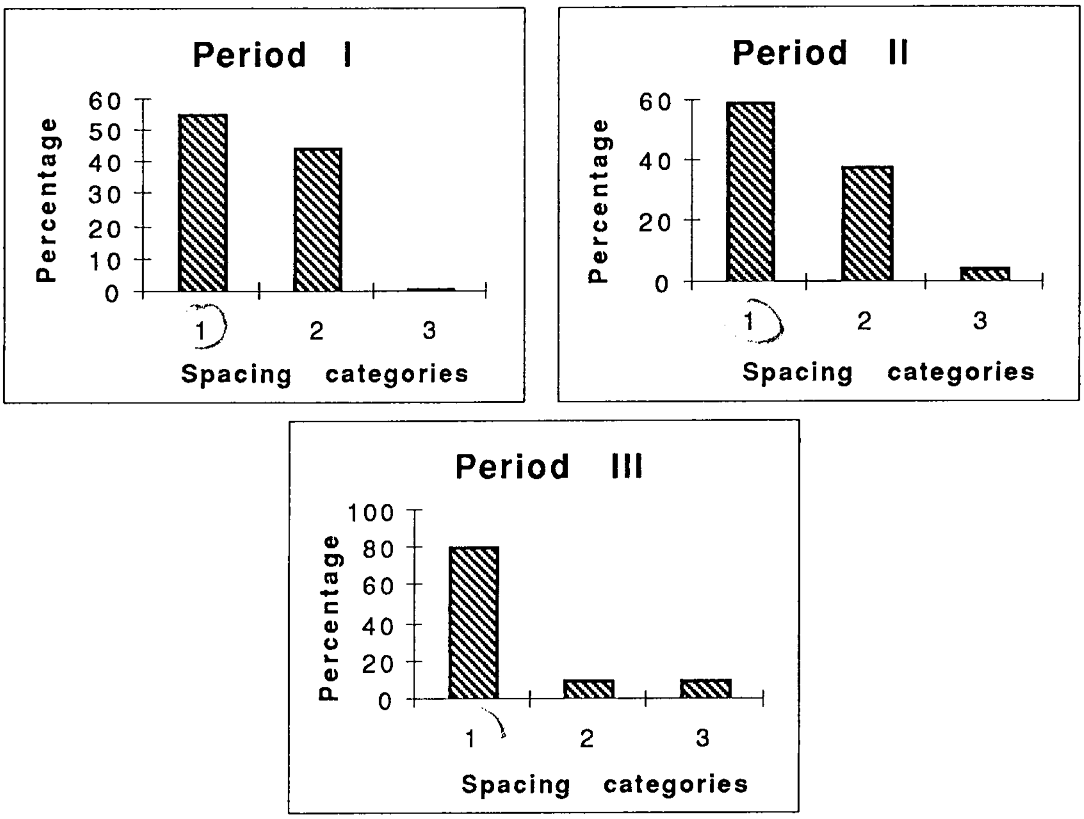


Figure 6. Touchstone. Distribution of spacing categories for three periods.
1 = No individual more than 2 m apart; 2 = all individuals within 30 m;
3 = all individuals within 50 m.

Other reserves

Interviews conducted at 24 different reserves showed that 50% (12/24) of the juvenile groups split after being released and 16.7% (4/24) did not regroup during the first year. In one reserve a very young individual walked off on his own and died soon afterwards.

DISCUSSION

Although elephants may bunch up in a seemingly uncoordinated group, certain individuals tend to stay nearer together than others. Some dyads which had formed in the boma stayed together throughout the observation period, others may find other partners. In both the Venetia and Touchstone groups there was a tendency for the younger males to keep away from the main female, or "family", unit. This is particularly interesting for Touchstone, where the juveniles were all young. In both groups one young female stayed with these males and did not participate in looking after the youngest individual or in group defence. At Mashatu Game Reserve a similar behaviour was observed in a 15 - 20 year old, non-lactating and probably nulliparous female, who was often apart from the family unit or seen together with older males. It appears then, that what keeps females together at the centre of the unit are the young individuals which have to be taken care of.

It seems that splitting can be expected in a group of translocated juveniles. However, in general the juveniles will eventually join up and form one group. What are the factors that influence group cohesion? A matriarch or leader will have a strong binding effect on the group members as was seen at Venetia and Touchstone. At Venetia the matriarch was aggressive to many of the juveniles and only allowed certain individuals near her. Many young males and one female were pushed to the periphery and eventually formed a subgroup which even split off at times. It would appear that one adult female cannot cope with such a large group. In order to ensure protection and best resources for a few, others have to be ignored. It was interesting that these individuals formed a subgroup which was cohesive in itself. There was no aggression among these members, but also no affiliative interactions. However, movements appeared coordinated. The fact that a female joined the males was unusual (compare Chapter 3 section on juveniles) and it would be interesting to see how this affects her behaviour in the long term. The two small groups at Mokolo were also cohesive, each group making separate decisions as to group movements and locality on the reserve. There was no definite leader in these groups.

Fragmentation seemed to occur in many cases. If nervousness and stress were binding factors one would expect the newly translocated individuals all to keep in a close-knit group, however, this is not always the case. It appears that social factors are more important to group cohesion if there is no matriarch or leader, although nervousness cannot be excluded. Bonding between individuals is probably a strong constituting factor. The two females that split off in 1991 in Venetia had formed a special relationship in the boma. It was however surprising, that they only joined the main group after 3 years and after more adult females had arrived. The members of the younger group at Mokolo all originated from one family unit and were probably related, this could have influenced their behaviour, as there did not appear to be anything else preventing them from permanently joining the older elephants. The two young individuals at Touchstone that split off initially had been penned together and, although they had known the others, walked off on their own after their release.

The individuals at the periphery of a group appear the most vulnerable. Each individual seemed to follow its own strategy to optimise security, some attempting to get closer to Jane at Venetia, one of them approached Jane's adopted juvenile; others formed a subgroup. At Touchstone one of the low ranking males reacted by displaying frequent threat behaviour to potential danger (in most cases the observer). The spatial arrangement of a group will depend on the social position of each individual relative to the other individuals. Female D at Venetia is an example, she was dominant in her group (Group B, see Chapter 4) in the boma, but lost her position in the large group. Dominance hierarchy is an important factor, but also the relationship to a leader or matriarch or possibly an allomother, as was clearly demonstrated by the juvenile Bb, who was at the periphery of the group until Jane started looking after him, but only after the death of her first adopted juvenile.

CONCLUSIONS

Certain individuals may bond at an early stage and remain together over a long period. Others will seek new partners. Young males tend to stay apart from the main "family" unit. Young females which do not participate in taking care of the young may join these males. Groups of translocated juvenile elephants may split initially, but members are likely to join up eventually. A matriarch or leader will instigate group cohesion, but only to a limited number of individuals. Social relationships in a group of elephants, such as bonding and dominance hierarchies or the relationship with the matriarch, all seem factors which influence group cohesion, more so than nervousness or stress. This must be considered when juvenile elephants are translocated and they should always be moved in groups and allowed to form bonds, or preferably, be given an older female as matriarch before being released.

CHAPTER 7

ACTIVITY PATTERNING IN RELATION TO GROUP SPACING WITH SPECIAL REFERENCE TO RESTING BEHAVIOUR

INTRODUCTION

Few studies on activity patterns of elephants have been carried out to date (Guy 1976; Wyatt & Eltringham 1974). Only the latter authors collected data over a 24 hour period. Activity patterns will depend largely on habitat and climatic conditions. Each reserve in the present study had a different vegetation and climate, but water availability was not a problem, as artificial water was provided if necessary. No attempt was made to render an exact activity pattern as it was not relevant to any of the questions posed in this study, and a comparison would have been difficult given the different climatic conditions and habitats. However, spacing of individuals was an important factor as one addressed hypothesis was whether juveniles living in groups without an adult would keep closer together than groups containing one or more adults. Close proximity of the group was assumed to be an indication of insecurity or nervousness. Spacing may however, also depend on the activity patterns, for example one would expect elephants to disperse more when feeding in order to minimise competition.

METHODS

1. Study groups

For details see Chapter 2.

Venetia Limpopo Nature Reserve (VLNR)

Data were divided into following observation periods:

Period I: 14 Sep - 20 Nov 1992 (Total obs time: 146 hrs 50 min)
Earliest and latest observation time: 06H20 / 12H55

Period II: 8 Apr - 19 Jul 1993 (Total obs time: 179 hrs 25 min)
Earliest and latest observation time: 07H50 / 14H40

Period III: 15 Jan - 21 May 1994 (Total obs time: 93 hrs 25 min)
Earliest and latest observation time: 07H30 / 13H10

Touchstone Game Ranch (Touchstone)

Data were divided into following observation periods:

Period I: 19 Apr - 29 Jul 1993 (Total obs time: 171 hrs 30 min)
Earliest and latest observation time: 07H45 / 14H20

Period II: 1 Aug - 29 Nov 1993 (Total obs time: 95 hrs 35 min)
Earliest and latest observation time: 06H40 / 13H25

Period III: 15 Jan - 21 May 1994 (Total obs time: 104 hrs 10 min)
Earliest and latest observation time: 06H30 / 14H20

Mokolo River Nature Reserve (Mokolo)

Observation period: 20 Jan - 24 Oct 1995 (Total obs time: 218 hrs 30 min)
Earliest and latest observation time: 06H50 / 17H35

2. Observational data

Data from the 5 minute scans were used for the analyses (see Chapter 2 for details). Activities were grouped into the following encompassing activity categories: Feeding (fe) includes looking for and preparation of food such as digging out roots. Elephants are capable of doing more than one activity at the same time, therefore some categories contain two activities (e.g. feeding/walking and feeding/resting). Feeding/resting (fe re): the group was resting under the trees, but some individuals were still slowly pulling down twigs and feeding on them. Feeding/walking (fe wa): The group was moving faster than the usual slow browsing pace, but feeding at the same time. Certain double activities where n <10, such as feeding/sandbathing were placed together with feeding and comfort behaviour. Comfort behaviour (com): includes sandbathing, mud-wallowing and scratching against an object. Investigating (inv) includes exploring, manipulating and picking up of objects but not feeding. Social (soc): any form of social interactions. Walking (wa): walking at a fast pace in a particular direction without feeding. Standing (st): standing listening or doing nothing, if standing doing nothing was longer than 1 minute it was recorded as resting. Drinking (dr): ingestion of water.

Spacing categories were sampled as follows:
Category 1 = No individual more than 2 m away from another (all within 'touching' distance)
Category 2 = all individuals within a diameter of 30 m
Category 3 = all individuals within a diameter of 50 m
Category 4 = all individuals within a diameter of 100 m
Category 5 = some individuals further apart than 100 m
Category 6 = group divided into separate units, location of second group not known.
Correlations were tested using a Spearman's rank correlation (r_s) and Kendall's coefficient of concordance (W). Other relationships were statistically tested using a *chi*-square or a Binomial test (z).

RESULTS

Table 1 presents the results for all groups. Feeding was the main activity, followed by resting. Data were not collected over a full day, so the results only reflect activities during observation time, and not the actual diurnal activity patterns. Observation occurred mainly from early morning to about midday, only on a few rare occasions at Mokolo observations were made in the afternoon.

Table 1. Distribution of activities for the different study groups expressed as a percentage of the total activities for each group recorded during each period.

Group	fe	fe re	fe wa	re	com	st	wa	dr	soc	inv
					(% of total activity)					
Mokolo	60.1	2.7	3.2	18.8	2.5	2.7	3.5	0.2	2.9	3.4
T I	41.7	3.2	8.4	32.2	0.6	6.9	6.0	0.1	0.8	0.1
T II	38.2	5.3	4.6	38.0	2.0	3.9	5.0	0	1.4	1.6
T III	44.1	1.6	7.8	31.5	3.0	3.0	3.8	0.9	3.1	1.2
V I	49.0	6.7	5.9	34.2	0.1	0.8	2.6	0.9	0	0
V II	26.9	1.9	6.9	59.9	0.4	1.5	2.3	0.2	1.0	0
V III	28.0	3.7	25.2	33.9	0.8	0.6	4.3	0	3.5	0

Groups: Mokolo, T = Touchstone periods I - III; V = Venetia periods I - III.
fe: feeding; fe re: feeding/resting; fe wa: feeding/walking; re: resting; com: comfort; st: standing; wa: walking; dr: drinking; soc: social; inv: investigating.

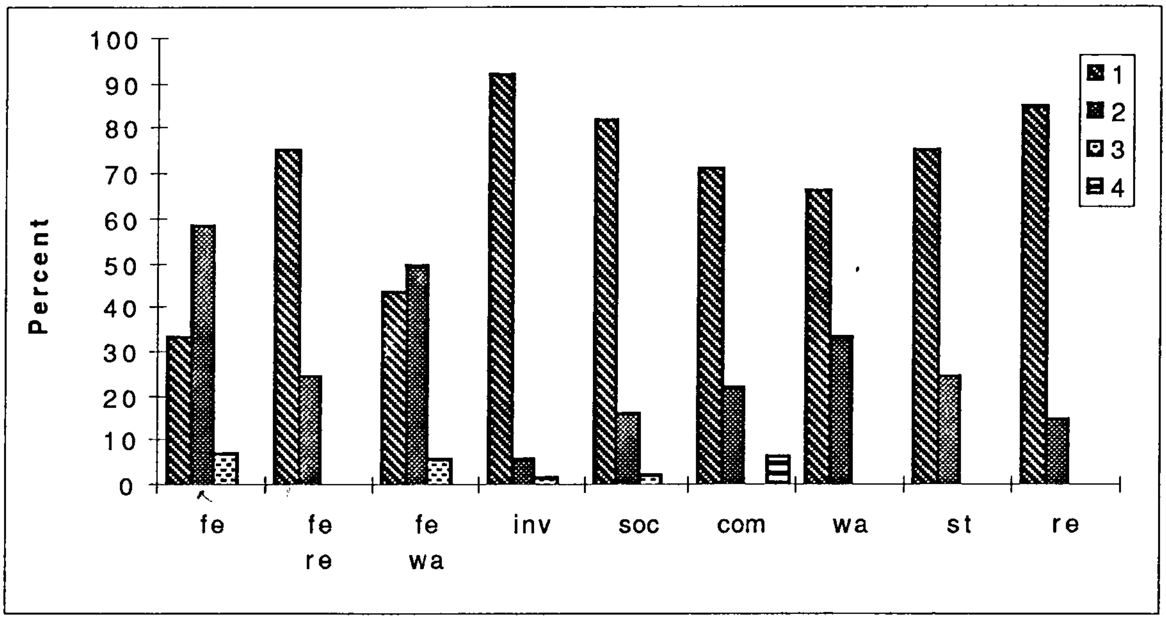


Figure 1. Mokolo River Nature Reserve. Distribution of activities (N = 1507) in relation to group spacing categories 1, 2, 3, 4 (1 = No individual more than 2 m away from another; 2 = all individuals within a diameter of 30 m; 3 = all individuals within a diameter of 50m; 4 = all individuals within a diameter of 100 m)

Mokolo River Nature Reserve

Feeding was the most frequent activity observed. If all double activities which included feeding are added up the elephants spent some 66% of the recorded time feeding. Figure 1 shows how the activities were distributed relative to group spacing. The elephants were spaced more than 2 metres apart from one another (category 2) only during feeding. All other activities mainly occurred when individuals were within touching distance of one another (category 1). Very rarely did the elephants disperse over 30 and 50 meters (categories 3 and 4).

Touchstone Game Ranch

These elephants spent only slightly more time feeding than resting. Feeding over all three periods amounted to 52% of the total observed time when all activities which included feeding were added. Figure 2 shows activities in relation to the spacing categories for all three observation periods. Data were pooled as they correlated significantly (Kendall's, W = 0.879, $x^2 = 23.7$, $p < 0.001$, df = 9). The elephants dispersed only during feeding and walking, but hardly ever more than category 2, rarely 3. They kept particularly close together when resting. A comparison between spacing category 1 and 2 shows a significant choice for category 1. (Binomial, z = -15.99, $p < 0.0001$, N = 774). Spacing category 3 was only recorded twice (2 five min scans) while the elephants rested.

Venetia Limpopo Nature Reserve

During period I there was more 'feeding' and during periods II and III more 'resting'. Feeding accounted for 44.4% of the time over all observation periods and when all feeding categories were included. The weather was very hot at Venetia and this could explain the relatively longer resting times observed in this group. Judging by the tracks found in the reserve, it also appeared that the elephants walked large distances at night. During daily observation periods they did not cover much ground.

Figure 3 illustrates the distribution of activities in relation to spacing categories. Results for periods II and III were pooled as there was a significant correlation between the two (Spearman; $r_s = 0.9348$, $p < 0.001$). Although one may have expected the elephants to keep close together when resting, they dispersed and were mainly at distance category 3. This was probably due to the fact that the mopane trees at Venetia provided little shade, and the individuals dispersed in small groups under various clusters of trees. Feeding, walking and even some resting occurred at spacing category 5. A subgroup of juveniles started to separate from the main group and this explains the more extensive spatial arrangement (see Chapter 6).

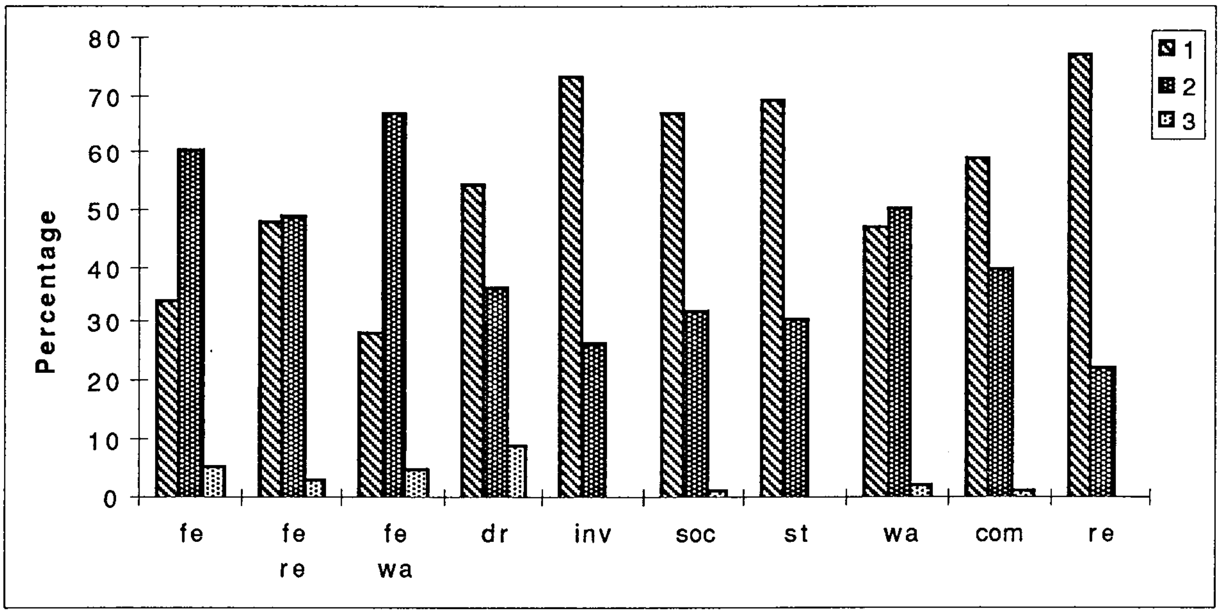


Figure 2. Touchstone Game Ranch. Distribution of activity in relation to spacing categories 1, 2, 3 (N = 3957). (1 = No individual more than 2 m away from another; 2 = all individuals within a diameter of 30 m; 3 = all individuals within a diameter of 50 m; 4 = all individuals within a diameter of 100 m

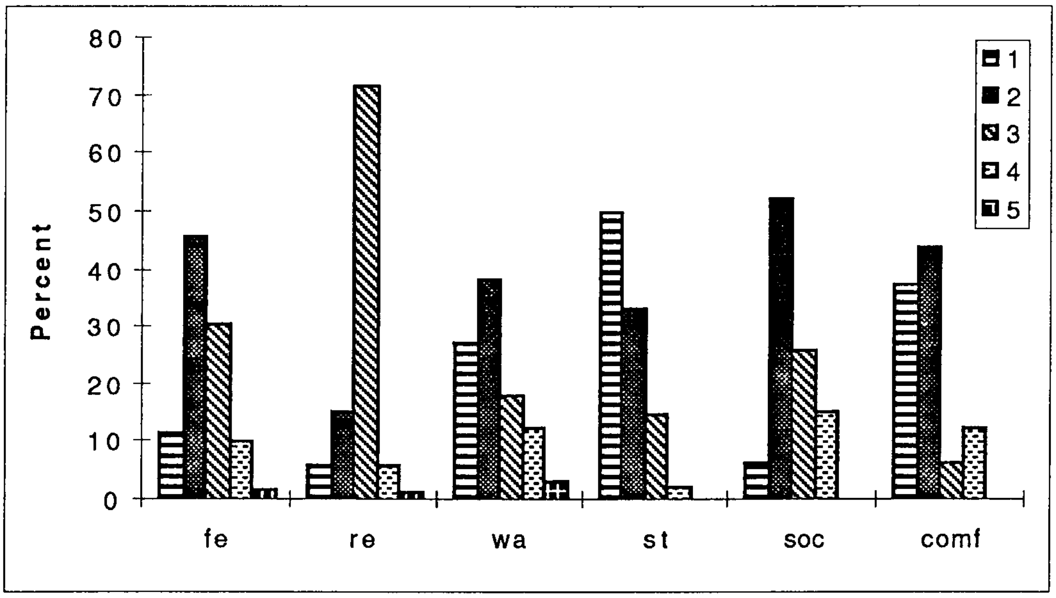


Figure 3. Venetia Limpopo Nature Reserve. Periods II and III, distribution of activities in relation to group spacing categories 1, 2, 3, 4, 5 (N = 3340) (1 = No individual more than 2 m away from another; 2 = all individuals within a diameter of 30 m; 3 = all individuals within a diameter of 50 m; 4 = all individuals within a diameter of 100 m; 5 = some individuals spaced over more than 100 m)

DISCUSSION

Compared with other studies, where elephants spent 66.7% - 75% (or 16 - 18 hours) of their time feeding (Guy 1976; Wyatt & Eltringham 1974; Carrington 1958) the elephants in the present study spent less time feeding and rather more time resting, but this is most likely the result of the actual observation times and not a reflection of the activity patterns.

The Venetia group consisted of more individuals than the other groups, therefore a larger spacing pattern is to be expected. However, despite this, at Touchstone and at Mokolo elephants kept in much closer proximity to one another. Particularly during 'resting' there was a marked difference in behaviour pattern. The individuals from the two groups without adults were within touching distance of one another when they rested. At Venetia many juveniles dispersed into small groups away from the adult Jane. Shade could have been a factor, but then there was no need to disperse as wide apart as they did, as the mopane *(Colophospermum mopane)* was very dense. In addition, the elephants would often rest out in the open mopane shrub (< 2 metres high) during the middle of the day, this seemed a surprising behaviour as there were plenty riverine areas, but is in agreement with findings by Guy (1976) where the elephants in Zimbabwe spent more time resting in the open during the hot season than during other seasons. The effect of convective cooling (Louw 1993) does not seem plausible as the landscape where the elephants stayed was completely flat and they did not rest on the hills. Therefore, the spatial arrangement could indicate that the elephants felt secure. Whether this was due to the presence of an adult or the fact that there were many more other elephants in the group cannot be determined with any degree of certainty. However, the presence of an adult female had a calming effect of the juveniles in the boma (Chapter 8). It would therefore seem reasonable to suggest that the same applies for the elephants in the reserve. In contrast, the behaviour of the Touchstone and Mokolo elephants may indicate some form of insecurity, especially during resting periods. As was illustrated in the chapter on Grouping Behaviour the Mokolo elephants appeared relaxed and did not permanently join up with the other group of juveniles, as may have been expected if they were nervous. Nevertheless, some form of insecurity could still prevail, especially during resting periods, when the elephants frequently lay down, and keeping in close proximity is likely to induce a feeling of security and in fact may provide tangible security to the individual.

II. RESTING BEHAVIOUR

INTRODUCTION

The only study on the sleeping behaviour of free ranging African elephants was conducted over seven nights in Uganda (Wyatt & Eltringham 1974). One of the principle sleeping periods appears to be during the early hours of the morning, however, elephants will frequently rest and sleep during the day as well (Wyatt & Eltringham 1974; Hendrichs & Hendrichs 1971, Abe 1994; Guy 1976). As has been shown in a young Asian zoo elephant total sleep time decreases during maturation (Tobler 1992). Lying down does not occur frequently in adult elephants during day time, and various factors could influence this behaviour. Adults may be more vigilant and recumbency would impair vision of any potential danger. Also the relatively large bulk of the animal does not allow it to stand up rapidly. It would seem reasonable to assume that an elephant will lie down only when it feels secure. The question was whether there would be a difference in resting and lying down behaviour between the different groups which may reflect a certain degree of insecurity.

METHODS

Resting times were calculated from the 5 min scans. Lying down periods were recorded *ad lib.* and the exact times were taken for each individual. These data were analysed separately. For study groups see page 74.

RESULTS

Table 2 presents the results for all groups and some individuals for times spent resting and times spent lying down. In all groups the elephants rested at any time during the daily observation periods, from as early as 6h25, which was the earliest record for Venetia. The three young elephants at Mokolo had a slightly longer mean resting time than the other groups, but this was not significant. The wide range of times for lying down in all groups was due to several factors. Sometimes another individual would disturb the recumbent one, or something gave them a fright which would induce them to stand, or an individual might stand up for a few minutes and then lie down again elsewhere. Some lying down bouts were less than 1 minute which obviously decreased the mean time. At Venetia, Jane frequently initiated moves when the juveniles were still sleeping and they subsequently followed her. This was seldom the case at Mokolo, where the three elephants waited for each other to wake up. The wide range in resting times was also dependent on several factors; the group may move to another tree and then resume resting, or simply feed or socialise for several minutes before continuing to rest. Alternatively, they may rest for a few minutes in between longer feeding periods.

Table 2. Resting times for various groups and individuals

Group	mean time resting (min) ±SD	range	mean time lying down (min) ±SD	range	N rest	N ld
T'stone	41.5 (27.9)	5m - 2h40m	11(17.4)	1m -1h17m	144	31
Venetia	46.3 (63.9)	8m - 4h55m	22.9 (21.8)	1m -1h37m	104	236
Jane			9.9 (7.0)	3m - 22m		14
Mokolo	54.8 (31.9)	5m - 2h25m			56	
P			39.6 (24.1)	1m - 1h18m		44
R			24.4 (20.5)	1m - 1h15m		33
C			13.4 (17.0)	1m - 1h 4m		41

Column 1: groups, Jane the adult at Venetia, three individuals P, R and C at Mokolo
Column 2 and 3: mean time spent resting (±SD) in minutes and range; h = hours, m = minutes
Column 4 and 5: mean time spent lying down (ld) (±SD) in minutes and range;
Column 6 and 7: total N for resting (rest) and lying down (ld) respectively per group or individual
N rest: total recorded resting periods; N ld: total recorded lying down bouts.

Male P at Mokolo lay down for longer periods than the other two individuals ($x^2 = 7.38$; $p < 0.01$). Female C had rather low values for lying down. It was not possible to determine why she lay down less than the others. The lying down bouts for Jane, the adult at Venetia, were shorter than those of the juveniles (Binomial, $z = 2.269$, $p = 0.012$). The longest resting times were recorded at Venetia where the climate was very hot and dry.

DISCUSSION

The lying down periods in this study are slightly shorter than those reported by other authors. Kurt (1960) found a mean duration of 49.2 minutes for adult Asian elephants and Tobler (1992) found 72.0 minutes to be the mean, however these were figures for captive elephants and there could be a difference in sleeping behaviour in the wild, where elephants have to rely more on their vigilance. Secondly, the present study only reflects resting behaviour during day time and night time results may well be different. There could also be a difference in sampling methods, in the present study if an animal got up and walked to another tree and lay down again, it was recorded as two different bouts.

Various authors have reported that adult elephants will lie down to sleep during the day (Asian: McKay 1973, African: Hendrichs & Hendrichs 1971; Adams & Berg 1980), but Wyatt & Eltringham (1974) in their study in Rwenzori National Park in Uganda never saw any of their study animals lying down during the day. However, they saw other elephants, mainly bulls, lying down in the Park. Similarly, Guy (1976) never saw any elephants lying down during his study in the Sengwa Area in Rhodesia (now Zimbabwe). Jane's results from the present study indicated shorter periods for recumbency than for other individuals. She was the only adult in the group and responsible for 21 juveniles and this may have been a factor influencing her recumbency behaviour. When she did lie down the juveniles stood around her, frequently touching her with their trunk. The oldest juvenile female B who had formed a special relationship with Jane (see Chapter 3) always stood next to her. On many occasions all 21 juveniles were lying down and only Jane was standing, and only on one occasion all 22 elephants were observed lying down and sleeping during the day. Jane had been habituated to humans from an early age and the juveniles had been habituated to the observer during 6 months in the boma and during the many months of observation in the reserve. At Mokolo the elephants had also been habituated during 6 months in the boma. The trust in the observer was reflected in the sleeping behaviour and probably accounts for the regular observations of recumbent elephants including Jane. This may explain differences found in the present study and the study by Guy (1976) who followed his elephants on foot, but had not habituated them. In the present study the elephants at Touchstone had to be habituated to the observer after they had been released from the boma for 2 years. First sampling was possible after 6 weeks of habituation (see Methods, Chapter 2), after which time it took another month for the first juvenile to lie down in the presence of the observer. Only after a further month did several juveniles lie down together, and it was not until period II (6 months after observations started) that the elephants lay down regularly in the presence of the observer. This serves to illustrate that elephants are more likely to lie down when they feel absolutely secure, either in the presence of an adult elephant or when they are at ease with human observers. The Touchstone elephants were very young when they were released, had been in the reserve for two years and were terrified of all other humans.

The elephants would rest at any time during the day. Casual observations and sampling during a few whole days showed that the elephants would increase their feeding and walking activities towards late afternoon, when they also walked to the water dams. Guy (1976) suggested that elephants rest during the day rather out of need to remain stationary than to keep cool in the shade. The elephants in his study would rest out in the sun more during the hot season. A similar behaviour pattern was seen in the present study at Venetia, where the elephants would frequently rest out in the open mopane shrub although riverine areas were nearby. Both at Mokolo and at Touchstone, however, the elephants chose an area with tall, shady trees for resting, especially during the hot season. Venetia was the only study site in which large carnivores were present. This might have had an effect on the behaviour of the elephants. Although visibility in the riverine areas was better due to the tall trees, lion activity was likely to be greater in this habitat, especially during Summer when there was relatively high grass. Another explanation for the difference in behaviour could be that it was not necessary for the adult Jane at Venetia to seek shade. The low surface-to-volume ratio in elephants prevents fast heating up or cooling off (Eltringham 1982). An adult elephant will have a larger surface area of the ear pinnae, relative to the juveniles, and this will increase the ability to give off heat to the ambient and in keeping the blood vessels cool through ear movement (Wright 1984, Wright & Luck 1984). So, maybe it was not so important for Jane to seek shade and the juveniles, who took their cues from her, rested near her and the very young ones stood in her shade. The elephants were frequently seen to blow liquid from their trunks, sometimes taken from inside their mouths, onto their ears as cooling devise, a behaviour which is known to occur in elephants. On the other hand, the juveniles at Touchstone and Mokolo (where there was no adult) preferred to seek shade for cooling effect, and maybe their smaller bodies necessitated them to do so. A third possibility is that Jane found a shady spot for her head and was not concerned whether the juveniles also found some shade or not. Her adopted calf rested in her shade.

It has been noted by other observers (Kühme 1962, Wyatt & Eltringham 1974) that elephants synchronised their resting behaviour, even when they were dispersed and could not see each other. In this study a series of rumblings could frequently be heard prior to resting, so that the observer could predict resting times by these vocalizations.

CHAPTER 8

STRESS RELATED BEHAVIOURS

INTRODUCTION

Stress is a psychological condition that results from excessive environmental or psychological pressures (McFarland, 1987). The usual response to stress is to attempt to maintain homeostasis. All sensory inputs pass through the limbic system, which is the seat of emotion and consciousness and determines behaviour. Stress can be divided into two types.

A. Short termed acute stress, generally called the 'flight and fight syndrome . This is governed by adrenaline and prepares the animal for immediate activity. Behavioural stressors (i.e. the causes of stress) are fright, conflict, frustration, anger etc. which elicit an unspecific reaction (e.g. flight, fight, displacement activity) by the animal.

B. Long termed chronic stress (or the 'general adaptation syndrome'), which is governed by glucocorticoids, Behavioural stressors could be social stress such as bullying, new environment, overcrowded conditions, insecurity, etc. which elicit a specific reaction by the animal. For the purpose of this study the word "stress" will be used as a general term, and "stress related behaviour" for any behaviours which appear to be a reaction to a motivational state within the functional contexts of insecurity and fear, although physical causes of stress, such as drought, adverse weather conditions, nutritional deficiencies and their influence on the general behaviour patterns cannot be totally excluded. The term "distress" will only be used when the negative connotation was apparent.

It seems reasonable to assume that juvenile elephants that have lost their family, gone though the trauma of capture and translocation and have been put into a boma with similarly aged and most likely unknown animals, have experienced a certain degree of stress. It will probably never be possible to determine how each individual experiences this stress, nor exactly how long it takes for an individual to adapt to the situation or whether it has a long term effect on their behaviour. An attempt was made in this study to define certain behaviour patterns as being stress related and to compare these among the different study groups.

I. AROUSAL BEHAVIOUR

In the following section the term "arousal" is used to describe certain behaviours related to nervousness and possibly stress, which became apparent in response to a specific and identifiable stimulus. Arousal is used as the opposite of "calm" and "relaxed". Low levels of arousal need not be experienced as stress and it is not possible to determine where the individual stress experiences lies on a gradient. If high levels of arousal are experienced in a negative manner, one may assume that it is experienced as stressful.

Study groups

Data of the following study groups were used for analyses. See Chapter 2 for details.

Venetia Limpopo Nature Reserve

Groups A, B, C, D in the bomas, 1992.
Jane: the 18 year old semi-tame female was introduced to the juveniles during their boma stay. Jane was penned with group C for one week , then with groups C and B together for a month before their release into the reserve.

Mokolo River Nature Reserve

Three juveniles (one male and two females) aged 4 - 5 years old were in a large paddock, *ca.* 2 ha in size for nearly six months before being released. Arousal data were collected in the first week after they arrived from the KNP.

Skukuza Boma

During one week in June 1995 observations were made at the Skukuza bomas in the Kruger National Park, into which the juveniles were put after being captured during the annual culling operations. There were several groups of juveniles and new individuals arrived daily and were either kept in a separate boma or penned with other groups. The criteria for grouping was age and sometimes sex, but also depended on the orders that had been placed by buyers. Similar aged juveniles were usually penned and sold together in a group, the size of which depended on the tender. Some males were captured and penned together for veterinary experiments.

METHODS

Group A at Venetia was very nervous during the boma stay and provided the opportunity to define what was termed 'arousal' behaviour. The behavioural elements were defined as follows (for definitions see Chapter 2): listening (ls), ears raised (er), ears spread and raised (es), head held high (hdh), tail up (tl up) walking around (wa ar), running (rn), clustering (cl), loud vocalising (trumpeting, screaming), diarrhoea (only if this occurs immediately after a stimulus), temporal gland secretion (tgs) and aggression (agg).

Significance was tested using a *chi*-square test for expected and observed values, df = 1 applies in all cases. Correlations were done with the Spearman's rank (r_s) correlation (Siegel 1987).

Sampling times for the four Venetia groups are as follows: (before and after the arrival of Jane respectively): A: 17h 35m / 7h 40m; B: 17h 53m / 10h 30m; C: 7h 10m / 15h 37 m; D: 10h 40 m / 13h 55 m. Sampling of arousal behaviour was done by the One-Zero method (Altmann 1974) for 30 sec intervals for all study groups i.e. arousal sampled as occurred (1) or not (0) within the past 30 sec.

RESULTS

Venetia Limpopo Nature Reserve

<u>Arousal symptoms</u>

The behavioural elements were placed on a gradient from being 'alert' over 'low intensity arousal' to 'high intensity arousal' as is shown in Figure 1. Not all elements need to occur. Temporal gland secretion is not shown by all individuals. It can occur with or without any other visible arousal symptoms (described in section III). One female in group A was particularly nervous and she secreted daily from the temporal gland, the others only occasionally when they received a fright.

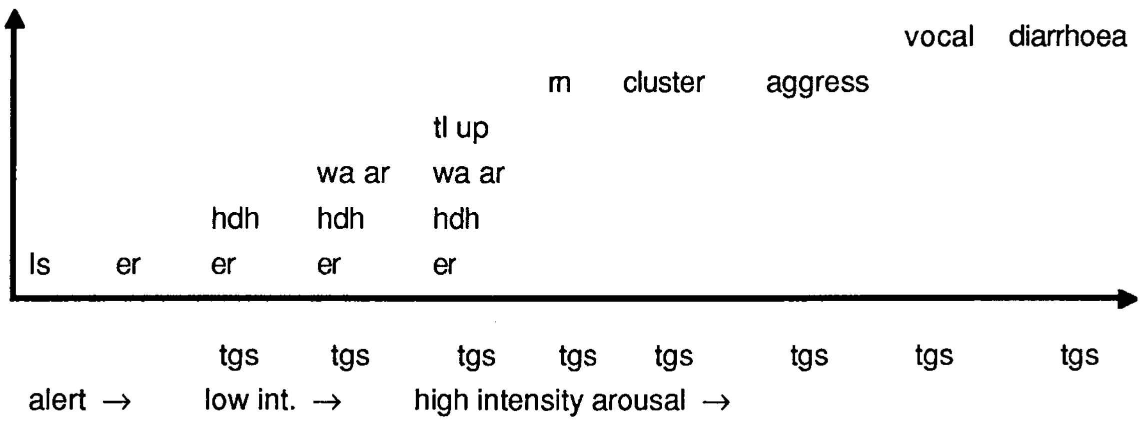


Figure 1. Arousal behaviour on a gradient from 'alert' through 'low intensity' to 'high intensity' arousal, horizontally and vertically.
ls = listening, er = ears raised, hdh = head held high, wa ar = walking around, tl up = tail held up, rn = running, cluster = all animals huddling together, aggress = aggressive behaviour, vocal = trumpeting or screaming, diarrhoea = immediate defecating reaction to a stimulus (for definitions see methods). tgs = temporal gland secretion: recorded in connection with any of the above arousal symptoms or not at all.

Group A, the oldest individuals, were nervous throughout their boma stay. They showed the most 'high intensity arousal' behaviour (Table 1). Particularly one female was very aggressive towards humans near the fence. There was also much aggressive behaviour in this group (see next section) and particularly one female constantly pushed the others, but at the same time was always near one of them and appeared very nervous.

Table 1. **Distribution of arousal behaviour (alert, low intensity arousal, high intensity arousal) expressed in percentage of the total arousal behaviour recorded within groups A, B, C and D respectively.**

Group	Alert %	Low intensity %	High intensity %
A	47.2	42.4	10.4
B	53.5	41.1	5.1
C	53.7	43.8	2.5
D	40.0	55.5	4.5

Groups: A: four females, 6 - 7 years; B: three males and five females, 4 - 5 years; C: five males, 2.5 - 3.5 years; D: five males, 18 months - 2 years.

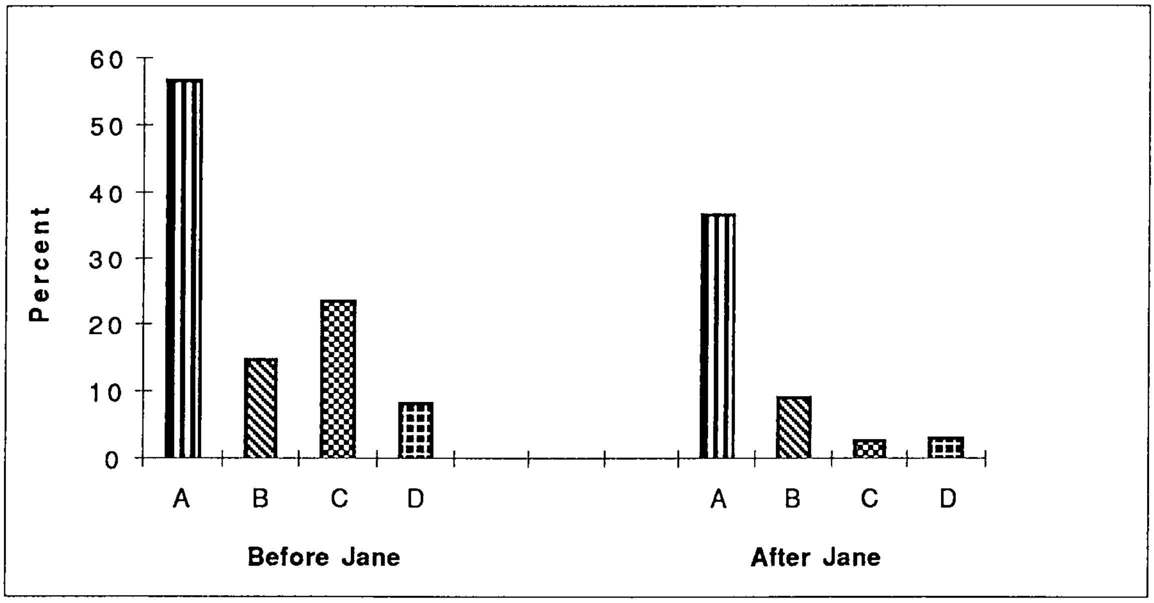


Figure 2. Occurrence of arousal behaviour before and after the arrival of the adult Jane for groups A to D expressed as a percentage of the total number of 30 sec scans observed.

Groups: A: four females, 6 - 7 years; B: three males and five females, 4 - 5 years; C: five males, 2.5 - 3.5 years; D: five males, 18 months - 2 years.

Figure 2 shows the difference in arousal behaviour before and after the arrival of the adult female Jane. There was a significant decrease in arousal behaviour after Jane was in the boma ($x^2 = 6.125$ $p < 0.005$; McNemar test, one sided). This was true for all groups, although Jane was penned with group C. The elephants in the other groups could see and even touch her through the inner fences.

Skukuza Boma

Table 2 shows the arousal behaviour expressed as a percentage of total 30 sec scans for the different groups in the bomas at Skukuza. One young female in group 4 tried to climb out of the boma and displayed aggression towards others and objects, and frequently screamed. A young female in group 7 spent her entire time showing stereotypic walking along the fence. She was in a bad physical condition and refused to eat for a long period. This female went to a zoo and was still in a bad physical and psychological condition two years after the capture. Group 2, the six males that were captured for experiments, showed signs of apathy rather than nervous behaviour, as did some other groups or individuals. These males had been in the boma for some weeks. They stood clustered in a tight group and showed little other behaviour. Only one male in group 2, separated from and bullied by the others, had values of 100% for arousal behaviour.

The three juveniles that went to Mokolo were observed in the boma at Skukuza and subsequently in the boma at Mokolo. The results are presented in Table 3. These three elephants were captured in the same family group and they were probably related.

Table 2. Occurrence of arousal behaviour expressed as a percentage of the total 30 sec scans recorded within each group in the Skukuza bomas

Group		Arousal %
1	1f, 4 -5 yrs	82.0
2	6m, 5 -7 yrs	43.0
3	1f, 2 yrs	43.0
4	2f, 2 yrs@	99.2
5	4f, 2 - 2.5 yrs	95.0
6	1f, 4 - 5 yrs	82.0
7	2m, 1f, 2 yrs	100.0

@ the female in group 3 was joined by another.

Table 3. Occurrence of arousal behaviour expressed as a percentage of the total 30 sec scans recorded for the Mokolo group in two different bomas

Individual	Skukuza Boma	Mokolo Boma
P	42.5	14.0
C	29.6	8.0
R	52.1	17.5

P is a male, C and R females
(For difference in boma construction see Methods, Chapter 2)

DISCUSSION

The calming effect of an adult female on the juveniles in the Venetia bomas was evident, even on those juveniles that were not in the same pen. The fact that the juveniles were in a boma with people walking around could have enhanced their nervousness (Garaï 1994). The females of group A calmed down quickly after their release. The results at Skukuza showed that juveniles are extremely nervous after capture, which was to be expected, despite all animals being under the effect of tranquillisers. Individuals used various strategies to cope with stress. The young female that tried to climb out of the enclosure screamed, kicked objects and other elephants and walked around continuously. The stereotypic behaviour shown by another young female could be indicative of suboptimal environmental conditions (Mason 1991) and suboptimal levels of psychological welfare (Marriner *et al.* 1994). The two groups of slightly older males had seemingly calmed down, but in reality appeared to show apathy. These males were subjected to veterinary experiments so it remains unclear whether their behaviour pattern was due to their age, longer duration in the bomas or specifically related to the experiments. It is interesting to note that the group that went to Mokolo showed relatively less arousal behaviour at Skukuza than the other groups. These elephants knew each other and were most likely related as they had been captured in the same family unit. They also calmed down more once they were in the Mokolo boma.

Apathy is difficult to describe in behavioural terms and may at best be an impression obtained. In the wild, elephants are always doing something (exploring, feeding, manipulating objects etc.), unless resting. It is unlikely that some of the juveniles in the bomas rested all day. Buirski *et al.* (1978) described depression as the 'failure to seek out or respond to social interactions'. Maybe apathy could be described as the 'failure to seek out any activity'. The lack of feeding by some individuals supports the argument that the juveniles were distressed. This behaviour was also observed in a group of very young juveniles at Kaia Ingwe, where two individuals were in a poor physical condition and hardly fed. One of them nearly died.

CONCLUSIONS

Translocated juvenile elephants will show arousal behaviour and some may show signs of distress after their capture. They will react to the situation individually and some may only calm down after being released into the reserve. Fear of people and animals walking on the outside of the boma will be enhanced by the fact that there is no escape route in a boma, more so if this is only a relatively small, closed construction (Garaï 1993, 1994). The presence of an adult female clearly induces security and calmness to the juveniles. Very young juveniles should not be translocated without mothers or at least an adult female. Some individuals may react with apathy and dejection to the situation and it is very difficult to assess the amount of stress afflicted to these individuals. Only long term studies or detailed physiological studies are likely to throw some light on this.

II. OCCURRENCE AND OMISSION OF CERTAIN BEHAVIOUR CATEGORIES WHICH ARE POSSIBLY RELATED TO STRESS

Group living automatically increases the chance of two or more individuals coming into conflict over resources (Cords 1988). Many species have developed strategies to ensure that aggression does not escalate and reach harmful levels, but many of these probably have to be learned through experience. Keeping to rules permits an individual to avoid aggression, however, in a group of translocated elephants these rules need to be established. Therefore one can expect aggression, which can have various causes: establishment of a dominance hierarchy (Chapter 4), food competition, nervousness or lack of adults. In the following section aggression will be compared among various study groups.)

Alados and co-authors (1996) have shown that stress can lead to a reduction in complexity of exploratory behaviour and they state that loss in variability appears to be a general characteristic of stress. It follows that one may assume a reduction or absence in certain non-relevant behaviour patterns and an increase in behaviour patterns necessary to cope with the stressful situation (i.e. feeding, defence behaviour etc.), and other behaviour patterns might become important as coping strategy, for instance displacement behaviour, stereotypes (Mason 1991; Marriner & Drickamer 1994) and other abnormal behaviour patterns. A group of rhesus monkeys showed cessation of play behaviour after being transplanted to a new site (Morrison & Menzel 1972). Play behaviour is a 'low priority' behaviour (Burghardt 1984) and occurs when no other more important behaviour predominates and is probably a good indication of a relaxed animal which has time to indulge in play. It follows that absence of play behaviour, especially in captive groups of animals which do not have to spend time looking for food, could be an indication that the animal is not relaxed, i.e. stressed, afraid, nervous and generally ill at ease.

1. Study groups

Data of the following study groups were used in this chapter, for details see Chapter 2.

Venetia Limpopo Nature Reserve 1991 - Boma
Venetia Limpopo Nature Reserve 1992 - Four groups in the boma
Venetia Limpopo Nature Reserve 1992-1994 - Free
Touchstone Game Ranch - Free
Thornybush Game Lodge - Free
Spektakel Game Ranch - Boma
Mokolo River Nature Reserve - Boma and Free
Kaia Ingwe - Two groups in the boma
Mashatu Game Reserve - Free, family groups

2. Observational data

In this section the following methods and data were used. For details see Chapter 2, and Appendix 1.

- Interaction categories: Affiliative, Aggressive, Dominance, Submissive, Investigate, Play-fight and Play.
- Data from the questionnaires.

Analyses were carried out using a *chi*-square test. Significance between aggressive and affiliative behaviour was tested with a Binomial test, two sided. The ratio for the total of these two behaviours for all study groups was near 0.5 (0.46 : 0.54; N = 8800), so that the assumption was made, that p = q = 0.5, using the formula $z = \frac{(x \pm 0.5) - NP}{\sqrt{NPQ}}$ (Siegel, 1987).

RESULTS

Table 4 shows the distribution of the behaviour categories in each study group:

Venetia Limpopo Nature Reserve 1991

The elephants in this group had been together *ca.* 5 months at the beginning of sampling, but were still in the boma, although they spent most time in the outside enclosure and only went into the pen for feeding. Play behaviour (40.6% of total behaviour) was the most frequent category (x^2 =1531; $p < 0.001$, n = 1810). This included all play-fighting, most of which occurred between female B and male R (54.3% of all play-fighting). Without play-fighting, play elements accounted for 9.4% only. It is not always possible to discern when play escalates into serious fighting. However, on a subjective grading 1 - 4, most play between individuals remained at level 1 (gentle play), sometimes 2 (sparring), but play-fighting between B and R escalated to levels 2, 3 and 4 (hard fighting) in 68.75% of the recorded incidents. Female Ch played least of all individuals (only 3.2% of all play bouts). She often stood at the bottom of the enclosure and looked out of the fence. Male R was involved in 30.5% of play bouts (56.4% of which were with female B), and female B was involved in 25.2% of play bouts (67.9% of which were with male R). Female P was involved in 19.7% of play bouts (of which 49.2% were with female S). Interestingly male E was only in 8.8% of play bouts (of which 88.9% were with male R).

Table 4. Distribution of behaviour categories for the different study groups expressed as a percentage of the total behaviour observed for each group

Group	agg	aff	dom	subm	inv	play	N
Venetia 91	17.8	18.3	7.3	3.0	12.9	***40.6**	4459
Venetia 92 A	***65.9**	16,3	1.1	13.2	3.5	-	546
Venetia 92 B	***31.8**	*24.4	13.4	10.3	13.3	6.8	1395
Venetia 92 C	***61.5**	6.2	9.2	6.2	16.9	-	65
Venetia 92 D	***46.8**	*30.3	3.9	4.7	14.3	-	363
Venetia I	***44.1**	*41.8	2.5	3.5	8.1	-	593
Venetia II	20.1	***35.3**	8.3	5.1	7.7	23.5	896
Venetia III	12.9	***49.4**	7.5	6.1	14.0	10.1	358
Venetia IV	8.8	*30.2	15.4	5.7	4.5	***35.4**	441
Spektakel	*21.5	*21.9	13.1	1.3	***22.3**	*19.9	4654
Thornybush	24.4	**40.77**	2.5	3.3	14.8	14.3	789
Touchstone I	*23.8	***27.4**	9.4	3.9	18.4	17.1	685
Touchstone II	*21.1	***30.4**	13.2	4.9	20.8	9.6	668
Touchstone III	13.3	*25.6	7.5	2.1	14.3	***37.2**	818
Mokolo boma	20.8	21.8	12.4	2.1	***31.2**	11.7	572
Mokolo free	6.2	***34.8**	13.4	3.2	*21.2	*21.2	748
Kaia Ingwe 1	27.7	18.2	2.9	3.7	***47.5**	-	137
Kaia Ingwe 2	***63.7**	29.5	-	-	6.8	-	44

For description of groups see methods, Chapter 2.
agg = aggressive behaviour; aff = affiliative behaviour; dom = dominant behaviour; subm = submissive behaviour; inv = investigating what a partner is doing or feeding, play = any form of play or play-fighting. N = total of behavioural elements categorised in above table. Elements which could not be placed with certainty in any of the above behaviour categories were grouped as "other" and left out of the table. In each group the highest percentage has been highlighted in bold type. Significant occurrence of behaviour categories for each study group, compared to a mean expected occurrence, at $p < 0.001$ is marked with a " * ".

Venetia Limpopo Nature Reserve 1992, boma

All four groups were kept mainly in the smaller pens, not in the paddock (see methods) and observations started from the time of their arrival from the Kruger National Park. In all four groups aggressive behaviour was the most frequent behaviour (A: $x^2 = 576$, $p < 0.0001$, df = 4; B: $x^2 = 190$, $p < 0.0001$, df = 5; C: $x^2 = 56$, $p < 0.0001$, df = 4; D: $x^2 = 130$, $p < 0.0001$, df = 4) but groups B and D also showed significant high values for affiliative behaviour (B: $x^2 = 49.7$, $p < 0.001$; D: $x^2 = 19.26$, $p < 0.001$). A comparison between affiliative and aggressive behaviour showed significantly more aggressive behaviour than affiliative behaviour for all four groups (Table 5)(Binomial, A: $z = 12.7$, $p < 0.00006$, n = 449; B: $z = -3.645$, $p = 0.0003$, n = 783; C: $z = -5.27$, $p < 0.00006$, n = 44; D: $z = -3.525$, $p = 0.0004$, n = 280). Play behaviour was absent in three groups, and only occurred infrequently in group B.

Groups A and C which displayed much intragroup aggressive behaviour, showed more affiliative behaviour to non-group members through the fence than to their own group members (Binomial, A: $z = -3.36$, $p < 0.001$, n = 230; C: $z = 19.63$, $p < 0.00001$, n = 12) (Table 5). Hardly any aggression was observed at communal fences. Groups B and D showed more intragroup affiliative behaviour (B: $z = -11.69$, $p < 0.00001$, n = 435; D: $z = -6.145$, $p < 0.00001$, n = 145).

After Jane joined group C aggressive versus affiliative behaviour was 44% and 56% respectively, but this was not significant ($z = -1.427$, $p = 0.15$, n = 159). However, there was still significantly more aggressive (73.5% of the two combined behaviours) than affiliative (26.5%) behaviour among the juveniles in this group (Binomial, $z = -3.759$, $p < 0.0002$, n = 68). Therefore, it was mainly Jane who showed affiliative behaviour towards the juveniles (46% of the total affiliative behaviour). After group B was allowed to join group C and Jane, aggression versus affiliative behaviour was 53.2% and 46.8% respectively, but again this difference was not significant ($z = -1.35$, $p = 0.18$; n = 491).

Most aggression was seen during feeding time but could occur at any time of the day. Some of the weaker individuals were prevented access to the feeding troughs, for instance female M in group B never managed to get any pellets but was able to feed on the Lucerne and branches which were dispersed. This female was at the bottom of the hierarchy and eventually showed abnormal behaviour by joining a group of males (Chapter 4). In group D the youngest individual would not eat during the first few days and had to be enticed to do so, after which he had to be fed separately as the others pushed him away from the feeding troughs.

Table 5. Aggressive and affiliative behaviour for the four groups A - D at the Venetia Limpopo Nature Reserve expressed as a percentage of the two combined behaviours

Groups: A: four females, 6 - 7 years; B: three males and five females, 4 - 5 years; C: five males, 2.5 - 3.5 years; D: five males, 18 months - 2 years.

Columns 2 and 3: aggressive and affiliative behaviour expressed respectively as a percentage of the combined aggressive and affiliative behaviour observed within a group.

Columns 4 and 5: affiliative behaviour within a group (intragroup) and between different groups at the fence (intergroup) expressed as a percentage of the total observed affiliative behaviour for each group.

	1		2	
Groups	Aggressive behaviour	Affiliative behaviour	Affiliative behaviour Intragroup	Affiliative behaviour Intergroup
A	*80.3	19.7	38.7	*61.3
B	*56.6	43.4	*78.2	21.8
C	*90.9	9.1	33.3	*66.7
D	*60.7	39.3	*75.9	24.1

Binomial test: significance: = * **1.** aggressive versus affiliative behaviour: A: $p < 0.0006$, B: $p = 0.0003$, C: $p < 0.0006$; D: $p = 0.0006$. **2.** affiliative behaviour intragroup versus intergroup: Intergroup: A: $p < 0.001$, C: $p < 0.0001$. Intragroup: B: $p < 0.0001$, D: $p < 0.0001$.

Venetia 1992 - 1994, Periods I - IV

During the first period after the release there was no significant difference between aggressive and affiliative behaviour (Binomial, $z = -0.531$, $p = 0.59$). In periods II, III and IV affiliative behaviour exceeded aggressive behaviour (II: $z = -7.702$, $p < 0.00001$, $n = 540$; III: $z = -8.7$, $p < 0.00001$, $n = 223$; IV: $z = -7.09$, $p < 0.00001$, $n = 172$). Play behaviour increased in period IV ($x^2 = 92.6$, $p < 0.001$, $n = 156$) and was never seen to escalate.

Spektakel Game Ranch

The elephants had been in a large boma together for 4 - 5 months when observations were initiated. The most frequent behaviour was investigating. There was no significant difference between aggressive and affiliative behaviour (Table 4; Binomial, $z = -0.378$, $p = 0.71$, $n =$

2022). This group showed much play behaviour and play-fighting occurred mainly between the males (33.1% of play was play-fighting). There was much aggression during feeding time (not recorded) and the weakest individual was prevented access to the feeding troughs and had to be fed separately. This female never played with the others and was too frightened to go into the dam with them.

Thornybush Game Reserve

The elephants had been together and free ranging for many years when observations commenced. Both aggressive and affiliative behaviour occurred significantly more frequently ($x^2 = 27.8$, $p < 0.001$; $x^2 = 273$, $p < 0.001$ respectively) than other behaviour categories, but affiliative behaviour exceeded aggressive behaviour (Binomial, $z = -5.65$, $p < 0.00001$, $n = 192$). However, as has been shown elsewhere (Chapter 3), most of the affiliative behaviour was directed towards the juvenile S. Play-fighting occurred between the oldest female A and the male B and escalated occasionally.

Touchstone Game Ranch Periods I - III

This group had been released from a boma and together for two and a half years when observations started. In period I aggressive and affiliative behaviour occurred significantly more than other behaviours ($x^2 = 20.88$, $p < 0.001$; $x^2 = 47.7$, $p < 0.001$), but there was no significant difference between the two frequencies (Binomial, $z = -1.28$, $p = 0.2$). In periods II only affiliative behaviour was significantly more frequent ($x^2 = 75.4$, $p < 0.001$) and in period III affiliative and play behaviour occurred significantly frequently ($x^2 = 206$, $p < 0.001$). Play had increased in relative frequency by period III (Table 4) and never escalated.

Mokolo River Nature Reserve

Boma: The first 6 months after arrival the three elephants were kept in a *ca.* 2 ha sized enclosure. The ratio aggressive versus affiliative behaviour was 48.8% to 51.2 % (Binomial, $z = -0.32$, $p = 0.749$) with no significant difference. The most frequent behaviour was investigating (31.2%, $x^2 = 71.69$, $p < 0.001$). Play behaviour could be seen. Female R was the one to show the most interactions towards others. She was responsible for 79.8% of the aggressive, 72.8% of the affiliative and 88.7% of the dominance behaviours.

Free: After the release there was very little aggressive behaviour compared to affiliative behaviour (15% to 85%) (Binomial, $z = -12.17$, $p < 0.0001$, $n = 306$) and play behaviour increased (from 11.7% to 21.2% of the respective total behaviour) and always remained gentle.

Kaia Ingwe

These small elephants had been a problem for the owner. Especially the two very small ones in group 2 were in poor physical condition, one of them had nearly died. It was clear to any observer that they were also in poor psychological condition, not feeding, depressed (definition after Buirski *et al.* 1978: " Failure to seek out or respond to social interactions") and obviously unable to cope with the situation. The female had an abscess in her tooth and the male had bad skin burns from exposure, as they were too young to be able to throw mud on themselves. In this group aggressive behaviour exceeded affiliative behaviour (Binomial, $z = -2.186$, $p = 0.029$, $n = 41$). In group 1 there was no significant difference between affiliative and aggressive behaviour ($z = -1.511$, $p = 0.1$). Investigating was the most frequent behaviour ($x^2 = 51.5$, $p < 0.001$, Table 4). Play was not seen in either group.

ABNORMAL BEHAVIOUR

Group D at Venetia 1992 consisted of very young individuals which would still have been suckling in a normal family unit. The youngest individual (probably no more than 18 months), who received most aggression from the others, repeatedly "suckled" or "attempted to suckle" at the ear pinna of another group member. These two behaviours together constituted 80.4% of his entire interactions, (or 36.1% and 44.3% respectively; n = 424). When prevented from "suckling" he emitted rumbles, growls and frustration screams with an average frequency of one vocalization per four minutes (or 14.67 per hour, see Chapter 9). This individual subsequently died after being relocated a second time. The recipient of the "suckling" behaviour seemed to have learned this behaviour, which he in turn displayed at another locality after also being relocated (Jim Stockley pers. comm.).

Results of the Questionnaires

Aggressive behaviour in the boma was reported by nearly everyone interviewed (82.2%, n = 25). In a number of cases the weakest and most bullied individual had to be separated, especially during feeding time.

DISCUSSION

Aggressive behaviour was the most frequently observed behaviour in the four boma groups at Venetia and also during period I after the release. In the latter case it was mainly the adult female Jane that showed aggressive behaviour. Aggression was also high in group 2 at Kaia Ingwe. Higher levels of aggression in the boma could be related to captivity but also to increased nervousness following the translocation. Aggressive behaviour in the boma was reported by all owners interviewed, which supports this statement. The fact that Jane was so aggressive could also reflect nervousness on her part, as she was now responsible for thirteen, and later twenty-one, juveniles in an unknown environment, and this was also her first contact with such a large group of elephants probably for a long time. Her aggression however, also served to maintain order in the group (see Chapter 3).

Observations on wild elephants will show that very young animals frequently play whenever they get together (own observations at Mashatu; Lee 1987). This was clearly not the case in the Kaia Ingwe group. There was also no play behaviour in three of the boma groups at Venetia (except in group B) or in the first period after the release. In all free ranging groups and the groups which had been in a large paddock, for several months, play behaviour occurred. There was a general trend in play behaviour to increase over time relative to the total behaviour in the Venetia group after the release, the Touchstone group, as well as in the Mokolo group after the release. An emotional state such as fear or insecurity can be expressed through the non-occurrence of a particular behaviour. All animals take precautionary measures to avoid danger. These will require more time the more an animal anticipates danger, such as in a new situation and new environment. On the other hand "feeling secure" will allow more time for other activities, such as social interactions. It would therefore seem that the assumption made at the beginning of the study, that play will occur only when an animal is relaxed, feels secure and is not nervous, was confirmed Alternatively, one can then assume that the non-occurrence of play reflects nervousness, unease, insecurity or some other form of emotional stress. This would confirm that some single individuals, such as female Ch at Venetia 1991 and the young female at Spektakel which both showed little or no play, were in a suboptimal psychological condition.

Rougher play-fighting was observed in the Spektakel group (3 - 4 years of age) and at Venetia in the 1991 group (in the large paddock). This latter group was the only one where play-fighting escalated to higher levels. Play-fighting is probably not connected to the dominance hierarchy (Chapter 4). Elephants in a captive situation have to spend less time foraging, therefore they have more time available for social interactions; this, possibly coupled with a certain amount of frustration due to captivity, might have been the cause of more severe play-fighting. Play-fighting in the pair which escalated most, female B and male R, was never seen to escalate after their release from the boma. There was also harder play-fighting between a male and a female in the Thornybush group. These elephants were slightly older (12 - 15 years) and there was only one male at the time, so he had no other partner to play-fight with (a normal behaviour among teen-aged elephant males).

CONCLUSIONS

From the above it is apparent that newly translocated juvenile elephants need time to adapt to their new surroundings. The frequency of aggressive behaviour is high in a newly translocated group. Aggression can be stressful to submissive individuals, and particularly so where they are prevented access to the food. The results of this study suggest that play behaviour can be used as indication of an animal's welfare, reflecting a relaxed psychological condition. Elephants will react individually to a stressful situation, some obviously having higher thresholds for stress than others, and coping strategies vary from reduction or loss of some behaviour patterns such as play, to increased aggression.

III. TEMPORAL GLAND SECRETION

The temporal glands are situated on either side of the head between the eye and the ear orifice and is unique to African and Asian elephants (Estes & Buss 1976; Buss, Rasmussen & Smuts 1976). In the African elephant two types of secretion can be observed, the one type is watery and evaporates due to highly volatile components (Adams, Garcia & Foote 1978; Gorman 1986), the second is sticky, remains visible for longer periods and is only produced by males during musth (Poole 1987). It is commonly known that elephants secrete from this gland when subjected to stress and fear, such as during culling operations (Adams *et al.* 1978; Buss *et al.* 1976). Various studies have been carried out on the temporal gland secretions and its relation to musth (Pool 1987; Poole & Moss 1981; Hall-Martin & van der Walt 1984), however, few quantitative behavioural studies of temporal gland secretions in relation to stress have been carried out. Adams & Berg (1980) found that the temporal glands secreted under conditions of stress, fear and / or excitement. The present study is an attempt to look at various situations when temporal gland secretion occurred and to appraise its connection to stress and other possible emotional states in the African elephant.

1. Study groups

Venetia Limpopo Nature Reserve, Periods I - IV
Skukuza Boma
Mokolo River Nature Reserve, boma and free
Touchstone Game Ranch periods I - III
Kaia Ingwe
Mashatu Game Reserve

2. Observational data

The presence or absence of temporal gland secretion, or TGS (Poole 1987) was noted as either fresh (shiny) or old (dark dry streak or patch). The amount of secretion was noted on a scale 1 - 5 based on the classification by Poole (1987), but with the addition of one more category (1). Categories 2 - 4 are taken from Poole:
1) small dark patch around the orifice of the gland; 2) from the gland orifice to the lower extend of the eye; 3) to the top of the upper jaw; 4) to the corner of the mouth; 5) to the base of the lower jaw. In addition the width of the secretion was described as being thin or thick. Whenever possible the situation and likely causes of TGS was noted. In the Venetia and Touchstone groups the state of TGS was noted daily at every first sighting of each individual.
Where applicable changes in TGS over different periods for the whole group were tested with a Wilcoxon test (T; two-sided).

RESULTS

There seemed to be a variety of causes of TGS and an attempt was made to categorise the ones observed in the present study (Table 6).

In all observed instances where the cause and reaction were visible, the secretion occurred within seconds of the cause. The secretion remains shiny for a relatively short period (minutes), but the dark streak will be visible for at least a day, after which it is usually rubbed off due to sand bathing or mud-wallowing. Animals which show a continuous dark streak on their cheeks are obviously secreting more frequently. There appeared to be great individual variation in TGS, which supports the statement made above that individuals vary in their disposition to experience stress. Both glands seem to operate separately, as sometimes only one side may be active, or, when both are active, the degree of secretion can differ.

Venetia Limpopo Nature Reserve (VLNR)

Table 7 shows the TGS for all four periods expressed as a percentage of days observed. Jane showed relatively high values for all periods, the highest for the period after the release from the boma.

Bb was the second youngest individual and was pushed to the periphery of the group (Chapter 6) and frequently walked alone. He showed high frequency of TGS especially in period I. He subsequently attempted to get nearer to Jane and in period IV was near Jane after Sq had died (Chapter 3). Ll who also showed relatively high values was another very young male pushed to the periphery of the group. He eventually joined the subgroup of males (Chapter 6). Female D (48.5% in period I) had been dominant in her group in the boma (Chapter 4) but was pushed out of the group by Jane in the beginning after the release and she joined up with the subgroup of males for a while.

The only significant change was from period II to period III were there was an increase ($T = 30$, $p < 0.01$). In period III the two highly nervous females from Zimbabwe joined the group, which may possibly have affected the overall behaviour of the juveniles.

Table 6. Observed contexts in, and causes of immediate TGS

1. Fright	
Observed causes	Additional reactions
Other game (baboons scream, zebras warned, kudus bark, nyala, warthogs, wildebeest)	Being alert, running, cluster formation, face danger, vocalization
Man induced (vehicles, the observer, other people, aeroplanes, being chased, unknown noise)	Being alert, running, cluster formation, face danger, vocalization, aggression, threat behaviour
2. Social aggression	
Observed causes	Additional reactions
Recipient of aggression	Vocalizing, show submissive behaviour
Actor of aggression(when recipient cried)	
3. Social excitement	
Observed causes	Additional reactions
Play-fighting	
Families meet at water (Mashatu)	Vocalization, greeting behaviour
Large males approach (Mashatu)	Submissive behaviour
Mud-wallowing and playing	
Other group nearby (Mokolo)	Nervous, running
4. Feeding in boma	
Observed causes	Additional reactions
Food arrives	running to troughs
Pushing during feeding	
Anticipating food, waiting for food (hungry?)	vocalization, investigating
5. Resting	
Getting up after sleeping	
6. Physical	
Diarrhoea	

Table 7. TGS for the VLNR expressed as a percentage of total observed days
Column 1 = individuals, Columns 2 - 5 the different observation periods (see methods) Sq had died by period IV. Ga and Z are two adult females that joined the group after having been translocated from Zimbabwe.

Ind	Period I %	Period II %	Period III* %	Period IV %
J	70.0	47.4	44.4	62.5
Sq	16.7	2.6	16.7	
Bb	80.0	21.1	44.4	30.4
Lt	50.0	23.7	40.0	40.0
Tb	16.7	2.6	11.1	18.2
F	26.7	7.9	27.3	19.0
B	3.3	18.4	42.9	17.4
S	33.3	36.8	41.2	36.4
R	19.4	18.4	42.9	17.4
E	0	7.9	36.8	26.4
Ro	6.7	5.3	0	15.8
K	23.3	10.5	38.9	30.0
L	3.3	2.6	0	12.0
St	13.3	34.2	33.3	31.8
A	19.4	31.6	33.3	31.8
G	19.4	15.8	23.5	25.0
Sa	13.3	2.6	16.7	4.8
T	6.7	2.6	17.6	28.6
Lt	16.7	5.3	22.2	8.3
Ba	0	10.5	17.2	0
M	13.3	13.2	30.0	14.3
D	48.5	13.2	36.8	21.7
Ga			85.7	88.0
Z			100	100

* significant change from period II to period III, Wilcoxon test, two-sided, $p < 0.01$

Touchstone Game Ranch

Female C, the leader of the group, showed the highest relative TGS frequencies for all periods (Table 8). Male A was often at the rear end of the group together with male P. However, A was a very nervous individual. Both female C and male A displayed most alertness and threat behaviour (see Chapter 3). There was a significant decrease in TGS from period I to period II ($T = 8$, $p < 0.05$) and a significant increase in TGS from period II to period III ($T = 0$, $p < 0.005$).

Mokolo River Nature Reserve

The results from this group are provided in Table 9. During the time in the boma and the first months after the release, the values were relatively high. Then there was a marked decrease. As was shown in Table 3, this group displayed very little arousal behaviour when they were in the boma at Mokolo. They showed TGS when the vehicle with food arrived and they would run up to the section containing the feeding troughs. Possibly this could indicate some form of anticipation or excitement not necessarily related to distress. One female of the other group showed continuous secretion (at every sighting) for at least two years after the release. Thereafter secretion seemed to decrease (anecdotal evidence).

Table 8 . TGS for Touchstone expressed as a percentage of total observed days (For observation periods see methods). Top row: individuals C, K, F, D are females

Periods	C	K	F	D	B	P	T	J	M	A
I	34.6	7.7	3.8	19.2	7.7	11.5	11.5	7.7	7.7	38.5
II*	20.0	0	0	2.2	2.2	20.0	13.3	4.4	0	13.3
III**	50.0	32.1	10.7	25.9	14.3	39.3	28.6	18.5	11.1	57.1

* significant decrease from period I to period II, $p < 0.05$
** significant increase from period II to period III, $p < 0.005$

Table 9. TGS for Mokolo expressed as a percentage of total observed days
P is a male, C and R females (For periods see methods)

Situation	**P** %	**C** %	**R** %
Boma	72.9	93.8	89.6
Free 1.	73.3	66.7	80.0
Free 2.	46.7	46.7	53.3

Free 1. and 2. = total observation days divided into two periods

no test for significance could be carried out in this small group

Table 10. Average TGS grading for Mokolo

	Boma	Free
P	1.8	2.6
C	2.5	3.3
R	1.8	2.7

for grading of TGS see page 100

Kala Ingwe

The two groups at this reserve showed TGS infrequently although particularly the individuals in group 2 were in poor physical condition and showed signs of being depressed and fed very little (see previous section). This led to the assumption that they were also in poor psychological condition. Some of these individuals were probably less than two years old. Therefore TGS can occur in juveniles of that age.

Skukuza Boma

The individuals in the different groups showed varying occurrence of TGS. Observations were only done during one week and data are too few to draw conclusions. As was seen at Kala Ingwe, however, the individuals showing apathy and depression did not secrete, whereas individuals showing high degree of nervous behaviour did.

Mashatu Game Reserve

Figure 3. shows the results for the family groups. As from category f4 upwards the females show higher values than the males. Only category f5 and the musth males showed secretion grading 5.

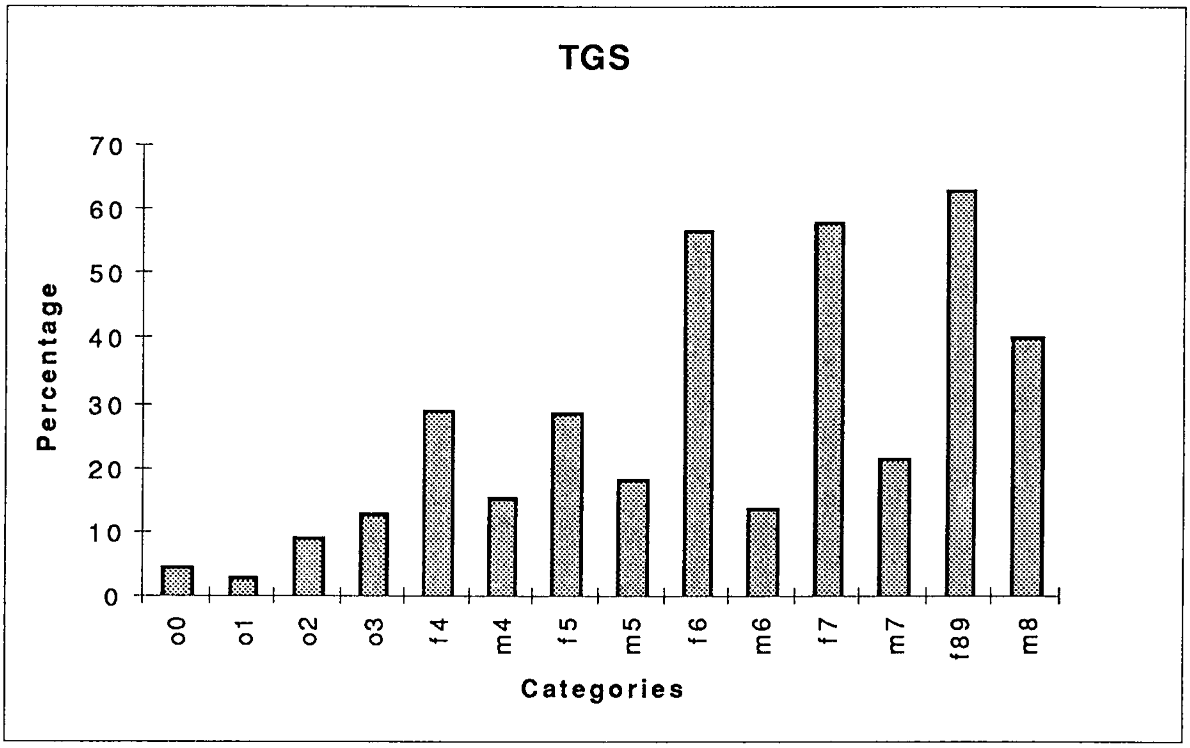


Figure 3. TGS values for the different age/sex categories at Mashatu expressed as a percentage of total TGS recorded (n = 6550). (o0 - o3: f and m combined for each of those age categories; see methods for age categories)

DISCUSSION

Temporal gland secretion was observed in a variety of contexts, not all necessarily related to a negative experience. Anticipation of food triggered TGS as well as certain social situations i.e. approach of a dominant male or the meeting of two family units. The meeting of families seems to be cause for great excitement, with the animals vocalizing and urinating (Moss 1988). TGS also occurred when the animal was afraid, such as culling operations (Buss *et al.* 1976), unexpected happenings and other forms of excitement (present study). This confirms the findings by Adams & Berg (1980) on captive elephants that the temporal glands secreted under conditions of stress, fear and / or excitement. In addition the present study showed that certain social events and anticipation can trigger TGS.

Temporal gland secretion in this study occurred in all age and sex groups. This confirms findings by other authors that elephants secrete from the temporal glands from as early as one year of age (Adams *et al.* 1978). Results (Mashatu data) indicate that secretion occurs below the age of one, and that females secrete more than males do and that older individuals secrete more than younger ones. If secretion was correlated to size of the gland and age of the individual, one would expect males and females to secrete equally, if anything males more frequently. This raises the question whether females experience more stress or are more nervous than males. Females have the responsibility of looking after calves and older females have the added responsibility of ensuring the safety of the whole family and finding water and good foraging areas. Jane, the matriarch of the Venetia group, and female C (a seven year old), the leader of the Touchstone group (Chapter 3), both had high levels of secretion. Other plausible causes of more secretion in females could be the oestrus cycle or pregnancy. It seems unlikely though, that all females at Mashatu cycle simultaneously and casual observation of the pregnant female at Thornybush who showed no TGS also negates the latter. The increase of TGS with age, might additionally reflect an increase in awareness of danger. There was no correlation between rank within the dominance hierarchy and TGS. To date there is no evidence that secretion is used for communication, but cannot be excluded.

Interpretation is made more difficult by the fact that the occurrence and degree of TGS appears to be individual, i.e. in the same situation some individuals will secrete, others not, which confirms that individuals have varying heights of thresholds for stress, nervousness or excitement and may even react differently to different situations, depending on their genetic make up and previous experiences, behaviour of the mother, etc. The varying reactions of the juveniles at Skukuza and the individuals in the Venetia bomas serve to illustrate this (e.g. apathy, nervousness, aggression). It would be interesting to find out which hormones trigger TGS.

CONCLUSIONS

TGS can be used with some degree of caution as measure for acute stress, fear, nervousness and excitement. TGS can also occur during certain social events. Females seem to secrete more frequently than males do. Elephants living in secure conditions will probably have a higher threshold level for reacting to unknown situations. On the other hand elephants living in insecure conditions will probably have a lower threshold and therefore secrete more frequently. A hypothesis to be tested is that females carry more responsibility than males and have lower thresholds of nervousness and possibly stress, and that particularly females that lead (matriarchs) experience higher levels of stress.

CHAPTER 9

SOME BEHAVIOURAL AND ACOUSTICAL ASPECTS OF VOCALIZATIONS OF TRANSLOCATED JUVENILE AFRICAN ELEPHANTS

INTRODUCTION

Elephants have a large repertoire of vocal communication (McKay 1973; Berg 1983) which have been associated to specific behavioural contexts (Berg 1983; Poole, Payne, Langbauer & Moss 1988; Poole 1996; Langbauer, Payne, Charif & Thomas 1989; Langbauer, Payne, Charif, Rapaport & Osborn 1991). Particularly the low frequency "rumbles" have been the focus of several studies and science is only beginning to understand the complexity of this form of communication. Elephants have true, elastic vocal cords which are ±7.5 cm long (Sikes 1971), compared to ±1.3 cm for an adult human, and as the frequency of vibration is inversely proportional to the mass of the cord, one may expect the elephant to produce low sounds. Low frequency sounds have less attenuation than higher frequency sounds and therefore an elephant will perceive low frequency sounds better at distances over 100 - 300 m (Wiley & Richards 1978; Payne *et al.* 1986). High-frequency hearing is directly correlated with the functional distance between the two ears (Heffner & Heffner 1982), which means that elephants, which have relatively large heads and ears set widely apart, will hear low frequencies better than high frequencies. Low frequency calls in the range of 14 - 35 Hz (Berg 1983; Payne *et al.* 1986; Poole *et al.* 1988) have been identified and are audible to the elephant at distances over several kilometres (Langbauer *et al.* 1991). The upper limit of hearing in elephants appears to be 12 kHz (Heffner *et al.* 1982). For comparison the upper limit for humans is in the region of 20 kHz and the lower limit is between 30 - 40 Hz. A study by Garstang, Larom, Raspet & Lindeque (1995) has shown that the efficiency of elephant communication is also a function of weather conditions and that low frequency communication is optimised during dry and cool conditions and the authors suggest that a range of over 10 km at night are likely. It has also been shown that at 1 m above ground, the lower the frequency the further the sound will travel (Marten & Marler 1977).

During this study an attempt was made to obtain some information on vocalizations of juvenile elephants. The main aim was to see whether vocalizations of stressed elephants differed from those of unstressed ones. In order to find a possible difference, the following parameters were used: occurrence of vocalizations per unit time, type of vocalization and acoustical manifestation.

METHODS

1. Study Groups

Data from the following study groups were used, for details see methods, Chapter 2.

Skukuza Boma
Kala Ingwe
Mokolo River Nature Reserve Boma
Knysna Forest, large boma
Venetia Limpopo Nature Reserve 1992, Boma

Venetia Limpopo Nature Reserve (VLNR) 1992-1994, Free
Touchstone Game Ranch, Free
Thornybush Game Reserve, free

The free ranging elephants at Venetia and Touchstone were assumed to be unstressed as these elephants had been free for a number of years and well habituated and relaxed in the presence of the observer. Other behavioural data supported this assumption (see sleeping behaviour, Chapter 7). Therefore data from these groups were used for comparison.

2. Data recording and Analyses

2. 1. Behavioural sampling and analysis

Throughout the entire study period the occurrence and type of all vocal sounds were noted *ad lib.*, as well as the situation during which the sound occurred and the individual that called and reactions to the call when possible. The sounds were grouped into the following categories (McKay 1973, Berg 1983, Poole *et al.* 1988; Payne *et al.* 1986; Langbauer *et al.* 1989; 1991): Rumble, growl, trumpet, cry, bellow, snort. The use of this terminology is not always consistent throughout the literature. In the present study the growl is applied to a more intense sound than the rumble (termed "low rumble" in the following), with a distinct guttural roll to it (see results). A cry is a short very loud sound, a bellow is a low-pitched loud sound. The 'squeak', 'chirp' and 'bounce trunk-tip on ground boom' (McKay 1973, Garaï own observations) known from Asian elephants was never heard during the present study. Many other sounds have been described and heard during this study, but data were too few for distinct grouping and were therefore omitted. Vocalizations were grouped and the occurrence per individual per hour calculated. Behavioural data were grouped with the type of vocalization. Significance was tested using a *chi*-square test.

2. 2. Audio - recording procedure and apparatus

Sound equipment was obtained in April 1994 and recordings started soon afterwards. Recordings were made with a Sony TCD-D10 PRO II DAT Recorder, a Sennheiser MKH110 microphone, and a microphone amplifier Electrosound SSU3. A test done by Timbre Audio Systems showed the frequency response of the recorder to be -3dB (standard DIN) @ ± 6 Hz, and the frequency response of the microphone to be -3dB @ ± 0,1 Hz. The amplifier had attenuation at 13 Hz (-3 dB).

Recording and analysis of elephant vocal communication optimally requires not only sophisticated technical equipment but also the help of several persons. During this study the observer walked on her own with the elephants, sometimes over many kilometres, and this limited the amount of recording equipment she could carry besides tracking equipment, binoculars, water bottles, weapon, etc. The bush was very dense in all reserves which made visibility of (i.e. identification of caller and distance to) the elephants very difficult. For this reason no intensity measurements were made and the Venetia acoustical analyses includes the vocalization of the adult female. Recordings of identified individuals were easier to obtain at the bomas. Wind is a source of low frequency noise and this proved to be a problem, especially during the hot season, when there was significant air turbulence, particularly at Venetia.

2. 3. Acoustic analyses of recordings

The acoustic analyses were done on a digital sound processor from Kay Elemetrics Corporation, the DSP SONA-GRAPH, model 5500. The recordings were played back from the same digital sound recorder into the digital memory of the Sonagraph, analysed and then displayed on a RGB colour high resolution multi-sync monitor.

The analysis set-up included a display of the soundwave, a narrowband spectrogram and a dissection of the spectrogram based on the computed mean of a specified portion of the vocalization. This multiple type of display and information enhances the reliability of measurements obtained by means of adjustable time and frequency cursors on the various displays. A great deal of time was initially spent in structuring an optimum analysis set-up for the different types of vocalization. The frequency range of the analysis set-up was adjusted for the different types of vocalizations in order to obtain the maximum information, e.g. 0 - 250 Hz (Fig. 1), 0 - 2 kHz, 0 - 4 kHz (Fig. 4 & 5) and 0 - 8 kHz (Fig. 3). DC coupling was used to accommodate the low frequencies of these vocalizations.

Duration measurements were done on the spectrogram and checked on the soundwave. The fundamental frequency (Fo) was derived from the difference between the overtones on the narrowband spectrogram (Fig. 1, 2 and 5) and checked with a peak count per time calculation on the waveform, where the time axis could be expanded so that the peaks could be counted (Fig. 1 and 2), as well as the frequency of the first peak on the dissection (or amplitude spectrum). The fundamental frequency modulation (Fo modulation) was calculated as the difference between maximum and minimum frequency of the dominant overtone on the narrowband spectrogram throughout the vocalization. By looking at the narrowband spectrogram and the dissection thereof, a subjective indication of the spectrum of highest energy concentration was derived and the maximum frequency estimated. This is not an absolute measurement but gives an indication of the area and range of the spectral energy for a specific type of sound. The same type of information was also obtained by noting the frequency of the dominant overtone (Dominant frequency) on the dissection of the narrowband spectrogram (highest peak; see Fig. 1, 2 and 5), which provides information on the relative amplitude of the different overtones. Approximately 30 hours were spent on the actual analyses of 349 vocalizations. Each sound taking about 4 - 6 minutes to analyse, as some sounds were analysed on two different set-ups (e.g. 0 - 250 Hz for Fo and 0 - 4 kHz for Spectrum).

RESULTS

1. Behavioural data on occurrence of vocalization per unit time

Table 1 provides the results for the distribution of vocalization types for the different study groups (bomas and free-ranging). To answer whether there was a difference in vocalization occurrence per hour, the data from all Venetia and Touchstone periods were taken and the mean calculated thereof (0.53) to reflect the baseline rate of vocalization. Both these groups had similar means when analysed separately (Touchstone: 0.43; Venetia: 0.63). Compared to this mean some of the other groups showed significantly more vocalizations per unit time (Table 1).

Group D at Venetia, the Mokolo elephants in the boma and the very young individuals at Kaia Ingwe all showed significant more vocalizations than the mean. At Skukuza four of the eight groups showed significantly high vocalization frequencies. These were either very young individuals (2 years or below) or a single individual. The four groups that showed no significant increase were two groups of males which displayed apathy and had been in the boma for some time (Chapter 8), and two groups of females over 2 years. The small females showed extreme signs of frustration, by walking around aimlessly continuously, throwing objects and kicking objects or other elephants and often crying out. One of them consistently tried to climb out of the boma. Cries from these individuals were heard throughout the night over several kilometres.

At Venetia boma the five males in Group D were under 2 years of age and one individual (Ru) displayed abnormal behaviour by suckling at a partner's (N) ear pinna (Garaï 1993, 1994). Ru accounted for 68.5% (n = 391) of all this group's vocalizations (n = 571), which gives a rate of one call every 4 minutes (or 14.67 per hour). Many of his calls were frustration cries (17.4% of his vocalizations) when he was not allowed to suckle at his partner's ear. Both these individuals emitted many growls (Ru: 19.7%, N: 37.3% of each individual's vocalizations). The Kaia Ingwe elephants were also very young, especially the two individuals in group 2 were under two years of age. They were in bad physical and probably poor psychological condition. Particularly the male emitted many growls whenever the female pushed him (49.3% of his vocalizations). He also emitted cries frequently(23.4%). In the other groups the amount of growls were much less than the rumbles.

In the free ranging group at Venetia the youngest male emitted 81.4% of the total growls and 81.9% of all the known cries (n = 317 and n = 193 respectively). Many of his vocalizations were emitted when he was prevented from suckling by his adopted mother Jane, when she either moved a leg or started to walk while he suckled (Chapter 3). At Mokolo the young male emitted 83.3% of the growls and was the only one to cry.

Table 1 Distribution of vocalization types expressed as a percentage of total vocalizations recorded in each study group

Group	lr %	gr %	tm %	cry %	time active	N	rate/ hr/ ind
Kaia Ingwe 1	40.0	45.5	1.8	12.7	9h45m	55	*1.88
Kaia Ingwe 2	64.3	26.4	0	9.3	9h10m	193	***10.53
Skukuza bomas:							
4F (±2 yr)	53.8	29.0	3.2	14.0	3h17m	93	***7.09
1F (5-6 yr)	61.9	9.5	28.6	0	2h30m	21	***8.40
3F (2-3 yr)	59.4	21.9	9.4	9.4	9h47m	32	1.31
6M (4-5 yr)	0	0	80.0	20.0	2h15m	5	0.37
6M (6-7 yr)	25.0	25.0	50.0	0	3h15m	4	0.21
2M (±18 mth)	21.7	52.2	0	26.1	2h17m	23	***5.00
2M 1F (±2 yr)	43.7	46.9	0	9.4	4h20m	128	***9.85
3F (±4 yr)	100	0	0	0	1h00m	2	0.67
Mokolo free	90.2	8.1	1.2	0.5	177h25m	410	0.80
Mokolo boma	88.5	8.0	0.5	3.0	51h10m	425	**2.45
VLNR Group A	100	0	0	0	56h40m	23	0.10
VLNR Group B	100	0	0	0	46h25m	77	0.21
VLNR Group C	100	0	0	0	11h00m	11	0.20
VLNR Group D	64.6	22.8	0.2	12.4	26h40m	571	***4.28
Venetia I	58.3	19.0	0.2	22.3	97h38m	1702	0.79
Venetia II	79.4	11.7	1.3	7.6	71h57m	1515	0.96
Venetia III	72.4	23.1	0.4	4.1	61h45m	221	0.16
Touchstone I	96.8	2.1	0.2	0.9	116h17m	437	0.38
Touchstone II	89.4	6.7	2.8	1.2	59h16m	254	0.43
Touchstone III	97.4	2.0	0.6	0.3	71h23m	345	0.48

lr = low rumble, gr = growl, tm = trumpet, cry = all forms of bellow, scream, cries etc.
Time active = total active time excluding resting, N = total vocalization recorded, rate / hr / ind = rate per hour per individual. F = female, M = male, estimated age given in years (yr) or months (mth). * = $p < 0.25$; ** = $p < 0.01$; *** = $p < 0.001$: significantly higher rates compared to the mean derived from Venetia and Touchstone free-ranging.

2. Acoustic analyses of type of vocalization at the different sites

This was differentiated by means of a descriptive definition and acoustic analyses. Table 2 presents the results of the acoustic analyses of the various types of vocalizations at the different study sites.

1. Low rumble:

Definition: A relatively soft, low, monotone rolling sound, the mouth appears closed. The monotony of this sound is illustrated in the spectrogram and waveform in Figure 1.

Acoustic characteristics: The mean duration of low rumbles were shortest for the very young elephants at Skukuza and Kaia Ingwe (range: 0.4 - 7 sec), slightly longer at Mokolo (range: 1.7 - 9.5 sec) and longest for the Venetia and Knysna elephants (range: 2 - 21 sec). Most calls at Venetia were emitted by Jane, one of the other adults or by one of the older juvenile females, however not all calls could be identified. Whether the difference in duration was related to the age or the different meanings of the calls cannot be assessed.

Both the Skukuza and Kaia Ingwe fundamental frequency (Fo) ranged between 18 Hz - 27.5 Hz, with a mean above 20 Hz. At Mokolo (4 - 5 years of age) slightly lower, 17.5 - 20 Hz. At Knysna where the elephants were between 8 - 10 years old, the Fo range was 13.5 - 18.45 Hz (mean: 16.26). The Fo was lowest for the Venetia elephants (range: 14 - 22.5 Hz) with a mean of 16.77 Hz (this group included older juveniles and an adult). It is interesting that the mean fundamental frequency for Mokolo is in between the very young and older elephants.

The Fo modulation was very low for all groups, the highest being 11.25 Hz, but mainly below 5 Hz, which illustrates the extreme monotony of the call (Fig. 1).

The mean dominant frequency was lowest for Venetia and highest for the young elephants at Skukuza and Kaia Ingwe. The spectrum in all groups did not exceed 2000 Hz.

2. Growl:

Definition: A more guttural, rolling, periodic, slightly louder sound than the low rumble, the mouth is generally open. The periodic, rolling effect is illustrated on the waveform in Figure 2.

Acoustic characteristics: The duration of a growl is generally slightly shorter than that of a rumble, the shortest being at Venetia (range: 1 - 1.7 sec; mean: 1.7 sec) where the growls were emitted mainly by the youngest individual (Chapter 3). The young elephants at Kaia Ingwe and Skukuza had slightly shorter durations for the growl than the low rumble (range: 0.56 - 3.7 sec).

Table 2. Duration and frequencies for various vocalization parameters at each reserve
(See text for explanation of parameters)

Place	Vocal.	Duration (sec)				Fundamental frequency (Hz)				Fo modulation (Hz)				Dominant frequency (Hz)				Spectrum	
		mean /	range /	SD/	n	mean /	range /	SD/	n	mean /	range /	SD/	n	mean /	range /	SD/	n	(Hz)	n
VLNR*	rumble	5.87	2 - 21	3.63	37	16.77	14 - 22.5	1.9	42	5.75	<5 - 15	2.45	20	27.69	15 - 45	10.83	39	1335	40
	growl	1.7	1 - 2.7	0.89	3	23.5	20 - 28	4.1	3				0	98	20 - 230	114.71	3	1720	3
	cry	1.13	0.5 - 1.7	0.49	4	271.25	105 - 395	121.34	4	195			1	438.75	390 - 560	81.28	4	8000	4
	trumpet	1.01	0.7 - 1.4	0.31	4	206.66	85 - 450	210.73	3				0	256.25	40 - 800	363.4	1	6500	3
Knysna	rumble	5.36	2.4 -12.25	2.52	32	16.62	13.5 - 18.45	0.94	32	5.83	<5 - 10	2.04	6	33.56	30 - 38	1.78	32	1405	32
Mokolo	rumble	3.77	1.7 - 9.5	1.97	15	18.09	17.5 - 20	0.72	18	<5	<5		2	35.5	35 - 40	1.32	16	1025	17
Skukuza	rumble	2.51	0.9 - 4.7	0.81	23	21.58	18 - 27.5	2.55	24	<5	<5		8	43.69	36 - 50	3.44	23	2000	23
	growl	2.14	0.7 - 3.7	0.83	74	25.55	19 - 30	5.15	75	21.6	15 - 45	12.58	39	69.06	40 - 365	78.32	70	4200	75
	cry	2.08	0.5 - 3.5	0.85	26	339.89	57.7 - 505	128.5	18	237.5	75 - 465	119.29	11	495	60 - 1165	236.2	23	8000	24
	squeal	2.0	2	0	2	640	600 - 680	56.52	2	367.5	365 - 370	3.54	2	675	670 - 680	7.07	2	5000	2
	bellow	2.26	1.62 - 2.77	0.59	3	212.3	22.5 - 330	166	3	258	236 - 280	31.11	2	441.67	350 - 645	176.4	3	5000	2
Kaia Ingwe	rumble	2.52	0.4 - 7	1.27	65	21.3	20 - 24.75	1.77	66	6.35	<5 - 11.25	1.49	56	42.4	40 - 49.5	2.63	57	2000	64
	growl	1.77	0.5 - 3.04	0.99	24	22.09	20 - 28	4.72	25	10.5	<5 - 50	12.95	21	44.4	41.8 - 50	2.69	16	2000	24
	cry	1.5	0.7 - 1.9	0.47	5	260	50 - 4437	175.2	4	227	60 - 470	160.92	5	513.75	235 - 935	297.9	4	8000	5

Vocal. : type of vocalization; Fo modulation: modulation of fundamental frequency; Spectrum: maximum only
* Group with adult female

The mean Fo was over 20 Hz for all groups and the upper range was also slightly higher than that of the rumble. The greatest range was at Skukuza (19 - 30 Hz). Growls were emitted mostly by young individuals, as was shown in Table 1.

The Fo modulation showed more variation than the rumble and the dominant frequency was higher, except at Kaia Ingwe. The spectrum went up to 4200 Hz, showing that a growl has more energy than a low rumble.

3. Cry:

Definition: A very loud, relatively short, very noisy sound, the mouth is wide open.

Acoustic characteristics: The mean duration of a cry is short, the longest recorded were at Skukuza (range: 0.5 - 3.5 sec). A cry can start abruptly or start off with a growl (Fig. 3) and usually ends abruptly but can end with a growl. The mean Fo was above 260 Hz in all groups and the large range (50 - 4437 Hz) shows how vastly different cries can be, the highest being for the Kaia Ingwe juveniles.

The mean Fo modulation, with the lowest at 195 Hz and a range of 60 - 470 Hz, illustrates the large difference in pitch of the vocalization, which can start as a low growl and rise up to a high, very loud sound and then drop again to a low frequency.

The mean dominant frequency was above 438 Hz, with a range of 60 - 1165, and the spectrum was the highest of all vocalizations with up to 8000 Hz.

4. Bellow and Squeal:

Definition: The bellow is a low pitched loud sound, the squeal is very high pitched and loud. Available data were too few to adequately differentiate and define the various loud sounds, therefore they have been grouped in Table 2 under 'cry'.

Acoustic characteristics: These vocalizations were only recorded at Skukuza and the sample size is very small, but bellows were slightly lower than a cry and squeals higher (Fig. 4). Both had relatively high differences in modulation, high dominant frequencies, the squeal the highest, and the spectrum went up to 5000 Hz.

5. Trumpet:

Definition: a blast of air through the trunk, resulting in a high frequency, high intensity sound, resembling the quality of a trumpet instrument.

Acoustic characteristics: The few trumpets that were recorded at Venetia, uttered by juveniles, showed the shortest duration of all vocalizations, a mean and dominant frequency over 200 Hz and a spectrum up to 6500 Hz (Fig. 5).

3. Situations and type of vocalization

Various vocalizations were heard in different contexts: (see Appendix 2 for a detailed list of behaviours and associated type of vocalization).

Low rumbles:

These calls could be heard in very different situations, when elephants were feeding or walking, when people approached, when individuals walked away, during friendly social encounters, when they appeared to be calling other elephants, during play or resting bouts or when they were expecting food. A series of low rumbles could be heard prior to resting periods with an average of 5 low rumbles per minute (range 4 - 22 calls, usually within 1 or 2 minutes).

Growls:

This vocalization occurred in the following contexts: when individuals were being pushed or received some other form of aggression; occasionally when a dominant individual investigated the food of a subordinate one the latter one growled; when the elephants were nervous; when females encountered males on the other side of the fence and there were high levels of excitement. In general growls were emitted more by young individuals in a group. The young male at Venetia growled frequently during suckling, when he was prevented from suckling and when another individual touched him on the lips while he suckled.

Trumpeting:

This sound occurred when the elephants ran; when a young individual was pushed over by an adult; when young individuals chased birds or played in the water, when an individual was lost and highly excited.

Cries, Bellows and Squeals:

These were heard as a reaction to aggressive behaviour by others, when the elephants ran away, when a young individual was prevented from suckling, when individuals were lost or frustrated. The various names and definitions given to loud vocalizations (roar, bellow, bark, cry, gruff cry, squeal) in the literature (McKay 1973; Berg 1983) and the present study appear to be individual to elephants and possibly age categories. This serves to illustrate that elephants are capable of many sound variations. However, all these loud calls are generally associated with discomfort, frustration, fright or fear.

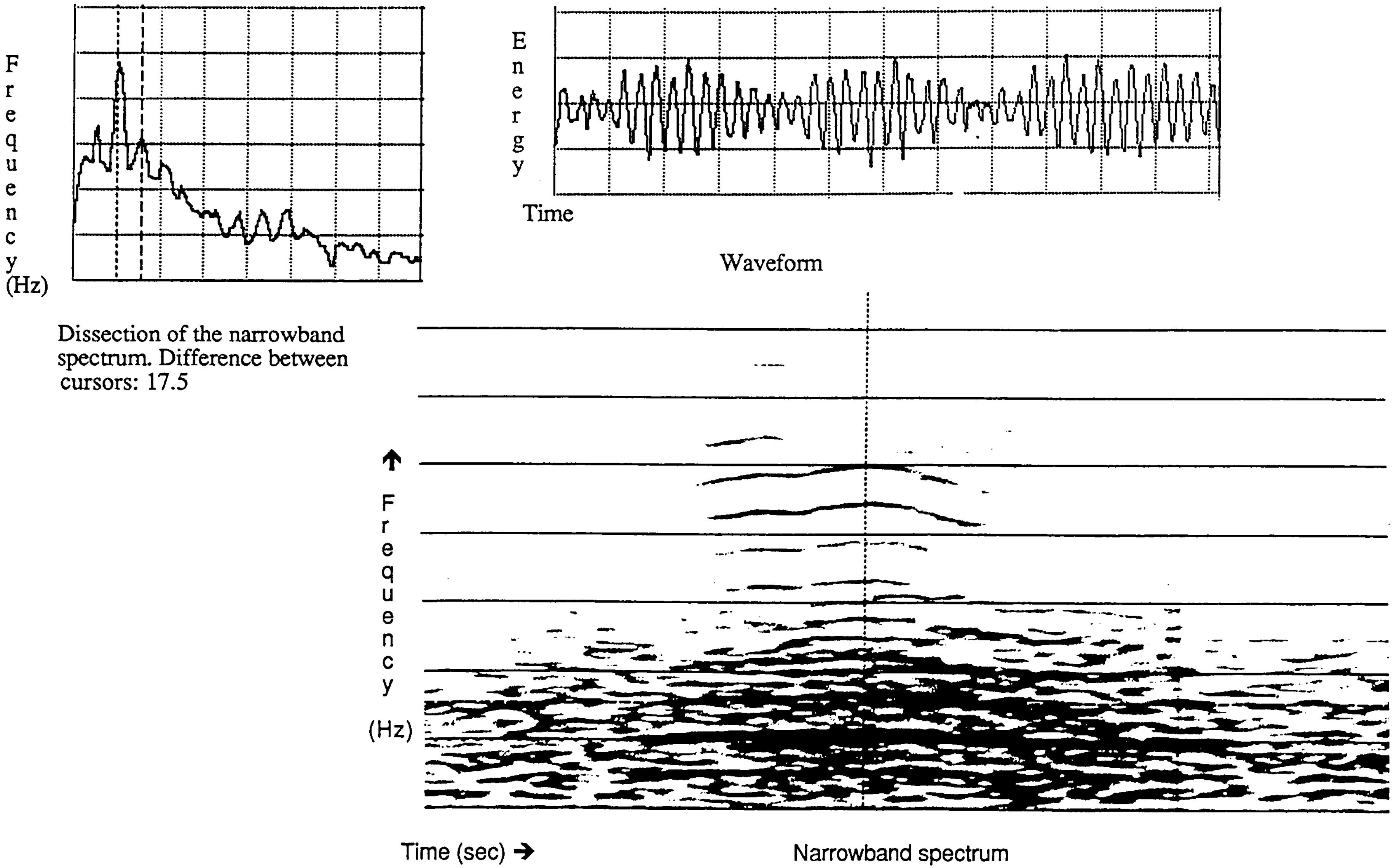
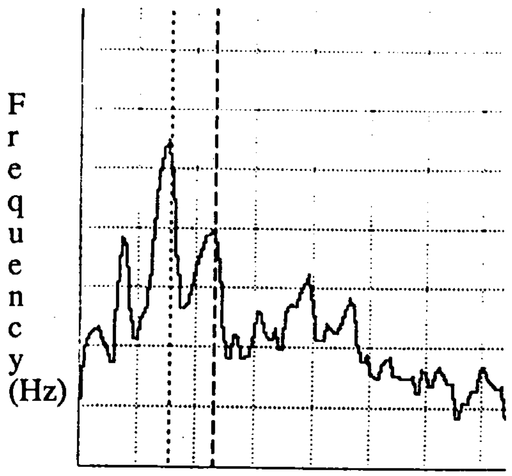
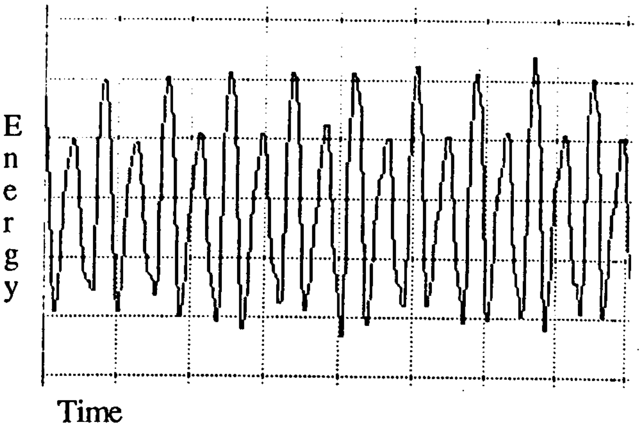


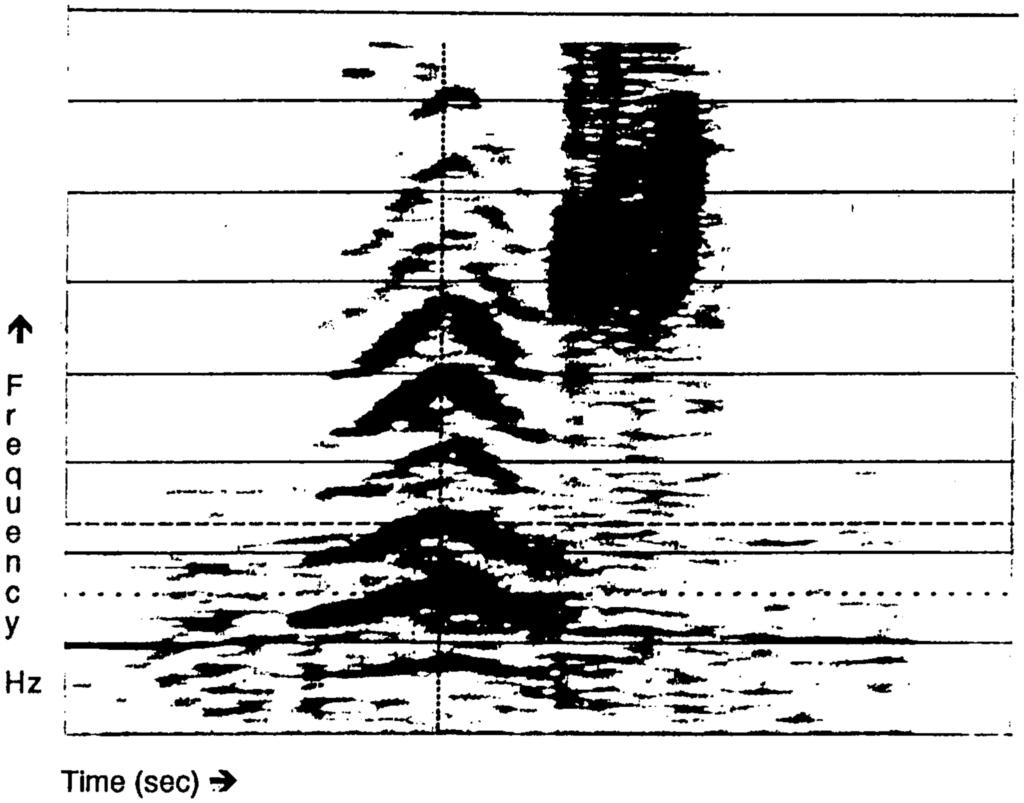
Figure 1. Example of a low rumble from Knysna. Scale: 0 - 250 Hz. Time: 9 sec
Fundamental frequency: 17.5 Hz. Dominance frequency 31.25 Hz



Dissection of the narrowband spectrum. Difference between cursors: 23.75 Hz.
Dominant frequency 48.75Hz

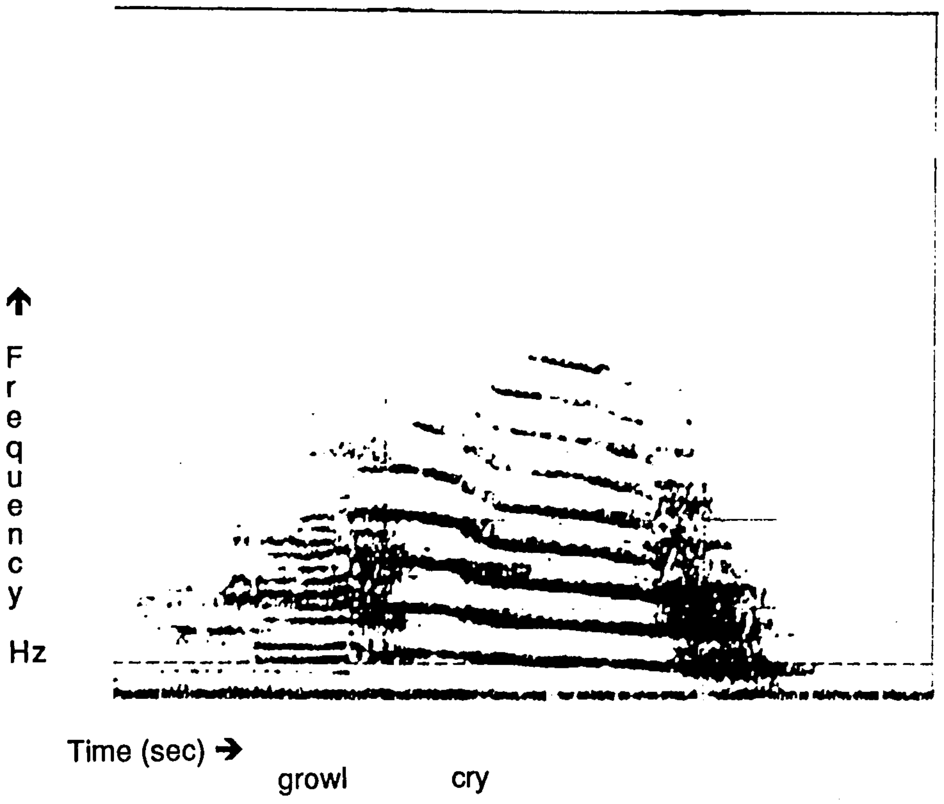


Waveform



Narrowband spectrum

Figure 2. Example of a growl from Skukuza. Scale: 0 - 250 Hz. Time: 2.6 sec. Fundamental frequency: 23.75 Hz.



Narrowband spectrum

Figure 3. Example of a cry with preceding growl from Kaia Ingwe. Scale: 0 - 8000 Hz. Time cry: 1.2 sec. Fundamental frequency: 400 Hz.

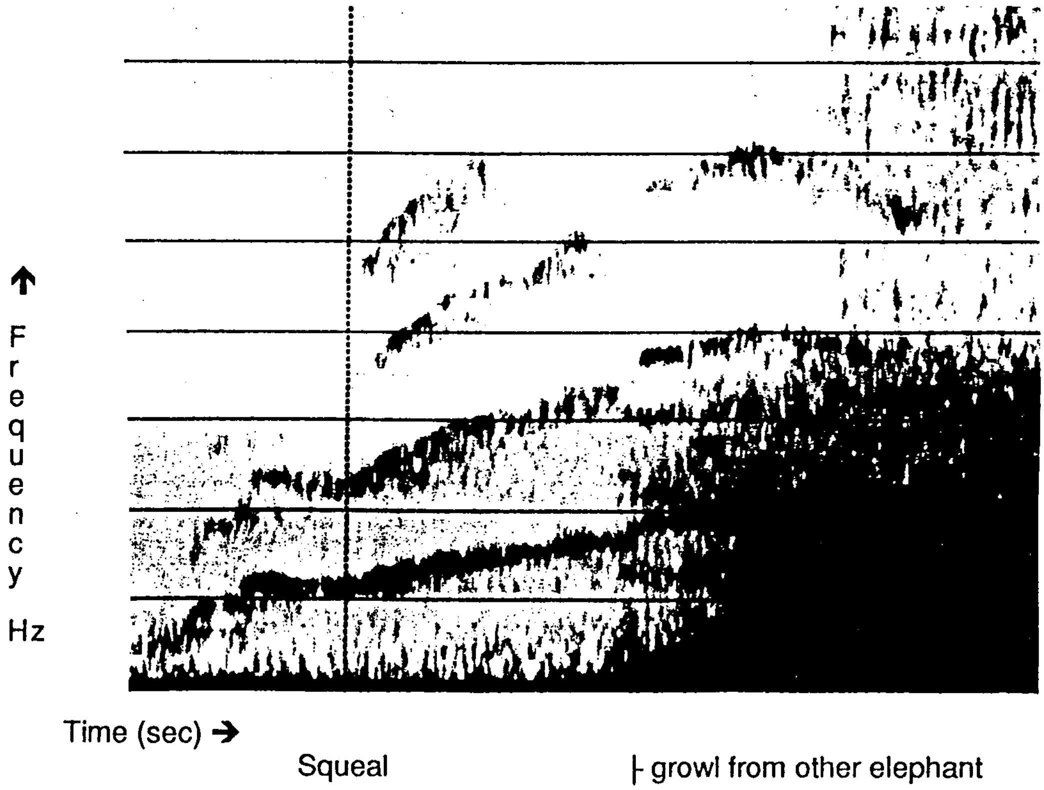
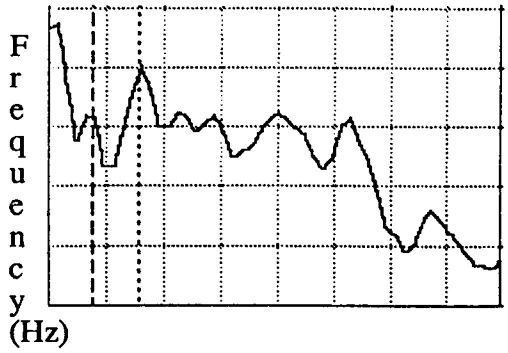
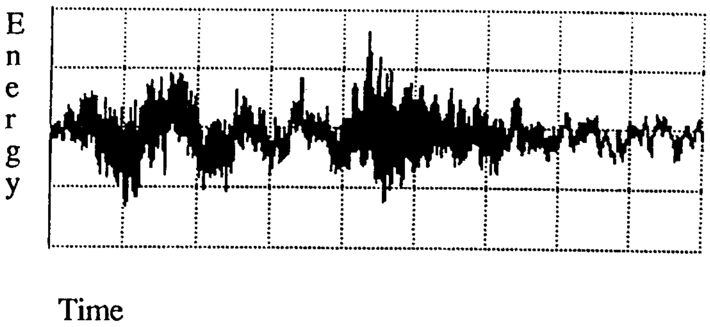


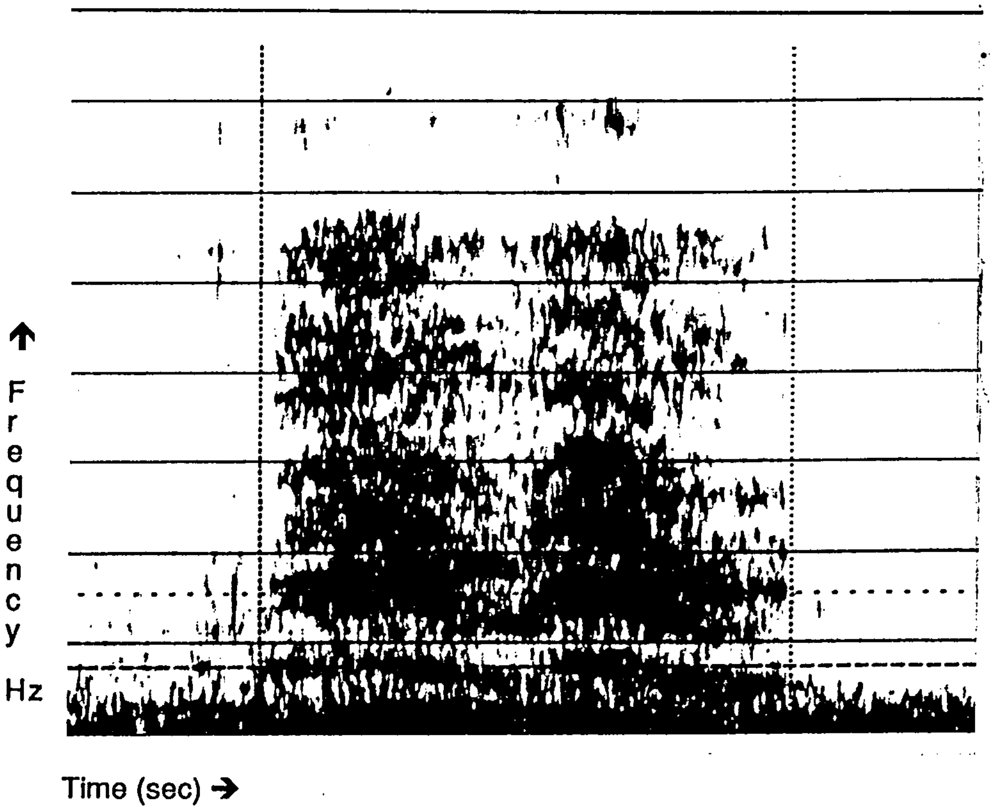
Figure 4. Example of a squeal from Skukuza. Scale: 0 - 4000 Hz. Time of squeal: 2 sec. Fundamental frequency: 680 Hz.



Dissection of the narrowband spectrum. Difference between cursors: 400 Hz.
Dominant frequency 780 Hz



Waveform



Narrowband spectrum

Figure 5. Example of a trumpet from VLNR. Scale: 0 - 4000 Hz.
Fundamental frequency: 400 Hz (Difference between cursors).
Time: 1.36 sec (difference between vertical cursors).

DISCUSSION

There was a significant difference between the rate of vocalization per hour between very young or single individuals and older or grouped individuals, as well as between a group in a boma and the same group after their release. It appears that individuals below the age of 2 years or individuals that are penned alone vocalize more frequently. Only one of the boma groups at Venetia showed a significantly high rate of vocalizing. This group was extremely nervous and had been used to define arousal behaviour (Chapter 8).

A look at the details of the type of vocalization shows that the elephants at Skukuza, Kaia Ingwe and group D at Venetia tended to use more of the louder vocalizations (growls, cries, trumpet) which reflect a higher level of emotional turmoil, such as aggression, frustration, fright etc. which supports the assumption that these individuals were more stressed. High values for cries were also obtained at Venetia I, which was mainly due to the small male (Chapter 3).

Low rumbles were heard in all types of situations. This is the most frequent type of vocalization used to convey a specific message (Poole *et al.* 1988). In general it is the young individuals that growl more, but also those that are pushed most (which usually are the youngest). Growls were heard also as protest to being pushed or as sound of frustration (e.g. prevented from suckling) or when an individual approached another who was feeding. It would appear that growls are more a sound of protest or frustration. In all groups the youngest individual cried (or bellowed). Cries were heard when an individual was pushed or received some other form of aggression by other group members, or was frightened.

The differences in time and frequency between the low rumbles at Venetia and Knysna as opposed to the younger groups could have been due to a difference in meanings of the calls. Lower frequencies are probably used for long distance communication, which is possibly why they were heard more at Venetia where the elephants dispersed and less in the bomas, where it might not have been necessary to use low frequencies. The messages conveyed may also have been different in the wild than in the boma, e.g. contact calls not used in the boma. At Knysna the wild elephant was in the vicinity of the boma and possibly the elephants were communicating, although this is speculative. In both Venetia and Knysna groups, many low rumbles appeared to be warning calls when the observer approached, these may have lower frequencies. However, one could also expect elephants in the boma to emit contact calls to the elephants in the other pens or even try to call their lost families or mothers, and also to emit warning calls when people approached. Therefore a more plausible explanation for the difference in frequencies between Venetia, Knysna and the other groups, may be that the small elephants (2 years) have smaller vocal cords and therefore the sound produced could be higher-pitched than that of an older elephant. The 4 - 5 year old elephants had in between values, which supports the hypothesis. This hypothesis has to be tested with many more recordings. If the amplifier was the limiting factor, the low sounds at Venetia, which were further away than in the boma groups, should have been attenuated and the low frequencies of the boma animals should have been more easily picked up from so short a distance to the microphone, despite attenuation at 13 Hz. However, it cannot totally be ruled out that the very young groups simply did not use very low frequencies in the bomas.

The difference in duration of the rumbles from the Venetia and Knysna groups as opposed to the younger groups, could also reflect a difference in the meaning of the call. On the other hand the longer calls could also have been a means to overcome the habitat properties (foliage, air turbulence, temperature) which would induce absorption, reflection and refraction, and only show a difference of use in transmission of sound in a natural habitat versus the boma environment (Waser & Waser 1977).

The growls were generally slightly higher, both in fundamental and dominant frequency, than the low rumbles, had more energy and a slight rise in pitch in the middle of the vocalization and therefore more modulation. These calls were uttered more in anger, protest or frustration and from this aspect the higher energy input is plausible. Generally the mouth is more open during a growl than during a low rumble, which would result in a more audible vocalization.

Cries and other loud vocalizations were heard more from the younger than the older juveniles and had much higher frequencies and energy, and were relatively short. The high frequencies reached with the squeals shows the great variation possibility that young elephants have with their vocal cords.

CONCLUSIONS

The study indicated that young newly captured elephants which were more stressed in terms of anger, frustration and fright, vocalized more than less stressed elephants. Two translocated groups in bomas also showed higher values for vocalization rates per unit time than the free ranging groups. One of these boma groups was extremely nervous which supports the hypothesis that stressed elephants vocalize more than less stressed ones. Individuals up to about 2 years tended to vocalize more than those above 2 years, possibly they coped less well with the situation, as did an individual which was confined alone, or simply expressed their emotion through vocalizing. Older juveniles might have other means of coping with a stressful situation. Present results suggest that juveniles below 2 years have slightly higher fundamental frequencies for the low rumbles, which could be explained with the fact that their vocal cords are smaller than in adult elephants, however this should be tested with further recordings. A follow-up study should attempt to obtain adequate recordings of low rumbles from very young calves, juveniles and from adults. To be absolutely sure of the origin or caller this study should ideally be done in a captive situation, or on a well habituated group in open veld conditions.

CHAPTER 10

GENERAL DISCUSSION

1. SOCIAL STRUCTURE AND ORGANIZATION

Each species has evolved its particular social structure through phylogenetic adaptations. However, each species' genotype allows for adaptive modifications. Environmental factors will determine the structure of a population (i.e. size, spatial and temporal patterning, and cohesiveness) and will influence the strategies used to fulfil the two basic requirements of nutrition and avoiding harm. Each society is made up of different roles (Bernstein & Sharpe 1966; Bramblett 1973). The intricate social network of individual interactions and the adherence to the rules of these roles will determine how individuals achieve their social organization and social structure The social structure in African elephants appears to be centred around the role of the matriarch (Douglas-Hamilton 1972; Moss & Poole 1983). It has been stated that without this figure the social structure disintegrates (Moss 1988).

Juvenile elephants which have been captured and translocated in groups with unfamiliar conspecifics not only have to adapt to new environmental conditions, but need to reorganize and restructure. The assumption was made at the onset of the study that certain aspects of role play could be innate and others might have to be learned through experience.

The results of the present study show that an adult female (Jane at Venetia) will readily take on the role of matriarch, allomother and even adopted mother, to a group of non-kin juveniles. One could argue that she had no choice as the juveniles followed her step by step from day one and took their cues from her. They immediately all perceived her as matriarch and allomother, so that she even had to use aggression to maintain order in the group. However, Jane herself was prepared to take on the roles as was clearly seen in her reactions towards the adopted juvenile male and also in the way she defended and led the group. One older juvenile female took on the roles of helper and allomother to the adopted juvenile and formed a special relationship with the matriarch. These three individuals started the core of a typical elephant family structure (Moss 1981; Moss & Poole 1983; Lee 1987).

In the other study groups various stages of role play were observed. Only one juvenile female seemed to take on the role of leader and allomother. In the other groups, individuals, females and males, shared the role of leading. Allomothering and helping to defend the group appeared where the first components towards a normal family structure were present: a leader who also allomothered the youngest individual. Where this core was present other roles such as that of 'helper', started to fall into place, as was seen at Venetia and Touchstone. However, non of the other older juvenile females in the large group at Venetia showed allomothering tendencies, although there were many very young juveniles present. From an evolutionary point of view, it would not be adaptive to care for alien young unless these form part of the family. Although the elephants in the various groups tried to form a normal social structure it was only possible to do so, where the core of the structure, namely the mother-infant unit, was present. This core appears to be the strongest pillar of elephant society and to establish this even a non-kin juvenile will be adopted, and a juvenile female may even attempt to establish this core. The role of leader to a group appears to have to be learned. Only one juvenile female achieved this. In the other groups individuals appeared to share the responsibility of leading. In view of the responsibility and the environmental and social knowledge required, it is not surprising that only older individuals are able to fulfil this role more adequately.

The other juveniles individually attempted to build relationships and find a niche within the group which allowed them to pursue their normal behaviour patterns. To this end a dominance hierarchy was formed, or was in the process of being formed, imitating the dominance hierarchy in a normal group, which is dictated by age (Moss 1988). This hierarchy is probably linear, where males and females form separate dominance hierarchies. Males started to split off from the main family core and form loose bonds with one another. Females showed tendencies to remain near the family core (where possible), reflecting temporal patterns seen in a normal family unit.

Spatial patterning was dependant on the activity and to a certain degree on the composition of the group. To optimise their feeding strategies the juveniles dispersed when foraging. This was apparent in all groups. Typically the youngest individual was permitted to feed next to the matriarch or leader. Security measures were taken during resting periods, when vigilance is low, and the juveniles kept in a close-knit bunch. This behaviour was not always seen at Venetia, although some small groups of juveniles congregated during resting periods and the group around the matriarch was tight. This could either be an indication that one adult cannot look after too many individuals, but more likely reflects a more relaxed attitude of these juveniles, either due to the size of the group or the presence of the adult. In the other groups the juveniles kept very close together most of the time, but particularly during resting periods, which might be a form of security and probably induces a feeling of comfort. In a normal family unit this sense of comfort and security would be provided by the mother.

2. STRESS RELATED BEHAVIOURS

Despite the difficulty to define stress in behavioural terms, the assumption made in the introduction, that juveniles that have lost their family and have been placed in an unfamiliar surrounding experience stress, was supported by the results from the present study. Arousal behaviour was defined and a grading system proposed and the assumption made that high frequencies of arousal behaviour could be an indication of stress. Stress response and coping strategies are individual, however, omission of certain behaviour patterns such as play, and increase of other behaviour patterns such as aggression, appear to be good indicators of suboptimal conditions. Because play behaviour is difficult to define and describe, it has largely been neglected in the past. Play does not feature as one of the important behaviours to optimise survival and reproductive strategies. However, play forms an integral part of the socialisation process, which is the basis for a functional group of individuals. During play the social requisites are learned, actions and reactions are tested in various configurations and between various individuals which have the opportunity to reverse their roles. In this manner individuals learn to cope with different situations and learn how to handle problems in the future. It may even induce security, as they are well prepared for unforeseen social events. Therefore play behaviour not only reflects a relaxed individual, but is an important part of the socialisation process.

The secretion of the temporal gland was shown to be an indicator of some form of excitement or arousal, and is not restricted to a negative form of stress. The function of this phenomenon is not yet understood. There was no indication throughout the study that elephants gain information through the secretion of others, but this cannot be excluded. Studies on Asian female elephants, which do not secrete from this gland, or very rarely, showed that they placed their trunk tip on the orifice of the temporal gland of partners (Garaï 1989). Vocalization may be an attempt to give vent to frustration, as was seen after the capture at Skukuza, but also to express fear and loss. The frequent monotonous calling of the small, distressed and sick elephants seem to confirm this. Stress is not easy to define in behavioural terms, however the results of the study indicate that elephants are stressed after the capture operation.

As was shown above translocated elephants will attempt to achieve a social structure according to their phylogenetic adaptation. Loss of a mother or matriarch will not only have immediate effects on the animal, but where this figure, or a substitute thereof, is non existent the structuring of a 'normal' family unit is not possible. This implies that certain behavioural patterns and even certain roles will not be fulfilled. A restriction in behavioural complexity and possibly even deprivation of certain emotional requisites, could lead to long lasting psychological deficiencies, or inadequacies in certain situations, but deprivation to perform certain innate behaviour patterns could also be experienced as frustrating. In this case the individual would turn to other behaviour patterns e.g. aggression and possibly even abnormal behaviour as was shown by a very young individual. This raises the question whether the aggressive behaviour by some bulls in some reserves which are currently observed, are not a result of this deficiency in the socialisation process and resulting frustration.

All animals have mechanisms to try and regain homeostasis, without these they would die of the consequences of stress. It appears that the manner in which this is attained is individual, within the given genetic make up. Behavioural plasticity must be present in a species which can easily adapt to various habitats and which has a relatively long learning period. Individual character and experience, but also the new situation, composition of and relation to the new conspecifics, will lead to different coping strategies, which can be anything from apathy and depression, to nervousness and aggression; or even positive, by attempting to re-establish phylogenetic adaptive structures with role substitutes.

Animals which were below or around 2 years of age seemed the least well equipped to cope with the situation. These individuals displayed distress, depression, abnormal behaviour, and loss of appetite. One can only speculate about the psychological effect on these individuals. It would appear that this is the age limit which should not be translocated without their mothers. Older individuals, from 3 years and above, appear to cope if they are given a substitute and a group which may resemble a family unit and where they are looked after by older individuals. Having said this, however, there are no guarantees that these individuals will develop normal social abilities and not retain psychological scars.

The compositions of the groups and subgroups as well as the splitting behaviour seen and reported from various reserves indicate that juvenile elephants will attempt to achieve a social organisation and grouping formation which is governed by social relationships, roles and ultimately the normal structure of a family group, rather than by nervousness, insecurity or fright.

In conclusion, it appears that elephants should preferably be translocated in family groups. Where this is impossible, they should at least be translocated in a group, which comprises sufficient older females to enable a restructuring that resembles a family unit, where individuals can take on their specific roles and feel some form of security within the group and where all roles are present. It would not be surprising to see problems arise in translocated groups where this was not possible. The most difficult question to answer is, what is the minimum size that this group, or even a family unit should constitute. This will depend on various factors, for instance the origin of the elephants and what the average family unit size is in that population. Social interactions occur regularly between families (Moss 1981, 1988) and these encounters may be important for further social development. It may be important to learn how to react with conspecifics outside of the family unit. Males will need to form a dominance hierarchy outside of the family units and learn to cope with male strategies and typical male behaviour, such as musth (Poole 1987, 1989). It seems in this light, that translocation represents much more than just moving a few individuals, and ideally should comprise a small population. It follows also that translocation of single or even only two or three individuals is totally undesirable and will disrupt the normal socialisation process. Where animals are not permitted to follow their genetically acquired behaviour patterns and roles this could lead to psychological deficiencies and even abnormal behaviour patterns.

3. MANAGEMENT RECOMMENDATIONS

The lessons learned from this study, over and above the usual considerations, are the following:

Elephants preferably should be acquired in family units. This unit should consist of individuals of varying ages and include the matriarch. A few adult bulls should also be translocated with the family unit to ensure breeding. If a delayed breeding activity is desired, then only juvenile bulls should be translocated with the unit. A strong electrified fence surrounding the reserve will be imperative.

Translocated family units must be offloaded into a large electrified paddock (min 2 ha) and left alone. It is important that the electric wires also cover the gates. Care should be taken not to frighten the elephants during and after offloading with noise, people or lights. It is imperative that the elephants are kept calm, as they may otherwise panic and break out of the paddock. This would teach them to break through electric fencing and could have catastrophic results later on. Sufficient browse must be available in the paddock to last for two days. Cut branches can be placed inside prior to the arrival of the elephants. Sufficient water must also be supplied, either in a large concrete trough or, if available, by a small stream or natural dam inside the paddock. Especially after the excitement of the translocation the animals will be thirsty. The paddock should have shady areas, either with large trees or else a shade cloth construction must be erected. The gates can be opened after one or two days and the elephants left to leave the paddock at their own leisure. People must leave the area immediately.

If it is not possible to translocate the entire family, and juveniles are translocated without an adult female, the following should be considered: The social environment is important for a normal social development process, therefore the group should be composed in such a manner that will allow the individuals to reorganize into a seemingly 'normal family group'. The group should preferably consist of an equal number of males and females with at least one, preferably two, older females (7 years and above) who will be able to lead the group and, if necessary, look after a very young individual and be able to assist one another in group defence. In order for the different roles to be constituted a group should not comprise less than six individuals. Elephants below 3 years of age should not be translocated without their mothers or at least another adult female. If large predators are present or will be introduced within a short period, no elephant should be below the age of 7 - 8 years (unless a few adult females are present). One should allow at least two years before introducing large predators, so that the elephants have time to completely calm down, familiarise themselves with the environment and form a close-knit unit.

The juvenile elephants should be kept in an electrified boma (3ha) for several weeks or even months, to allow them to calm down and form bonds within the group. This is important, as familiarity within a group and between individuals will induce a feeling of security. The time in the boma will also allow them to familiarise themselves with the game on the reserve, especially if predators are present. Where the elephants are very young, care must be given to the boma fence, so as to prevent large carnivores such as lion from entering the boma. During the boma stay the juveniles must be looked after intensively. Apart from special feed such as cubes or lucerne, the animals must be given branches daily. This is important not only for the digestion, but also provides a welcome pastime in the otherwise bare and not very stimulating boma environment. Elephants are intelligent and like to manipulate and play with objects. A natural dam would be preferable so that the elephants can play and make mud to throw onto themselves. Fresh drinking water must be supplied in concrete drinking troughs, which have to be cleaned out daily for hygienic reasons. The same applies to the feeding troughs. Release from the boma should take place when the vegetation on the reserve is green. All elephants should be released simultaneously. The elephants should be left to leave the boma at their own devise without being chased out.

If it is desired that the juveniles are calm in the presence of people and vehicles, then it is suggested that they come into regular (daily) contact with people and vehicles at the boma. Talking to the elephants has a calming effect and will enable them to get to know individual persons. Following the release they must continue to have regular contact with vehicles and people in them, or else they will become nervous again. The familiar voices and vehicles will help them calm down quickly. The elephants should never be hand-fed once they have been released. If supplementary feeding is necessary in winter, a mixture of lucerne and grass can be placed somewhere near the elephants and then they must be left alone.

In a few reserves which have had translocated elephants long enough for the juveniles to reach maturity, some problems have been experienced, such as killing of rhinos and even other elephants. One can only hypothesis on the causes of these unusually aggressive behaviour patterns. It appears that the translocated bull elephants come into musth at an earlier age than would be expected in a normal population and this may influence their behaviour, moreso as there usually are no older bulls present. Bulls form a dominance hierarchy within a population and older bulls can surpress musth in younger ones. Musth bulls announce their state (Poole 1987; 1989) and other bulls keep out of their way to avoid lethal confrontations. In a reserve with a dense rhino population the chances of rhinos and elephants meeting is greater and rhinos are easy targets for the elephants to demonstrate their strength. It could also be that the socialisation process was inadequate due to lack of sufficient adult females in the group. Rhino killing and aggressive behaviour by two elephants was observed in a reserve which had only a male and a female, supporting the statement that two elephants is an inadequate number. Only experience and time will tell whether the introduction of older bulls will alleviate the problems. It could well be that it would be more advisable to translocate older bulls together with the family unit.

Finally, a few points should be considered before acquiring elephants. The most important thing to do is a detailed habitat assessment prior to buying elephants. Next, a long-term management plan must be implemented which will allow for a possible habitat change by the elephants. Careful consideration must be given to the fact that the elephants will eventually multiply and that they may overutilise sensitive habitat areas inside the reserve. It is also important to consider the neighbours surrounding the reserve, whether these are rural communities or farmlands, or another reserve with elephants in it. Where rhinos are present it must be considered that problems between these and the elephants could arise in the future.

CHAPTER 11

SUMMARY

The present study evaluated how translocated juvenile elephants would re-organize and restructure socially and whether specific individuals would adopt certain roles (Chapter 3). The following roles were investigated: leadership, maternal care, helpers, juveniles. Only one group included an adult female. She adopted the youngest male and following his death the next youngest individual. In all groups allomothering behaviour was shown. Leadership probably has to be learned but a 5 year old female prematurely took on this role. Special relationships between females were formed from the age of 6 - 7 years. In some groups the roles were divided amongst males and females.

It was determined that a dominance hierarchy can be measured by the direction of aggressive and submissive behaviour (Chapter 4) and that dominance is transitive. Placing the trunk tip into a partner's mouth was seen mainly during play and play-fighting (Chapter 5). The behaviour is not a submissive behaviour but appears to be one of appeasement to prevent escalation of aggressive motivation.

Nearest Neighbour analyses illustrated the changing social positions of some juveniles relative to others (Chapter 6). In the group containing the adult some young males and one female formed a subgroup. Comparison showed this group to be more dispersed than another group where the juveniles were mostly within 'touching' distance (2 m) of each other. In a third group six juveniles remained in two distinct units. It appears that dominance hierarchies, individual social relationships and caretaking of young are important factors which effect group cohesion and a more central position within the group. Tight grouping was assumed to be an indication of insecurity but was dependent on activity (Chapter 7). The individuals of two groups without adults were within touching distance of one another when resting. In the group with the adult female the juveniles dispersed.

The results showed that juveniles are extremely nervous after their capture. Stress related behaviour patterns were defined and compared among the groups (Chapter 8). Arousal behaviour decreased significantly after the arrival of the adult female. Aggression was the most frequently observed behaviour in the boma and during the first period after the release, whereas play behaviour was absent. In all free ranging groups and the groups which were in a large paddock play occurred and tended to increase gradually after the release. Abnormal behaviour was seen in a young male (< 2 years) who "suckled" at the ear pinna of another. Temporal gland secretion (tgs) occurred in all age and sex classes and in a variety of contexts including stress, excitement, anticipation and certain social situations. Data indicated that females secrete more often than males, and older individuals more often than younger ones. Analyses of vocalizations confirmed that stressed animals vocalize more frequently than relaxed ones (Chapter 9) as do calves below 2 years of age who tend to use louder calls. Acoustic analyses of four vocalizations are presented.

OPSOMMING

Die huidige studie het die wyses waarop jong olifante sosiaal herorganiseer en herstruktureer gemonitor en vasgestel of individue spesifieke rolle sou aanneem (Hoofstuuk 3). Die volgende sosiale rolle is ondersoek: leierskap, ouersorg, helpers en jeugdiges. Slegs 'n enkele groep het 'n volwasse koei bevat. Sy het die jongste bulletjie aangeneem en na sy dood die naas jongste bulletjie. In alle groepe is pleegouergedrag waargeneem. Leierskap blyk aangelerde gedrag te wees maar 'n vyfjarige vers het op 'n onvolwasse stadium hierdie rol aanvaar. Spesiale verhoudings is tussen ses tot sewe jaar oud verse gevorm. In sommige groepe is hierdie rolle tussen beide bulletjies en verse vervul.

Daar is vasgestel dat 'n dominansie hierargie by middele van die rigting van aggressiewe en ondergeskikte gedragspatrone vasgestel kan word (Hoofstuk 4) en dat dominansie tydelik is. Die plasing van die punt van die slurp in die mond van 'n ander olifant is hoofsaaklik tydens speel en speel-gevegte waargeneem (Hoofstuk 5). Hierdie gedragtpatroon behels nie 'n ondergeskikte gebaar nie, maar blyk een van toenadering te wees wat dien om die eskalering van aggressiewe motivering te verhoed.

Nabyheids ontleding illustreer die veranderende sosiale posisies van sommige jong olifante (Hoofstuk 6). In die groep wat die volwasse koei bevat het 'n aantal bulletjies en een vers 'n subgroep gevorm. Vergelykende studies demonstreer dat laasgenoemde groep meer ruimtelik versprei was as 'n ander groep waar die kalfies meestal binne raakafstand van mekaar was (< 2m). In 'n derde groep het ses kalfies in twee kenmerkende subgroepe verkeer. Dit blyk dat dominansie hierargieë, individuele sosiale verwandskappe en ouersorg belangrike faktore is wat die hegtheid van groepe sowel as 'n meer sentrale posisie van individue binne groepe moontlik maak. Noue groeperings was aanvaar as 'n indikasie van onsekerheid maar was afhanklik van die heersende aktiwiteit (Hoofstuk 7). Die individue van twee groepe sonder volwassenes het binne raakafstand van mekaar gerus. In die groep met 'n volwasse koei het die kalfies meer verspreid verkeer.

Die resultate dui daarop aan dat kalfies senuweeagtig is na hul vangs. Spanningsverwante gedragspatrone was gedefinïeer en die voorkoms daarvan tussen groep vergelyk (Hoofstuk 8). Na die aankoms van die volwasse koei het die senuweeagtige aard van klein kalfies se gedragspatrone betekenisvol afgeneem. Aggressiewe gedrag was meer dikwels waargeneem in die aanhoudinghokke en gedurende die eerste periode na vrylating, terwyl speelgedrag afwesig was. In alle vrylewende groepe sowel as die groepe wat in groot aanhoudingkampe aangehou is was speelgedrag teenwordig en het geleidelik toegeneem na vrylating. Abnormale gedrag was in 'n jong bulletjie (< 2 jaar) bespeur wat gereeld aan die oor van 'n ander bulletjie gesuig het. Temporaalklier afskeidings was opgemerk in alle ouderdomsklasse, in beide geslagte onder verskeie omstandighede, insluitend spanning, opgewondenheid,

afwagting en in 'n aantal verskillende sosiale omstandighede. Die data dui aan dat koeie meer dikwels as bulle en dat ouer individue meer gereeld as jonger diere temporale afskeidings produceer. Selektiewe klankanalises word aangebied en vertolk (Hoofstuk 9).

REFERENCES:

Abe E.L. 1994. The behavioural ecology of elephant survivors in Queen Elizabeth National Park, Uganda. PhD Thesis. University of Cambridge, Cambridge.

Acocks J.P.H. 1975. Veld types of South Africa: with accompanying veld type map. Pretoria: Botanical Research Institute.

Adams J. & Berg J.K. 1980. Behavior of female African elephants (*Loxodonta africana*) in captivity. *Appl. Anim. Ethol.* 6, 257-276.

Adams J., Garcia A. III, & Foote C.S. 1978. Some chemical constituents of the secretion from the temporal gland of the African elephant (*Loxodonta africana*). *J. Chem. Ecol.* 4 (1), 17-25.

Adams D.C. & Anthony C.D. 1996. Using randomization techniques to analyse behavioural data. *Anim. Behav.* 51, 733-738.

Alados C.L., Escos J.M. & Emlen J.M. 1996. Fractal structure of sequential behaviour patterns: an indicator of stress. *Anim. Behav.* 51, 437-443.

Altmann J. 1974. Observational study of behavior: Sampling methods. *Behaviour* 49, 227-267.

Appelby M.C. 1983. The probability of linearity in hierarchies. *Anim. Behav.* 31, 600-608.

Arzt V. & Birmelin I. 1993. Haben Tiere ein Bewusstsein? C. Bertelsmann Verlag, München.

Berg J.K. 1983. Vocalizations and associated behaviors of the African elephant (*Loxodonta africana*) in captivity. *Z. Tierpsychol.* 63, 63 -79.

Bernstein I.S. & Sharpe L.G. 1966. Social roles in a rhesus monkey group. *Behaviour* 26, 91-104.

Bischof N. 1975. A systems approach toward the functional connections of attachment and fear. *Child Devel.* 46, 801-817.

Bramblett C. A. 1973. Social organization as an expression of role behavior among old world monkeys. *Primates*, 14(1), 101-112.

Buirski P., Plutchik R. & Kellerman H. 1978. Sex differences, dominance, and personality in the chimpanzee. *Anim. Behav.* 26, 123-129.

Burghardt G.M. 1984. On the origins of play. In: Play in animals and humans Ed: P.K. Smith. Basie Blackwell, Oxford. pp 5-42.

Buss I.O., Rasmussen L.E. & Smuts G.L. 1976. The role of stress and individual recognition in the function of the African elephant's temporal gland. *Mammalia* 40 (3), 437-451.

Buss I.O. & Smith N.S. 1966. Observations on reproduction and breeding behavior of the African elephant. *J. Wildl. Manage.* 30(2), 375-388.

Carrington R. 1958. Elephants. A short account of their natural history, evolution and influence on mankind. Chatto & Windus, London.

Cheney D.L.1977. The acquisition of rank and the development of reciprocal alliances among free-ranging immature baboons. *Behav. Ecol. Sociobiol.* 2, 303-318.

Cords M. 1988. Resolution of aggressive conflicts by immature long-tailed macaques *Macaca fascicularis*. *Anim. Behav.* 36, 1124-1135.

De Villiers M.S., Van Jaarsveld A.S., Meltzer D.G.A. & Richardson P.R.K. 1997. Social dynamics and the cortisol response to immobilization stress of the African wild dog, *Lycaon pictus*. *Horm. Behav.* 31, 3-14..

De Vries H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Anim Behav.* 50, 1375-1389.

De Waal F.B.M. 1987. Dynamics of social relationships. In: Primate Societies. Ed: Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham R.W., Struhsaker T.T. Univ. Chicago Press. 421-429.

Drews C. 1993. The concept and definition of dominance in animal behaviour. *Behaviour* 125 (3-4), 283-313.

Douglas-Hamilton I. 1972. On the ecology and behaviour of the African elephant. Ph.D. thesis, University of Oxford.

Douglas-Hamilton, I. & Douglas-Hamilton, O. 1975. Among the Elephants. Viking Press, N.Y.

Dublin H.T. 1983. Cooperation and reproductive competition among female African elephants. In: Social behaviour of female vertebrates. Ed: S. Wasser. Ac. Press N.Y., 291-313.

Eltringham S.K. 1982. Elephants. Blandford Press. Poole, Dorset

Estes J.A. & Buss I.O. 1976. Microanatomical structure and development of the African elephant's temporal gland. *Mammalia* 40(3), 429-436.

Ganslosser U. 1993. Stages in formation of social relationships - An experimental investigation in Kangaroos (Macropodoidea: Mammalia) *Ethology* 94, 221-247.

Garaï M.E. Social organization in translocated juvenile African elephants: The acquisition of roles. *Ethology* in review.

Garaï M.E. 1989. Special relationships between female Asian elephants in captivity. Diplomarbeit, Univ. Zürich.

Garaï M.E. 1992. Special Relationships between female Asian elephants (*Elephas maximus*) in Zoological Gardens. *Ethology* 90,187-205.

Garaï M.E. 1993. Erläuterungen zur Haltung von umgesiedelten juvenilen afrikanischen Elefanten. *Bongo* 22, 117-124. Sonderband, Berlin.

Garaï M.E. 1994. The effects of boma design on stress-related behaviour in juvenile translocated African elephants. *Pachyderm* 18, 58-60.

Garstang M., Larom D., Raspet R. & Lindeque M. 1995. Atmospheric controls on elephant communication. *J. Exp. Biol.* 198, 939-951.

Ginsberg J.R. & Young T.P. 1992. Measuring association between individuals or groups in behavioural studies. *Anim. Behav.* 44, 377-379.

Gittleman J.L. 1985. Functions of communal care in mammals. In: Evolution; Essays in honour of John Maynard-Smith. Ed: P.J. Greenwood, P.H. Harvey, M. Slatkin. Camb. Univ. Press. pp. 187-205.

Gorman M.L. 1986. The secretion of the temporal gland of the African elephant *Loxodonta africana* as an elephant repellent. *J. Trop. Ecol.* 2,187-190.

Gust D.A., Gordon T.P. & Hambright M.K. 1993. Response to removal from and return to a social group in adult male rhesus monkeys. *Physiol. Behav.* 53, 599-602.

Guy P.R. 1976. Diurnal activity patterns of elephant in the Sengwa Area, Rhodesia. *East. Afr. Wildl. J.* 14, 285-295.

Haemisch A. 1990. Coping with social conflict, and short-term changes of plasma cortisol titers in familiar and unfamiliar environments. *Physiol. Behav*. 47, 1265-1270.

Hall-Martin A.J. & Walt L.A. van der. 1984. Plasma testosterone levels in relation to musth in the male African elephant. *Koedoe* 27, 147-149.

Hammerstein P. 1981. The role of asymmetries in animal contests. *Anim. Behav.* 29, 193-205.

Hamilton W.D. 1964. The genetical evolution of social behaviour. I, II. *J. theor. Biol.* 7 (1), 1-52.

Hanks J. 1979. A Struggle for Survival: The Elephant Problem. Country Life Books. London, New York

Heffner R. & Heffner H. 1980. Hearing in the elephant (*Elephas maximus*). *Science*. 208 May, 518-520.

Heffner R., Heffner H., Stichman N. 1982. Role of the elephant pinna in sound localization. *Anim. Behav.* 30(2) 628-629.

Hendrichs H. & Hendrichs U. 1971. Dikdik und Elefanten. Oekologie und Soziologie zweier afrikaischer Huftiere. R. Piper & Co. Verlag, München.

Hinde R.A. 1969. Analyzing the roles of the partners in a behavioral interaction - Mother-infant relations in rhesus macaques. In: Annals of the New York Academy of Sciences 159 Art. 3, 651-667.

Hrdy S. B. 1976. Care and exploitation of nonhuman primate infants by conspecifics other than the mother. In: Advances in the study of behavior. N.Y. Vol 6,101-158.

Hrdy S.B. 1977. The Langurs of Abu. Havard Univ. Press, Cambridge Mass & Lond.

Jarman P.J. 1974 The social organisation of antelope in relation to their ecology. *Behaviour* 48 (3-4), 215-266.

Kawai M. 1958. On the system of social ranks in a natural troop of Japanese monkeys, basic and dependent rank. *Primates* 1, 111-130.

Kerr M.A. 1978. Reproduction of elephant in the Mana Pools National Park, Rhodesia. *Arnoldia* 8 (29), 1-11.

Kühme W. 1962. Ethology of the African elephant (*Loxodonta africana* Blumenbach 1797) in captivity. *Int. Zoo Yearb.* 4, 113-121.

Kummer H. 1975. Rules of dyad and group formation among captive Gelada baboons (*Theropitecus gelada*). Symp. 5th Cong. Int'l. Primat. Soc. (1974), Nagoya, Japan Sci. Press, Tokyo, pp. 129-171.

Kurt F. 1960. Le sommeil des éléphants. *Mammalia* 24, 259-272.

Kurt F. 1986. Das Elefantenbuch: Wie Asien's letzte Riesen leben. Rasch & Röhring Verlag, Berlin.

Lancaster J.B. 1971. Play-mothering: The relation between juvenile females and young infants among free-ranging Vervet monkey (*Cercopithecus aethiops*). *Folia Primat.* 15(3-4), 161-182.

Langbauer W.R. Jr., Payne K.B., Charif R.A. & Thomas E.M. 1989. Responses of captive African elephants to playback of low-frequency calls. *Can. J. Zool.* 67, 2604 - 2607.

Langbauer W.R. Jr, Payne K.P., Charif R.A., Rapaport L. & Osborn F. 1991. African elephants respond to distant playbacks of low-frequency conspecific calls. *J. exp. Biol.* 157, 35-46.

Laws R.M. 1966. Age criteria for the Afrcan elephant (*Loxodonta africana*). *East. Afr. Wildl. J.* 4, 1-37.

Laws R.M. 1969. Aspects of reproduction in the African elephant, *Loxodonta africana. J. Repr. Fert.* Suppl. 6, 193-217.

Laws R.M., Parker I.S.C. & Johnstone R.C.B. 1975. Elephants and their habitats: The ecology of elephants in North Bunyoro, Uganda. Clarendon Press, Oxford.

Lee P.C. 1986. Early social development among African elephant calves. National Geographic Research Vol. 2. 388-401.

Lee P.C. 1987. Allomothering among African elephants. *Anim. Behav.* 35, 278-291.

Lee P. C. & Moss C. J. 1986. Early maternal investment in male and female African elephant calves. *Behav. Ecol. Sociobiol.* 18(5), 353-361.

Leuthold W. 1977. Spatial organization and strategy of habitat utilization of elephants in Tsavo National Park, Kenya. *Z. Säugetierkd.* 42 (6), 358-379.

Louw G. 1993. Physiological Animal Ecology. Longman, Harlow. U.K.

Marriner L. M. & Drickamer L.C. 1994. Factors influencing stereotyped behavior of primates in a zoo. *Zoo Biol.* 13, 267-275.

Marten K. & Marler P. 1977. Sound transmission and its significance for animal vocalization *Behav. Ecol. Sociobiol.* 2, 271-290.

Mason W. A. 1979. Development of social interaction. (Chapter 7) In: Human Ethology. Ed: M. von Cranach K. Coppa W. Lepenies & D. Ploog. Camb. Univ. Press.

Mason G. J. 1991. Stereotypies: a critical review. *Anim. Behav.* 41, 1015-1037.

Masson J. M. & McCarthy S. 1994. When Elephants Weep: The emotional lives of animals. Jonathan Cape, London.

Maynard Smith J. & Parker G.A. 1976. The logic of asymmetric contests. *Anim. Behav.* 24, 159-175.

McFarland D. 1987. (Editor) The Oxford Companion to Animal Behaviour. Oxford Univ. press. Oxford, New York.

McKay G.M. 1973. Behavior and ecology of the Asiatic elephant in southeastern Ceylon. Smithsonian Contributions to Zoology 125, pp 67-69.

McKnight B.L. 1995. Behavioural ecology of 'hand-reared'African elephants (*Loxodonta africana* (Blumenbach)) in Tsavo East National Park, Kenya. *Afr. J. Ecol.* 33, 242-256.

Millar S. 1987. In: The Oxford Companion to Animal Behaviour. Ed: D. McFarland. Oxford Univ. Press, Oxford, N.Y. pp. 457-460.

Mitchell C.L. 1994. Migration alliances and coalitions among adult male South American squirrel monkeys (*Saimiri sciureus*). *Behaviour* 130 (3-4), 169-190.

Moore V. 1996. Life at the top: Animals pay the high price of dominance. *Science* 271 (292), 830-831.

Morgan B.J.T., Simpson M.J.A., Hanby J.P. & Hall-Craggs J. 1976. Visualising Interaction and sequential data in animal behaviour: Theory and application of cluster-analysis methods. *Behaviour* 56(1-2), 1-43.

Morrison J.A. & Menzel E.W. Jr. 1972. Adaptation of a free-ranging Rhesus monkey group to division and transplantation. Wildlife monographs No 31. Publication of the Wildlife Society.

Moss C.J. 1976. Portraits in the Wild: Behavior Studies of East African Mammals. Boston. Houghton Miffllin.

Moss C.J. 1981. Social Circles. *Wildlife News* 16(1) 2-7.

Moss C.J. 1988. Elephant Memories: Thirteen years in the life of an African elephant, Elm Tree Books, N.Y.

Moss C.J. 1994. Some reproductive parameters in a population of African elephants, *Loxodonta africana.* Proceedings of the Second Int. NCRR Conference on 'Advances in Reproductive Research in Man and Animals', Nairobi, May 1992. The Institute of Primate Research, National Museums of Kenya, 284-292.

Moss C.J. & Poole J.H. 1983. Relationships and social structure of African elephants. In: Primate Social Relationships: An integrated approach. Ed: R.A. Hinde, Blackwell Scientific Publ. pp. 315-325.

Nair P.V. 1989. Development of nonsocial behaviour in the Asiatic elephant. *Ethology* 82, 46-60.

Nicholson N.A. 1987. Infants, mother, and other females (Chapter 27). In: Primate Societies Ed: B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, T.T. Struhsaker. Univ. Chicago press.

Payne K. B., Langbauer W.R. Jr. & Thomas E.M. 1986. Infrasonic calls of the Asian elephant (*Elephas maximus*). *Behav. Ecol. Sociobiol.* 18 (4), 297 - 301.

Poole J. H. 1987. Rutting behaviour in African elephants: The phenomenon of musth. *Behaviour* 102 (3-4), 283-316.

Poole J.H. 1989. Announcing intent: the aggressive state of musth in African elephants. *Anim. Behav.* 37(1), 140-152.

Poole J. H. 1996 Coming of Age with Elephants. Hodder & Stoughton, London.

Poole J.H., Payne K., Langbauer W.R. Jr. and Moss C.J. 1988. The social contexts of some very low frequency calls of African elephants. *Behav. Ecol. Sociobiol.* 22,385-392.

Poole J.H. & Moss C.J. 1981. Musth in the African elephant *Loxodonta africana*. *Nature* 292 (5826) 830-831.

Rapaport L. & Haight, J. 1987. Some observations regarding allomaternal caretaking among captive Asian elephants (*Elephas maximus*). *J. Mammalogy.* 68(2), 438-442.

Riedman M.L. 1982. The evolution of alloparental care and adoption in mammals and birds. *Q. Rev. Biol.* 57(4), 405-435.

Sachser N. & Lick C. 1991. Social experience, behavior, and stress in Guinea pigs. *Physiol. Behav.* 50, 83-90.

Sapolsky R.M. 1990 Stress in the wild. *Sci. Am.* 106-113.

Sapolsky R.M. & Ray J.C. 1989. Styles of dominance and their endocrine correlates among wild olive baboons (*Papio anubis*). *Am. J. Primatol.* 18, 1-13.

Short R.V., Mann T. & Hay M.F. 1967. Male reproductive organs of the African elephant. *Loxodonta africana. J. Repr. Fert.* 13, 517-536.

Siegel S. 1987. Nichtparametrische Statistische Methoden. Methoden in der Psychologie Band 4. Fachbuchhandlung für Psychologie, Verlagsabteilung.

Sikes S.K. 1971. The Natural History of the African Elephant. London, Weidenfeld and Nicholson.

Sokal R.R. & Rohlf F.J. 1981. Biometry. W. H. Freeman and Company New York.

Tennessen T. 1989. Coping with confinement - Features of the environment that influence animals' ability to adapt. *Appl. Anim. Behav. Sci.* 22, 139-149.

Thompson K.V. 1993. Aggressive behavior and dominance hierarchies in female Sable antelope, *Hippotragus niger:* Implications for captive management. *Zoo Biol.* 12, 189-202.

Tobler I. 1992. Behavioural sleep in the Asian elephant in captivity. *Sleep* 15(1), 1-12

Trivers R.L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46(4), 35-57.

Van Schaik C.P. & Van Hooff J.A.R.A.M. 1983. On the ultimate causes of primate social systems. *Behaviour* 85(1-2), 91-117.

Walters J.R. & Seyfarth R.M. 1987 Conflict and Cooperation (Ch 24) In: Primate Societies. Ed: Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham W., Struhsaker T.T. 306-317.

Waser P.M. & Waser M.S. 1977. Experimental studies of primate vocalization: Specializations for long-distance propagation. *Z. Tierpsychol.* 43, 239-263.

Western D. & Lindsay W.K. 1984. Seasonal herd dynamics of a savanna elephant population. *Afr. J. Ecol.* 22, 229-244.

Whyte I.J. 1996. Population dynamics of the African elephant. Proceedings of a workshop on the management of the African elephant held by EMOA at Warmbaths, Nov 1995. 53-67.

Wiley R.H. & Richards D.G. 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3, 69-94

Williamson B.R. 1976 Reproduction in female African elephant in the Wankie National Park, Rhodesia. *S. Afr. J. Wildl. Res.* 6(2), 89-93.

Wilson E.O. 1975. Sociobiology: the new synthesis. Camb. Mass.: Belknap/ Harvard Univ. Press.

Wright P.G. 1984. Why do elephants flap their ears? *S. Afr. J. Zool.* 19(4), 266-269

Wright P.G. & Luck C.P. 1984. Do elephants need to sweat? *S. Afr. J. Zool.* 19(4), 270-174.

Wyatt J.R. & Eltringham S.K. 1974. The daily activity of the elephant in the Rwenzori National Park, Uganda. *East. Afr. Wildl. J.* 12, 273-289.

APPENDIX 1

ETHOGRAM OF BEHAVIOURAL ELEMENTS

used in this study and as grouped for the analyses

AFFILIATIVE

Element	Abb	Description
head on	hd on	lying down and placing the head on a recumbent partner
lean against	lnV	leaning against a partner
leg contact	lgc	touching a partner with the leg
foot on	ft on	placing a foot on a recumbent partner
push guide	pu^gu	directing a young juvenile with the trunk
rub against	rbV	rubbing any part of the body against a partner
smell genitals	smg	smelling a partner's genitals, holding the trunk tip in the direction and near the genitals of a partner
smell urin/faeces	sm ur/fe	extending the trunk tip towards urin or faeces
touch head	tc hd	touching a partner with the trunk tip
touch body	tc bd	touching any part of the head, trunk or body, i.e. face (tc fa), ear (tc e), eye (tc y), body (tc bd), leg (tc lg) etc.
trunk curved	tcv	holding the trunk tip in the direction of a partner
trunk genital contact	tgc	touching another on the genitals with the trunk tip
trunk lip contact	tli	touching another on the lip with the trunk tip
trunk over	tro	placing the trunk over the back of a young juvenile or a recumbent partner
trunk up	tu	holding the trunk curved upwards as a partner approaches, or when approaching a partner

DOMINANT

Element	Abb	Description
trunk over back	tob	placing the trunk on a partner's back
tusks over back	ts ob	placing the tusks on a partner's back
push away	puay	physically displacing a partner
push drive	pudr	placing the trunk along the spine of a partner, both animals in locomotion

Ethogram continued

AGGRESSIVE

Element	**Abb**	**Description**
chase	cha	chasing a partner, both individuals moving fast
kick	kk	kicking a partner with a foot
mock charge	moch	aggressive fast approach towards a partner
push	pu	pushing a partner with any part of the trunk or body
push hard	pu^{h}	pushing a partner with force and displacing him
trunk flick	tflic	flicking the trunk towards a partner
trunk whip	twip	hitting a partner with the trunk
threat	thr	lowering the head towards a partner or lifting the head so that the tusks face a partner horizontally
head shake	hdsh	vigorous shaking of the head towards a partner, sometimes with flapping the ear pinna against the body

INVESTIGATE

investigate food	if	touching or smelling at the food item of a partner
mouth inspect	mi	placing the trunk tip into a feeding partner's mouth
trunk lip feeding	tli^{fe}	touching the lip of a feeding partner
trunk up feeding	tu^{fe}	extending the trunk tip towards the mouth of a feeding partner
investigate	inv	approaching a partner and looking at or smelling what he is doing e.g. digging (inv^{dg}), pulling down (inv^{pubr}) or breaking branches (inv^{brbr}), pushing trees (inv^{puttr}) manipulating objects (inv^{mnob}) etc.

SUBMISSIVE

give way	giay	moving out of an approaching individual's way or being displaced from a spot without contact
presenting	pr	standing in front of a partner with the posterior or walking backwards towards a partner

Ethogram continued

OTHER

Element	Abb	Description
attempted suckling	at su	juvenile tries to suckle
approach	app	nearing a partner
*head contact	hdc	placing the forehead against a partner
*hold leg	ho lg	holding a partner by the leg with the trunk
*hold trunk	ho tr	holding a partner's trunk with the trunk
push gentle	pu[g]	placing the head or trunk against a partner and inducing him gently to move
suckling	su	juvenile suckling
**turn away	tnay	turning away from an approaching partner
*trunk contact	trc	placing the anterior part of the trunk against a partner without pushing
trunk mouth contact	tmc	placing the trunk tip into a partner's mouth

* these elements can be either affiliative or aggressive or be part of play
** this can be submissive or to end a play fight, but usually occurs when an individual is feeding and protects its food from an approaching partner

PLAY and PLAY FIGHT

trunk over head	toh	placing the trunk on a partner's head
chin over back	cob	placing the lower jaw on a partner's back
trunks entwined	tent	two individuals facing each other, both trunks held up and around each other
climb on	cb on	climbing on top of a recumbent partner
*mount	mt	placing the forelegs on a partner's back
play push	plpu	gentle sparring or pushing each other
sit on	si on	sitting on a recumbent partner
push trunks	putrs	pushing each other with the trunk
push heads	puhds	pushing each other with the forehead
trunk base contact	tbc	the proximal anterior part of the trunks of two individuals touching
trunk base protruding	tbp	curving the trunk inwards towards the body so that the proximal part forms a bulge in the direction of a partner

other elements could occur during a play sequence
* this is an element of sexual behaviour, but in juveniles is part of play behaviour.

Ethogram continued

VOCALIZATIONS

Element	**Abb**	**Description**
trumpeting	tm	loud trumpet like air blast through the trunk
snort	sn	exhaling air rapidly though the trunk
rumble	lr	low soft rumbling monotonous sound
growl	gr	low guttural rolling sound
scream	sc	high pitched very loud sound longer than cry
bellow	bel	low pitched very loud sound
cry	cr	short high pitched loud sound

APPENDIX 2

VOCALISATION TYPE IN RELATION TO BEHAVIOUR

Situation	rumble	growl	trumpet	cry, scream
<u>Spektakel</u>				
feeding	+			
touch lip of partner (tli)	+			
food is touched by partner				+
smell people	+			
individual lost			+	+
near observer	+			
nervous		+		
chase bird			+	
play in water			+	
inititate	+			
food arriving	+			
rough play	+			
mock charge observer	+			
resting	+			
being pushed				+
wake up	+			
aggresson	+			
<u>Thornybush</u>				
investigating empty food bag		+		
touch lip of another (tli)	+			
initiate move	+			
feeding	+			
young being pushed				+
individual being chased		+		
cross road	+			
calling males in other reserve	+			
near observer		+		
nervous		+		
walking	+			
young disturbed during sleep	+			
inspect food of young		+		
excitement at fence (males)	+	+		
individual approaches group	+			
two individuals approach e.o.	+			

APPENDIX 2 continued

Situation	rumble	growl	trumpet	cry, scream
leading walking	+			
observer arrives	+			
investigate people	+			
waiting for food	+			
<u>Touchstone</u>				
(series) before resting	+			
investigate observer	+			
nervous of observer	+			
two ind. approach each other	+			
alert	+			
being pushed		+		
run(fright)		+		
(series) all approach leader	+			
inititate move	+			
run		+	+	
aggression				+
walking	+			
feeding	+			
<u>Venetia</u>				
run	+		+	+
pushing in group		+		
individual being pushed		+		
leader initiates	+			
(series) before resting	+			
cluster formation		+		
2 individuals alone	+			
Jane while Sq suckles	+			
Jane initiates suckling	+			
juvenile suckling		+		
lip being touched during suckling		+		
Sq prevented from suckling		+		+
two females approach e.o.	+			
series before leading	+			
observer near / arrives	+			
Jane looks for and runs to Sq	+			
third individual near young suckling	+			

APPENDIX 3

EXTRACT FROM A DATA SHEET OF THE 5 MIN SCANS

Venetia					Date 10. 4. 1993									
Time	Fo	NN	DN	DJ	sbgr	J gr	Ø	Act	food	pt	Habitat	gr	ht	vis
8.45	J	Sq	1	-			2	fe wa	mop	lv	mop shrub	bare	1	70
8.50	E	R	2	3			3	fe wa	mop	lv	mop shrub	bare	1	70
8.55	J	K	1	-			2	fe wa	mop	lv	mop shrub	bare	1	70
9.00	Lt	E	1	2			2	fe wa	mop	lv	mop shrub	bare	1	70
9.05	B	Sq	1	2			2	fe wa	mop	lv	mop shrub	bare	1	70
9.10	Sq	J	1	-		10e 1	3	fe	mop	lv	mop woodl	bare	6	20
9.15	J	St	1	-		10e 1	3	fe	ac	lv	mop woodl	bare	6	20
9.20	E	B	2	2		10e 1	3	fe	ac	lv	mop woodl	bare	6	20
9.25	B	Sq	1	1		10e 1	3	fe	ac	lv	mop woodl	bare	6	20
9.30	Sq	J	1	-		10e 1	2	re			mop woodl	bare	6	20
9.35	St	J	1	-		10e 1	3	re			mop woodl	bare	6	20
9.40	A	Sq	1	2		10e 1	3	re			mop woodl	bare	6	20
9.45	J	Sq	1	-		10e 1	3	re			mop woodl	bare	6	20
9.50	Bb	Sa	1	2		10e 1	3	re			mop woodl	bare	6	20
9.55	A	J	1	-		10e 1	3	re			mop woodl	bare	6	20
10.00	Bb	Tb	1	2		10e 1	3	re			mop woodl	bare	6	20
10.05	G	Lt	1	2		10e 1	3	fe	gr		mop woodl	bare	6	20
10.10	Tb	Ba	1	1		10e 1	3	fe	gr		open gr ac river	gr	8	60
10.15	Ro	Lt	2	1		10e 1	3	fe	gr		open gr ac river	gr	8	60
10.20	Ll	F	2	3		10e 1	3	fe	gr		open gr ac river	gr	8	60
10.25	F	-	-	4		10e 1	3	fe	gr		open gr ac river	gr	8	60
10.30	Ro	Lt	1	3		10e 1	3	fe	gr		open gr ac river	gr	8	60
10.35	Tb	-	-	3		10e 1	3	fe	gr		open gr ac river	gr	8	60
10.40	Lt	S	1	2		10e 1	3	fe	gr		open gr ac river	gr	8	60
10.45	F	Ll	1	3			3	fe wa	gr		open gr ac river	gr	8	60
10.50	R	Ll	1	3			4	fe	ac		open gr ac river	gr	8	60
10.55	D	Tb	1	2			3	fe	gr		open gr ac river	gr	8	60
11.00	R	E	1	3	12e 1		3	fe	tree	lv	open gr ac river	gr	8	60
11.05	Sa	Lt	1	3	12e 1		3	fe wa	gr		ac woodl	gr	0	100
11.10	F	R	1	3			3	fe	gr		ac woodl	gr	0	100
11.15	Lt	F	1	2			3	fe	gr		ac woodl	gr	0	100
11.20	Sq	J	1	-			3	fe	gr		ac woodl	gr	0	100
11.25	D	Lt	1	2			3	re	gr		ac woodl	gr	0	100
11.30	T	M	1	2			3	fe	gr		mop woodl	gr	12	40
11.35	F	-	-	2			3	fe	tree		mop woodl	gr	12	40
11.40	M	Ll	1	3			4	fe	gr		mop woodl	gr	12	40
11.45	Ba	A	2	2			4	fe	tree	lv	mop woodl	gr	12	40
11.50	Bb	Ll	1	2			4	fe	mop	lv	riverine mop woo	gr	12	30
11.55	Ll	R	1	4			4	fe	mop	lv	riverine mop woo	gr	12	30
12.00	J	Bb	1	-			4	fe	mop	lv	riverine mop woo	gr	12	30
12.05	Sa	A	1	2			4	re			riverine mop woo	gr	12	30
12.10	Sq	J	1	-			4	re			riverine mop woo	gr	12	30
12.15	T	A	1	2			4	re			riverine mop woo	gr	12	30
12.20	D	St	1	2			4	re			riverine mop woo	gr	12	30