

To Grant, Adan and Andrea Cresswell  
and in memory of my father Dr. A. Baldellou

**IMPLICATIONS OF THE MULTI-MALE TROOP STRUCTURE IN VERVET  
MONKEYS** (*Cercopithecus aethiops pygerythrus*)

by

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## **P R E F A C E**

The observational work described in this thesis was carried out on a caged troop located in the Grounds Department of the University of Natal, Durban, from September 1985 to November 1986. In addition, a free-ranging undisturbed troop was studied from June 1987 to June 1988 at Windy Ridge Game Park, Heatonville. At that time the author was a student of the Department of Biological Science and Prof. W. Meester and Dr. S.P. Henzi had been nominated to supervise my work.

The analytical and logistic part of this work was carried out in the Department of Psychology of the above mentioned University with Prof. S.P. Henzi as supervisor.

These studies represent original work by the author and have not been submitted in any form to another University. Where use was made of the work of others it has been duly acknowledged in the text.

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## ABSTRACT

The aim of this study is to assess the advantages and disadvantages to all the troop members, of vervet males remaining in heterosexual groups outside the mating season. Extensive data on time budgeting and social interactions have been obtained for both a caged and a free-ranging undisturbed troop.

Some of the potential advantages males provide to other members of the troop are: improvement in predator detection, maintenance of the troop unity and interference in agonistic interactions involving females and immatures.

Special emphasis is placed on the analysis of seasonal changes in agonistic, social, sexual and proximity relationships of male-male and male-female pairs. The influence of male and female dominance rank and the vervet male genital signalling system are discussed.

Also a framework to achieve a better understanding of vervet monkey sexuality is provided. A detailed analysis of male inspection of female's genitalia (visual, tactile, olfactory and muzzling), female receptivity, attractivity and proceptive behaviour has been done in order to investigate male and female mate choice. These behaviours are expected to be related to time of conception, although it was found that male and female rank, mate choice and possibly the age of the mates influence their outcome. In addition, sexual consortships and other alternative male strategies (besides agonistic rank) to control access to receptive females are described for the first time in vervet monkeys.

The multi-male structure of vervet societies has been questioned by other authors, mostly because of the absence of male-male agonistic coalition against other males, and the absence of sexual consortships and other special friendly bonds between males and females. However, the results of this study do show that all the above patterns may also occur among vervet monkeys, therefore the multi-male structure of vervet monkeys is similar to the one found in baboon and macaque societies.

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## 1. THE VERVET MONKEY

The vervet monkey is an African cercopithecine which lives in multi-male multi-female groups. Females remain in their natal troops (female-bonded groups) while males migrate on reaching adulthood and continue to do so on average once every 3-4 years. The consequence of this is that non-related adult males coexist with females who are closely related to one another.

The objectives of this chapter are: first, to describe the relevant features of vervets, *i.e.* their taxonomy, distribution, ecology and social structure; second, to introduce the theoretical problems the multi-male nature of vervet society presents; third, to review the vervet male genital signalling system which appears to be the main mechanism regulating male coexistence; fourth, to review the implications of the absence of female sexual skin in vervet monkeys; fifth, to summarise the findings on male dominance and sexual behaviour in multi-male societies and finally, to detail the aims of this study.

### 1.1. TAXONOMIC AND DESCRIPTIVE NOTES

The Family **Cercopithecidae** consists of two subfamilies. First, the **Cercopithecinae** which includes the guenons (*Cercopithecus*, *Allenopithecus*, *Miopithecus*, and *Erythrocebus*), macaques (*Macaca*), mangabeys (*Cercocebus*) and baboons (*Papio*, *Mandrillus* and *Theropithecus*). Second, the **Colobinae** or leaf-eating monkeys, with its African (*Colobus*) and Asian (*Presbytis*) representatives (Fleagle, 1988). A distinguishing feature of this family is that the partition dividing the nostrils is narrow and the opening of the nostrils themselves are directed downwards and outwards (Forbes, 1896).

The subfamily **Cercopithecinae** is distinguished from the **Colobinae** by: i) the possession of 'cheek-pouches' which are sacs formed by distendable folds of skin in the cheeks, that serve as storing places (Forbes, 1896) and ii) the absence of a fermentative stomach which is an adaptation to process large quantities of leaves (Richard, 1985 p. 195-196).

The Genus *Cercopithecus* includes a larger number of species than any other Anthropoid genus (Tappen, 1960).

"Their tail is longer than the combined head and body length. Their face is short, the muzzle less elongated, the 'cheek pouches' larger than in the macaques. The nose is not prominent, and the nostrils are approximated, while whiskers are generally developed as well as a longer or shorter beard... their callosities are more developed than in the macaques " (Forbes, 1897).

In some respects, *C. aethiops* seems to be intermediate in adaptation and structure between the terrestrial patas monkey (*Erythrocebus patas*) and the forest dwelling guenons (Gartlan & Brain, 1968; Tappen, 1960). Kingdon (1988a) suggests that the hand and foot of *C. aethiops* have secondarily acquired some of the specialised terrestrial traits of the patas monkey.

### **1.1.1. Classification**

O. PRIMATES

S.O. ANTHROPOIDEA Mivart, 1864

Family **Cercopithecidae** Gray, 1821

Subfamily **Cercopithecinae** Gray, 1981

Genus *Cercopithecus* Linnaeus, 1758

Group species *Cercopithecus aethiops* Linnaeus, 1758

Subspecies *Cercopithecus aethiops pygerythrus* Schwarz, 1926

Hill (1966) and Napier (1981; Napier & Napier, 1985) recognise four genera of guenons: *Cercopithecus*, *Miopithecus*, *Allenopithecus* and *Erythrocebus*. But if one considers: first, their anatomical homogeneity (Kingdon, 1971; Tappen, 1960); second, their potential for interbreeding and their karyological phylogeny; and finally, the fact that the three last genera are closer to the ancestral guenons than the 'true' *Cercopithecus*, it is reasonable to retain only a single genus (review in Lernould, 1988).

At the beginning of this century it was customary to recognise five species of green-backed guenons, the grivet (*C. aethiops*), tantalus monkey (*C. tantalus*), the vervet (*C. pygerythrus*), the malbrouck (*C. cynosorus*) and the common West African green monkey or callitrix (*C. sabaes* or *C. callitrichus*). The group was revised by Schwarz who reduced all green backed guenons to the status of geographical races of a single polytypic species (*C. aethiops*) (cited in Hill, 1966; see also Thorington & Groves, 1970 p.636; Lernould, 1988).

Although the Napiers first opposed Schwarz's classification (Napier & Napier, 1967 p.372) they later reconsidered their position and regrouped all green monkeys into a single species with four subspecies (Napier, 1981; Napier & Napier, 1985). This classification is used in the present study.

### **1.1.2. Description**

The diagnostic characteristics of vervet monkeys are: "black hands and feet, scrotum turquoise blue, red subcaudal patch and black tip of tail, white and broad brow band confluent with the short white whiskers which blend with the crown" (Napier, 1981). The red penis contrasts with the blue scrotum and the white hairs surrounding the red perianus (Fedigan & Fedigan, 1988, p. 395). The ischial callosities are small and well separated and cheek-pouches are present (Forbes, 1897; Kingdon, 1971).

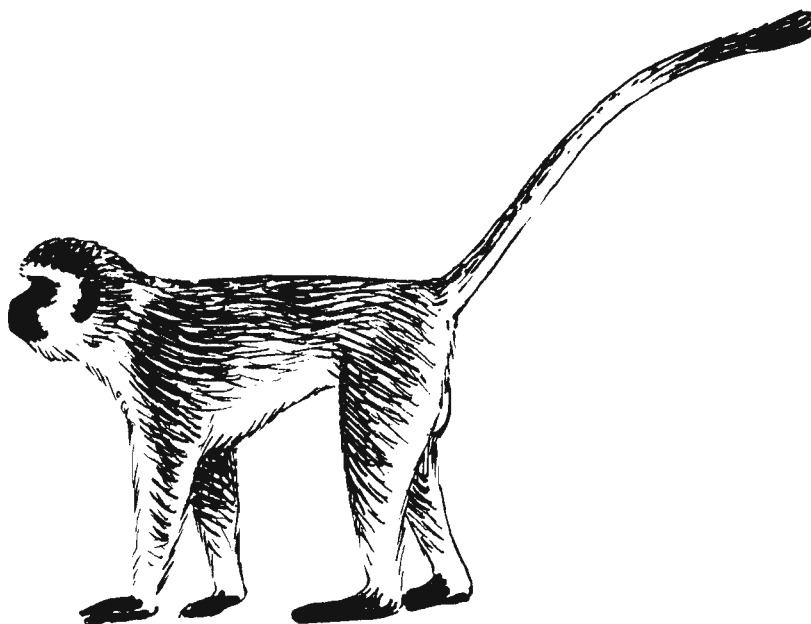


Figure 1.1. The vervet monkey.

The vervet monkey is a medium sized guenon with a slight sexual dimorphism (Napier & Napier, 1985). Male vervets (4.5 kg with a range between 3.7-5.2) are slightly bigger than females (3.4 kg. with a range between 3.0-3.7) (Bramblett & Coelho, 1987, p.76) and their canines are marginally larger (Fedigan & Fedigan, 1988).

### **1.1.3. Habitat**

Members of the genus *Cercopithecus* are mainly arboreal, spending most of its time moving through the forest canopy and occasionally descending to the ground. *C. aethiops* is semi-terrestrial and can spend hours foraging on the ground near bush cover.

Guenons are rare or absent where arid conditions prevail and from closed forest (Tappen, 1960; Gartlan, 1969; Kavanagh, 1980). The range of vegetation types inhabited by *C. aethiops*, apart from riverine gallery forest which is their preferred habitat (Gartlan & Brain, 1968), includes all types of savanna, woodland and lake-shore forests (Kingdon, 1971).

The adaptation of *C. aethiops* to such varied environments is mainly due to its lack of anatomical specialisations, slight sexual dimorphism and most important of all, its flexible social structure (Gartlan & Brain, 1968) and diet (Fedigan & Fedigan, 1988). Vervet monkeys are largely vegetarian and their diet is composed essentially of fruits, tender shoots, leaves, bark, flowers, seeds and gum from *Acacia* trees, supplemented with insects, spiders, birds' eggs and nestlings (Struhsaker, 1967a). They have been very successful in exploiting urban environments and are known to raid crops and cultivated trees.

#### **1.1.4. Distribution**

The guenons are indigenous to the African continent and the different species are confined to specific areas (Forbes, 1897). *C. aethiops* is the most widely distributed guenon and probably the most numerous (Tappen, 1960). Its representatives are found in savanna regions throughout Africa, from the highlands of Ethiopia and the semiarid regions of the Sudan to southern South Africa and from Senegal to Somalia (Gartlan & Brain, 1968; Hall & Gartlan, 1965). Next to baboons, vervets are the most abundant and widespread of the African monkeys (Struhsaker, 1967b; Fedigan & Fedigan, 1988).

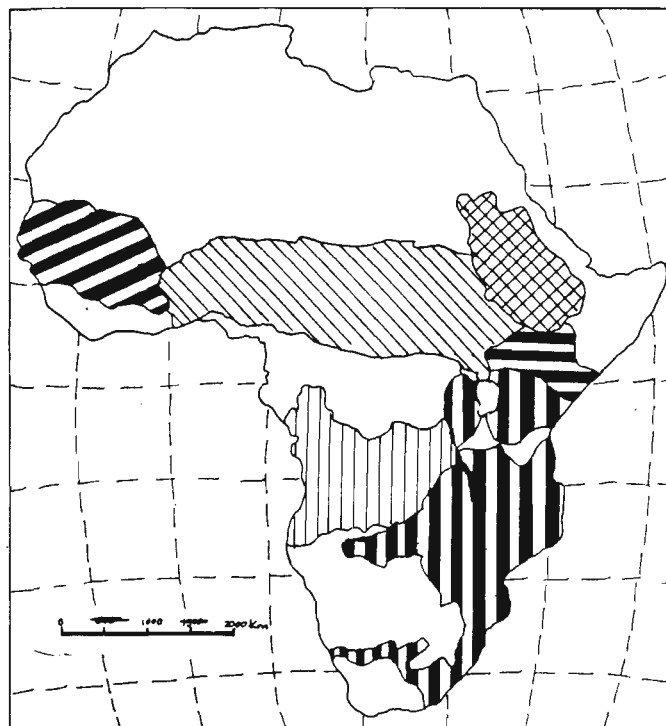
The southern savanna form, *C.a.pygerythrus*, extends from Ethiopia (Napier, 1981) to the Cape Province in South Africa and has at least two distinct but closely related peripheral populations. Those are *C.a.cynosurus* in Angola and *C.a. arenarius* in arid northeast Africa. The northern savanna type has an easterly population *C.a. aethiops* in Ethiopia, a more westerly population *C.a.tantalus*, and the West African type is *C.a.sabaeus* (Kingdon, 1971, p.213) (Fig. 1.2).

In South Africa, vervet monkeys occur as far south as the coastal areas of the Eastern Cape Province (Hall & Gartlan, 1965). They do not occur in the dry sand-plains and Karoo regions of central and western South Africa, except along the tree-fringed valleys of the Orange and Vaal rivers (Shortridge, quoted in Hill, 1966). Their most southern range ends in the surrounding areas of George and Knysna in the Cape



Province (A. Fourie of the National Parks Board, personal communication), although early reports showed an apparently extended distribution south (quoted in Forbes, 1897):

"The vervet is common in the forests along the Great Fish river, and other streams between Algoa Bay and Cape Town. Its range extends also along the Natal Coast, throughout the Amakozi country and Caffreland generally".









<i>C.a.sabaeus</i>	
<i>C.a.tantalus</i>	
<i>C.a.aethiops</i>	
<i>C.a.arenarius</i>	
<i>C.a.cynosurus</i>	
<i>C.a.pygerythrus</i>	

Figure. 1.2. The distribution of *Cercopithecus aethiops* (modified from Kingdon, 1971, p.213 and Lernoold, 1988).

### **1.1.5. Reproductive biology**

The vervet monkey is a seasonal breeder in the wild (Struhsaker, 1967a; Gartlan & Brain, 1968; Henzi & Lucas, 1980; review in Butynski, 1988) with a well defined mating season which, in Natal commences in March and lasts into June. Other multi-male species that breed seasonally are the rhesus monkey (Kaufmann, 1967), Japanese monkey (Takahata, 1980), macaques and talapoins (see review in Melnick & Pearl, 1987, p.126-128). In contrast, the olive baboon (Ransom & Rowell, 1971), chacma baboon (Hall & DeVore, 1965) and gelada baboon (Mori, 1979) do not show any clear peaks in reproduction.

Seasonality in breeding corresponds to seasonal changes in plasma levels of sexual hormones in both males and females (*e.g.* Loy *et al.* 1978). The duration of the birth season is more affected by the distribution of than by the total rainfall and mating occurs in the middle of the dry season (Butynski, 1988, p. 307; 311).

Female vervets are characterised by sexual cycles of approximately 1 month in length (Bramblett *et al.*, 1975). The mean gestation period is  $163 \pm 2$  days (Johnson *et al.* 1973; Bramblett *et al.*, 1975) and the age at first birth varies from 3 to 5 years according to environmental conditions (Fairbanks & McGuire, 1984). Females can potentially produce an offspring every year (Gartlan, 1969; Bramblett *et al.* 1975), but in dry areas females start reproducing later and give birth every two years (Cheney & Seyfarth, 1990). Young captive vervet females show longer interbirth intervals than older females (Rowell & Richards, 1979).

Although males are behaviourally adult at 4 years (Bramblett, 1978), they produce sperm at 3 years and do not attain full adult size until the age 6 plus (Fedigan & Fedigan, 1988, p. 405).

Many previous studies on Old World monkeys which documented a positive relation between female rank and reproductive success have been conducted on captive or provisioned populations (Japanese macaques: Fedigan *et al.* 1986; bonnet macaques: Silk, *et al.* 1981; rhesus monkeys: Drickamer, 1974; Sade *et al.* 1977; Wilson *et al.* 1978; vervet monkeys: Fairbanks & McGuire, 1984) or in areas where predators were rare (Dittus, 1979).

However, as a result of the non-random distribution of causes of death amongst female vervet monkeys in a declining, non-provisioned and heavily predated population (Amboseli National Park, Kenya), there was no correlation between dominance rank and reproductive success (Cheney *et al.*, 1981; see Altmann, 1980 for baboons and Meikle & Vessey, 1988 for rhesus). Deaths due to predation were concentrated among high ranking females and deaths due to illness among low ranking females (Cheney *et al.* 1981).

Mortality due to illness is more common among low ranking monkeys due to harassment (Dittus, 1977), competition for food (Dittus, 1979) and water (Wrangham, 1981) and primarily affects infants and juveniles (Altmann, *et al.* 1985). Therefore, dominance rank partly explains some of the variation in reproductive success (Silk, 1987). Finally, the distribution of deaths by sex in female-bonded groups affects females in the early stages of their life, and males when they reach adulthood and emigrate from their natal troop (*e.g.* Dittus, 1979 for toque macaques; Henzi & Lucas, 1980; Cheney & Seyfarth, 1983 for vervets).

## **1.2. THEORETICAL ISSUES CONCERNING PRIMATE SOCIETY**

I will review some of the hypotheses formulated to explain: i) why monkeys live in groups, ii) the socioecological classification of primate groups, iii) the characteristics of female-bonded groups, iv) why unrelated male competitors coexist in multi-male multi-female groups.

### **1.2.1. Living in groups**

The group integrative mechanism in non-human primate species was originally proposed to be sexual behaviour (Zuckerman, 1932). Later studies point out that the major determinants of social life are ecological, for vertebrates in general (Lott, 1984) and monkeys in particular (review in Fedigan & Fedigan, 1988), more specifically, these are location and defence of food resources (Wrangham, 1980; 1987; Robinson, 1982; Slobodchikoff & Schulz, 1988; Isbell *et al.* 1990), predation (Alexander, 1974; van Schaik, 1983; van Schaik & van Hooff, 1983; Anderson, 1986), or both (Chance, 1959; Hall, 1968; Gartlan & Brain, 1968; Eisenberg *et al.* 1972; Jolly, 1972; Clutton-Brock, 1974).

### **1.2.2. Female-bonded groups**

Vervet monkeys live in female-bonded groups and as it is characteristic of female-bonded societies females remain in their natal groups throughout their lives (Wrangham, 1980). One of the ultimate advantages of females not migrating is that the costs of predation in unfamiliar areas are reduced (Isbell *et al.* 1990). Females in these societies have highly differentiated networks of social relationships based on proximity, grooming and aggression and other interactions (Seyfarth, 1977, 1980; Bernstein, 1980; Wrangham, 1980; Lopez-Lujan *et al.* 1989).

Female vervet coalition in agonistic encounters has been correlated with female-female proximity (Fairbanks, 1980), grooming (Seyfarth *et al.* 1978; Seyfarth, 1980) and kin relationships (Seyfarth & Cheney, 1984). Therefore, high ranking females in female-bonded societies receive more grooming than lower ranking individuals because of their higher competitive ability (Fairbanks, 1980; Seyfarth, 1977; 1980). The use of grooming as an investment in future relationships is also apparent when considering the number of individuals immature females groom *versus* the number males groom in female-bonded primates (Cheney, 1978). In support of the idea, in species where the females migrate this does not occur (i.e. mountain gorillas: Harcourt & Stewart, 1983 p.318; hamadryas baboons: Abegglen, 1984).

The most characteristic features of matrilineal social organisation in many Old World Monkeys are that daughters rank just below their mothers (rhesus: Sade, 1967; vervets: Horrocks & Hunte, 1983a; Fairbanks & McGuire, 1984) and that younger sisters eventually outrank older sisters (Horrocks & Hunte, 1983b). Daughters seldom rise in rank above their mothers precisely because mothers reverse the rank of their daughters (Horrocks & Hunte, 1983b). Consequently, adult females in those groups tend to have stable dominance hierarchies (vervets: Seyfarth, 1980; review in Wrangham, 1980).

In contrast, males transfer to neighbouring troops at around sexual maturity and continue to do so throughout their lives (for vervets: Struhsaker, 1967 a,b; Gartlan & Brain, 1968; Henzi & Lucas, 1980; Cheney & Seyfarth, 1983; Japanese macaques: Eaton, 1976; toque macaques: Dittus, 1979; baboons: Chance, 1959, Packer, 1979a). Inbreeding avoidance occurs as a result of natal males migrating when they reach adulthood (Pusey & Packer, 1987) and non-natal males before the time their potential daughters are able to reproduce (e.g. Struhsaker, 1967b; Dittus, 1979).

This point is nicely illustrated by female residence being closely associated with intergroup transfer by males (Lindburg, 1969; Packer, 1979a; Clutton-Brock, 1989). In addition, preference to mate with unfamiliar conspecifics (Smith, 1987) and the fact that adult males ignore sexual presents by adolescent females (e.g. Smuts, 1985, p.15-16) also reduce the probability of inbreeding.

Wrangham (1980) reviews the species of non-human primates in the Old World in which females generally migrate (*Colobus badius*, *Papio hamadryas*, *Gorilla gorilla berengei* and *Pan troglodytes*). Clutton-Brock (1989) considers female migration as an alternative strategy to prevent inbreeding.

It has been argued that in female-bonded primates: first, investment by kin is greater in males than in females in the first stages of life although investment in males ceases at adolescence while it continues through the average duration of the generation for females (Dittus, 1979 for toque macaques); second, that aggression is one of the mechanisms matrilineal use in the socialisation of their infants (Bernstein & Ehardt, 1986); third, that juvenile females receive more aggression from adult females than do juvenile males (Horrocks & Hunte, 1983a for vervets); finally, male rank at puberty is independent of the mother's (Sade, 1967 for rhesus monkeys). All the above is in agreement with the migration pattern of these species.

The finding that adult males, living in female-bonded multi-male species, rarely interact among themselves in a friendly or positive way (Melnick & Pearl, 1987) is not surprising because. First, adult males are generally unrelated. Second, male dominance hierarchies are not as stable as those of females and change through agonistic disputes or by the arrival of new immigrant males (Cheney & Seyfarth, 1990, p.32). Third, male mate competition can account for a greater variance in male reproductive success than female mate competition (Emlen, 1973).

### **1.2.3. Socioecological classification of primate groups**

The relationship between environmental quality, primate social organisation and territoriality has been extensively discussed (Gartlan & Brain, 1968; Struhsaker, 1969; De Moor & Steffens, 1972; Fairbanks *et al.* 1978; Whitten *et al.* 1987; Dunbar, 1988). Primate grouping patterns are mainly related to food distribution (Slobodchikoff & Schulz, 1988) although predation pressure (Jones, 1981; van Schaik & van Hooff, 1983) and sexual selection also play a part (Crook & Gartlan, 1966).

Emlen and Oring (1977) present the following ecological categorization of mating systems. First, monogamous species or animals that live in family groups are characteristically found in uniform environments with a low density of individuals. Second, there are three forms of polygyny: i) resource defence polygyny in which the male defends resources, ii) female defence polygyny (or harems) is characterised by females being very gregarious and one male monopolising them, iii) male dominance polygyny, in which males sort out their rank and females choose males primarily on the basis of their dominance rank. Emlen and Oring conclude that when ecological conditions do not allow the existence of a polygynous mating system, mammals benefit by remaining with their initial mate and sharing the energetic burden of paternal care between the two sexes.

Uni-male species are those with only one reproductive adult male and are primarily found in species with long breeding seasons. Multi-male groups which typically contain more than one unrelated adult reproductive male and one or more matriline (Emlen & Oring, 1977; Clutton-Brock, 1989) are favoured when the groups are large (Clutton-Brock & Harvey, 1977a) and/or the breeding season is short (Ridley, 1986). Therefore, in polygamous species sex differences in intensity of mate competition are said to have selected for sexual dimorphism in body size and musculature (Trivers, 1972; Clutton-Brock & Harvey, 1976).

Age-graded groups are intermediate between uni- and multi-male breeding systems. They are characterized by the presence of more than one adult male of different ages who may partake in breeding (Eisenberg *et al.* 1972); as in the case of gorillas (Harcourt, 1978), these males are normally related.

Eisenberg *et al.* (1972) argue that a true multi-male system is restricted to those terrestrial, intermediate-sized primates living in large groups in which several functionally reproductive adult males co-exist with other non-reproductive males of different ages. On the other hand, the uni-male system and the age-graded system are characteristic of arboreal species. However, certain partial exceptions to these generalisations are apparent (see below) because, as van Schaik and van Hooff (1983) point out; a male may be unable to stop other males from feeding in their area although they can stop them from approaching a cohesive group of females.

The first exception is the terrestrial patas monkey (*Erythrocebus patas*) which is the biggest guenon (Butynski, 1988, p. 286) and males are twice the female weight (Napier & Napier, 1985, p.146). Breeding is seasonal and supernumerary males leave the troop at the end of the breeding season (Harding & Olson, 1986).

Second, the crab-eating macaque (*Macaca fascicularis*) is arboreal and lives in large troops which include many adult males (Wheatley, 1980).

Third, the arboreal talapoin monkey (*Miopithecus talapoin* also known as *C. talapoin*) is the smallest of all the guenons, breeds seasonally (Butynski, 1988 p. 304) and presents slight sexual dimorphism (Napier & Napier, 1985, p.144). Although talapoins have been described as living in large multi-male groups (Gautier, cited in Rowell, 1988, p.450), their multi-male system is questionable when considering reports that male and female talapoins travel in distinct subgroups during the non-mating season (Gautier-Hion, cited in Melnick & Pearl, 1987, p.126).

Fourth, the swamp monkey (*Allenopithecus nigroviridis*) is a forest dwelling monkey characterised by adult males and females having a similar size, with females presenting sexual swelling and males having a whitish blue scrotum (Napier & Napier, 1985, p.144). They live in multi-male groups (Melnick & Pearl, 1987).

Finally, the vervet monkey had been classified as a multi-male species (review in Fedigan & Fedigan, 1988). However, the multi-male nature of vervet society has been questioned (Eisenberg, *et al.* 1972; Henzi, 1985; Clutton-Brook, 1989), one of the reasons is that in some study troops only one fully grown adult male reproduced (Struhsaker, 1967b, but see Andelman, 1987; Cheney *et al.* 1988), while another is that males do not form agonistic coalitions among themselves (Henzi, 1985).

It is worth noting that the only three species of guenon that live in multi-male groups (talapoin, swamp and vervet monkey) are exceptions to the classical categorisation of multi-male systems (Melnick & Pearl, 1987).

Three more issues must be taken into account when considering the social structure of a species: first, intraspecific variation may occur in relation to the habitat (Eisenberg, *et al.* 1972; De Moor & Steffens, 1972; Wheatley, 1980; Lott, 1984); second, aggressive dominance can affect the size of the group and the number of males in a primate group (Slobodchikoff & Schulz, 1988) and finally, there may be variations in the ability of males to monopolise breeding females (Emlen & Oring, 1977; van Schaik & van Hooff, 1983; Ridley, 1986).

#### **1.2.4. Multi-male systems**

There are a few issues which are not fully understood about the nature of multi-male troops in monkeys. First, unrelated adult male mammals rarely co-exist in heterosexual groups, the exception being some species of non-human primates (Eisenberg, 1981). Second, why do adult females in a female-bonded species accept the presence of more than one adult male in the troop (Wrangham, 1980)? Third, it is not known whether the presence of more than one adult male in the troop (in the absence of receptive females) benefits additional males or other members of the troop. Finally, how do unrelated adult males co-exist in an arena of reproductive competition?

The classical socioecological explanation of why unrelated male primates coexist was that, through cooperative defence, they reduce the risk of predation (Crook & Gartlan, 1966). However, single males would be more economical in areas with scarce food resources, mainly for highly dimorphic species (Gartlan & Brain, 1968). These arguments were based on the group selection theory (Wilson, 1975).

Other, more favoured arguments are those of a demographic nature which are based on the assumption that males are attracted to receptive females. First, the distribution of females regulates the number of males living in a troop (Wrangham, 1980). Second, the degree of polygyny is related to the number of adult females in the troop and the difficulty adult males have in controlling the arrival and presence of additional males (Cheney, 1983a, p.234). Third, as the number of fertilisable females to sexually active males determines the intensity of sexual selection, birth synchrony will make it more difficult for high ranking males to monopolise females (Emlen & Oring, 1977; Ridley, 1986). Finally, it has been pointed out that cercopithecines may live in uni-male groups when there are less than six adult females and in multi-male groups when there are more than six females or less depending on environmental conditions (Andelman, 1986).

The demographic arguments can explain a multi-male 'moment', that is, an influx of males into an heterosexual troop during the breeding season (Henzi, 1988) as has been reported for samango monkeys (Cords *et al.* 1986; Henzi & Lawes, 1987), patas monkeys (Chism & Olson, 1982) and redtails (Struhsaker, 1977). This argument is supported by the fact that the influx of samango males is directly related to the availability of receptive females (Henzi & Lawes, 1988).



Male samango monkeys might not remain in the troop outside of the mating season because female samangos reproduce on average once every second year (Henzi & Lawes, 1988). In contrast, female vervets can potentially give birth every year (e.g. Gartlan, 1969; Fairbanks & McGuire, 1984), suggesting that vervet males stay in the troop in order to improve their reproductive opportunities.

If this is so, it might be expected that: i) a maintenance of male-female social relationships through the year occurs (see chapter 6) and ii) males would copulate more often with those females they associate more closely with during the non-mating season, as has been found for other multi-male species (e.g. Smuts, 1985).

A question which arises at this point is the following: why do adult females living in female-bonded groups accept the presence of more than one unrelated adult male in the troop throughout the year? Additional males may provide some benefits to other members of the troop (Kummer, 1968; Wrangham, 1980) and their numbers would depend on those benefits (Eisenberg, *et al.* 1972). Smuts (1987) points out that female baboons can respond differently to male sexual approaches and may also influence male membership. Considering that the limiting resource for females is food (Wrangham, 1979) and water resources (Wrangham, 1981), males can be valuable for territorial defence. Agreeing, Tsukahara (1990) proposes that female Japanese macaques choose males that are valuable for territorial defence.

On the other hand, van Schaik and van Hooff (1983) suggest that a reduction in the risk of predation is one of the most important factors regulating the number of males in primate societies (see also Clutton-Brock & Harvey, 1977a). Consequently, females may select helpful males (van Schaik & van Noordwijk, 1989 for capuchins). Finally, adult male defence of females and immatures during intratroop agonism has been considered to be what makes males most attractive as potential mates (Kurland, 1977 for Japanese monkeys). Since vervet males are slightly bigger than females (Bramblett *et al.* 1975) and do not have the metabolic demands imposed by pregnancy and lactation, they could be more successful than females in various areas (see below).

First, free-ranging vervet monkeys have generally been described as having well defined territories (*sensu* Davies & Houston, 1984) and defending them against conspecifics (Hall & Gartlan, 1965; Struhsaker, 1967a,b; Gartlan & Brain, 1968; Cheney, 1981; Harrison, 1983a; Henzi, 1985; Dunbar, 1988; but see McGuire, 1974; Chapman & Fedigan, 1984). Crook and Gartlan (1966) pointed out that vervet monkeys living in impoverished environments do not defend their territories.

Contradictory results on the relative participation of vervet males in intertroop encounters have been obtained (review in Fedigan & Fedigan, 1988). By defending their territory males protect their food and water resources as well as those resources for their potential mates and probable offspring (Isbell *et al.* 1991). However, preliminary results obtained in Natal by Henzi (1982) suggest that males primarily defend the females of their troop against extratroop males. Cheney (1981) argued that in slightly dimorphic species such as vervets, macaques and langurs, females - primarily the higher ranking individuals- actively participate in threatening males and females away from their territory.

Second, as the reduction of predation is one of the main reasons for living in groups and is accomplished by: i) a dilution effect (Pulliam & Caraco, 1984), ii) enhancing predator detection (van Schaik, 1983; van Schaik *et al.* 1983), and/or iii) by directly attacking potential predators (see chapter 4; but see Cheney & Wrangham, 1987), any significant contribution by males in those mechanisms of defence against predators would be beneficial to all members of the troop.

Some of the costs imposed upon animals by being vigilant are that their feeding time may be constrained (Kavanagh, 1980) and that by occupying exposed positions to scan their environment they are more vulnerable to predation (see chapter 4). However, the risks incurred by males are more obvious when they defend the troop (Hall, 1967; Poirier, 1972). As males partake in vigilance and defence of the troop to a higher degree, females can concentrate on feeding and caring for their infants, behaviours which also contribute to improving the reproductive success of males.

Third, there are no reports in the literature of infanticide committed by long term resident males, though there are accounts of adult males killing infants upon arrival or during intense intra- or inter-troop agonism (Dunbar, 1984, p. 209; review in Jolly, 1985, p. 259-264). In uni-male and age-graded groups infanticide seems to be more common than in multi-male societies, specially when the troop is taken over by new leaders (Trivers, 1972; Blaffer Hrdy, 1974; 1977). Therefore, adult resident males, could protect the infants from potential infanticides by preventing other males from entering the troop (see Dunbar, 1984, p.210-217).

Finally, for strictly reproductive reasons there might be other selective advantages to females by having more than one adult male in the troop during the breeding season. One of these might be that females in polygynous species can choose a high quality

male and compensate for a general reduction of male paternal care (Emlen & Oring, 1977, p.217).

The advantages to dominant and subordinate males by remaining in the troop outside the mating season could be explained in terms of individual survival, and of improving their chances of fathering offspring in the next mating season -'personal fitness' (Goss-Custard *et al.* 1972; Dunbar, 1988, p.18)- or in terms of increasing the survival and reproduction of their offspring -'collateral fitness' (Dunbar, 1988, p.18) by defending food resources (Isbell *et al.* 1991) and/or predator avoidance.

I predict that additional vervet males may improve their 'inclusive fitness' (Hamilton, 1964) by remaining in heterosexual groups when there are no immediate chances of fathering offspring. This benefit would outweigh the costs of food competition and harassment from higher ranking unrelated males.

A further question which arises is how unrelated adult males coexist. Whatever the evolutionary cause may be, the consequence of multi-male systems is that males need to invest more effort to maintain access to a group of females, and have come under strong selective pressure to evolve strategies to deal with the presence of male competitors. Therefore, a complex network of behavioural patterns which allow unrelated adult males to coexist in multi-male multi-female troops should exist.

Richards (1974) emphasises the usefulness of the concept of dominance and also points out the value of a recognised order of priority in reducing aggression (see also Chance, 1959).

Spatial segregation among males can also result in lower levels of antagonism. Among vervets, adult males are often found peripheral to the groups (Hall & Gartlan, 1965). However, vervet males are seldom found outside troops (Henzi & Lucas, 1980). Solitary males are either old males (Hill, 1966), or there has been a general reduction of the vervet population (Andelman, 1986 in Amboseli, Kenya) as a result of high rates of predation and food shortage (Cheney & Seyfarth, 1990). These drastic environmental conditions prompt group fission to such an extent that adult males have been observed in all-male bands (Isbell *et al.* 1990) something not previously reported for vervet monkeys (Andelman, 1986). All the above may suggest the importance of predator detection as a reason for unrelated males to coexist, especially in areas where the risk of predation is high (Henzi, 1988).

In other species, i.e. Japanese macaque, *Macaca fuscata*, (Chance, 1959), samango monkey, *Cercopithecus mitis* (Henzi & Lawes, 1987) and Nilgiri langurs, *Presbytis johnii* (Poirier, 1970 p.319) all male groups are commonly found.

Male macaques may form alliances with other male relatives with whom they have emigrated to other groups (cited in Melnick & Pearl, 1987). As vervet males may also emigrate with other male peers (Cheney & Seyfarth, 1983), it is surprising that male-male coalition has not been described for vervet males, with the exception of a pair of possibly related males (Cheney & Seyfarth, 1990, p.33).

On the other hand, unrelated adult and subadult male baboons may form alliances against higher ranking males (e.g. Hausfater, 1975; Smuts, 1985; 1987). Surprisingly, male-male coalitions are not exclusive to multi-male species (cited in Smuts, 1987, p.390). This together with the use of infants as buffers during intermale agonism in baboons (Packer, 1980; Strum, 1983, 1984; Dunbar, 1984) could be explained by the high levels of sexual dimorphism among baboons correlated to drastic differences in size and competitive power among males.

Some of the behavioural patterns vervet males have developed to tolerate each other's presence are based on their visual genital signalling system and displays of subordination (Henzi, 1981, 1982, 1985). Therefore, special attention will be paid to this issue in order to understand the evolution of multi-male systems.

### 1.3. MALE GENITAL SIGNALLING SYSTEM

Terrestrial guenons typically present bright genital signals, while the arboreal species tend to have bright colouring on their faces (Kingdon, 1980; 1988b). In general, arboreal primates seem to rely more heavily on acoustic than visual signals (Moynihan, 1967). The above is nicely illustrated in the mandrill that presents various coloured body parts that are used for communication in different contexts (Jouventin, 1975; Bowling, 1978).

The vervet monkey has a vivid blue scrotum (Hill, 1966; Napier & Napier, 1967), its blueness is due to the deep dermal deposition of melanin in melanocytes and is modulated by the state of hydration of the dermis (Price *et al.* 1976; see also Machida & Giacometti, 1967). The scrotum is clearly visible from the front and side if the animal is sitting or standing and from the rear when the animal is standing (Price

*et al.* 1976). The male's genitalia can be accentuated by the tail carriage and lateral movement or 'flashing' (Henzi, 1982).

Though Darwin (1876) pointed out that the colourful genitalia of some species of monkeys function as attractants, more recent studies suggest that the importance of genital signalling among monkeys is related to a social (non-sexual) context. The importance of the colour of the scrotum as a social marker was predicted by Price and co-workers (1976). The complex visual signalling system of the vervet monkeys' genitalia has been found to be associated with inter-male agonism (Struhsaker, 1967a,b; Henzi, 1982; chapter 5) and has developed independently for the penis and scrotum (Henzi, 1985).

The frequency of scrotal adductions increases with an increase of fearful behaviour. Alpha males adduct their testes for non-social reasons, while subordinates do so as a consequence of social events, more often when interacting with adult males (Henzi, 1981). By retracting (adducting) their testes, male vervet monkeys protect them from injury (Henzi, 1985) at the expense of an increase in temperature which is not beneficial to their viability (Waites, 1970).

It has been stated that the vivid scrotum of vervet monkeys pales when the animal falls in social rank (Gartlan & Brain, 1968; Bramblett, 1980). Price and his co-workers (1976) stated that these colour changes are regulated by the level of dermal hydration. In addition, the redness of the penis fades after castration in male patas monkeys (*Erythrocebus patas*) suggests that it is hormone dependent (Dixon, 1983 p.91). As a relationship between levels of plasma testosterone and agonistic rank exists (*e.g.* Rose *et al.* 1974), and patas are closely related to vervets, it can be hypothesised that dominance rank in vervets reinforces the visual signalling power of penile displays. If the colour of the penis in vervet monkeys is regulated by the sexual hormone testosterone, one would expect there to be either seasonal or individual (rank related) differences or both. Henzi (1985), however did not observe any variation in scrotal colour among the dominant or subordinate males, nor a seasonal variation as asserted by Wickler (1967).

Besides the vervet male's genitalia, blue colour is found in the skin of their abdominal wall and extends along the medial aspects of the upper arms and legs (Price *et al.*, 1976; Fedigan & Fedigan, 1988, p.395). In addition, the genitalia of female infant vervets resemble the genitalia of male vervet infants. However, upon closer examination the genitalia are seen to be different, but their form, size and colouration prevent accurate sex recognition in the field (Bramblett *et al.*, 1975). That

infants have their genitalia inspected (visual and muzzling) very often (Gartlan, 1969; Lancaster, 1971; Krige & Lucas, 1974) could explain sex differences in aggression received by immature vervets (Horrocks & Hunte, 1983a).

Finally, Hall (1967) reported a vicious attack by an adult male patas against a subadult male after the subadult male's penis became clearly visible. It is possible that this aggression was triggered by the genital colouring (see also Bolwig, 1978). A similar observation was made in a study on howler monkeys, males of this species present white spots in the scrotum when they approach adulthood (Young, 1983) and it could be hypothesised that the presence of the spots triggers adults males to attack other males.

#### 1.4. IMPLICATIONS OF THE ABSENCE OF FEMALE SEXUAL SKIN

A 'true sexual skin' in primate females is only found among Catarrhine or Old World primates (Dixon, 1983). The fact that the colour and swelling of the female sexual skin may occur in different parts of their genitalia has prompted some authors to propose an independent evolution for each group (Wickler, 1967). Moreover, *Theropithecus gelada* presents a bare skin patch on the chest in both sexes; it undergoes cyclical changes that could be advantageous for a species that spends most of its foraging time sitting (Crook & Gartlan, 1966).

Changes in the turgescence and colouring of the female's genitalia can provide certain information about the reproductive state of the female. The most common pattern is that the sexual skin signals the period of maximum sexual receptivity in females (e.g. Hausfater, 1975, p. 75) and attracts males (Bielert & van der Walt, 1982). It has been suggested that this visual cue tends to concentrate complete copulations by adult males, especially the most dominant, to around the time the female is ovulating (Hall & DeVore, 1965; Hausfater, 1975; Packer, 1979b, review in Dixon, 1983). However, the importance of visual cues in chacma baboon sexual interactions does not explain the reduction of attraction 2-5 days prior to skin breakdown (Chance, 1959).

Besides a visual component in female attraction, the importance of olfactory cues has been emphasised (see chapter 7). Moynihan (1967) argued that there is a need for olfactory signals to be reinforced by acoustic and/or visual signals.

It is surprising that only females of certain species of *Colobus*, *Cercopithecus* and *Macaca* have a sexual skin (Dixon, 1983). Some of the species that lack sexual swelling are: black and white colobus, toque and bonnet macaques (Napier & Napier, 1985 p. 130,150).

"It is possible that the development of sexual skin is a comparatively ancient feature, at least in certain groups and that it may have arisen in terrestrial ancestors of some species which now live in the trees" (Dixon, 1983 p.84).

In *Cercopithecus aethiops*, the colouration of the female outer surface of the labia majora is dark blue without the vividness of the male scrotum, and is not usually observed in any of the typical postures of the animal (Price *et al.*, 1976). In addition, some reddening in the clitoridal area and a slight turgescence of the vulva have been observed in some adult females (Gartlan, 1969; personal observation). However, in vervets these changes in the female's ano-genital area are not obvious (Struhsaker, 1967a; Rowell, 1971) and do not correspond to the female's midcycle (Andelman, 1987).

The fact that vervet males might obtain some information about the reproductive state of the female through olfactory cues can only be inferred from the available literature; these accounts normally refer to the male occasionally sniffing the female genitalia before mounting (Gartlan, 1969; Girolami, 1985).

Natural selection may have favoured the evolution of concealed ovulation in some species, in order to extend the mating period. Andelman (1987) examines some of the hypotheses that have been proposed and concludes that concealed ovulation may serve to reduce infanticide because newly immigrated males are responsible for most of the infanticides reported in the literature of Old World monkeys and females outside the fertile period were mainly observed mating with non-resident males. Andelman also hypothesises that other benefits for females would be the facilitation of mate choice. Finally, it has been pointed out that in general, concealed ovulation may reduce male competition (Blaffer Hrdy, 1977; Jolly, 1985; Andelman, 1987).

It has been argued that in multi-male multi-female species a reduction of estrus signals is related to a reduction in male paternal care, probably because of a low degree of paternity confidence (Hamilton, 1984). The absence of perineal swelling and colour changes in the female genitalia impedes a study of the distribution of successful copulations among undisturbed vervet monkeys and consequently, very little is known about alternative strategies in male mating behaviour.

Although morphological and colour changes to the vervet female's perineal area may not be obvious to the human observer, I hypothesise that vervet males may have other mechanisms (*e.g.* behavioural or olfactory cues) to detect the reproductive state of the females.

### 1.5. MALE DOMINANCE AND SEXUAL BEHAVIOUR

Altmann's model (1962) of male priority of access to reproductive females predicts that subordinate males of rank  $n$  stand some chances of mating when there are at least  $n$  females cycling at any one time. High ranking adult males benefit most when there is less overlapping in female sexual receptivity (Emlen & Oring, 1977). However, many exceptions have been found (DeVore, 1965; Smuts, 1985; Strum, 1982; 1987).

The result is that higher ranking males mate more often than lower ranking males in many multi-male multi-female species (Carpenter, 1942a; Hall & DeVore, 1965; Hausfater, 1975; Packer, 1979 a,b; review in Cowlshaw & Dunbar, 1991). The same applies to vervet monkeys (Struhsaker, 1967b; Andelman, *et al.* 1985; Andelman, 1987).

Besides, what is more important is the timing of the mating, successful mating can only occur when the females are in midcycle. Surprisingly, Andelman (1986) found that high, middle and low ranking male vervet monkeys in Amboseli did not differ in total number of copulations with females, not even during the week they were more likely to conceive (Andelman, 1987). These results are contradictory with those found for other multi-male species (for rhesus: Chapais, 1983a; *inter allia*: Dixon, 1983) and need to be extended to other study sites. In order to investigate this possibility, it is essential that a detailed description of the sociosexual behaviours that precede and occur during copulation is undertaken. The distribution of male and female initiated sociosexual bouts, relative to the reproductive state of the female is also required if we are to understand vervet monkey sexuality. Unfortunately, I could not carry out a physiological or cytological study to ascertain the reproductive cycles of the females in my study groups. Backdated dates of conception from successful births will provide some limited data.



The most extreme, although rare form of male mate competition is infanticide (Trivers, 1972; Blaffer Hrdy, 1974, 1977; Timmermans, *et al.* 1981). Stillbirths and early infant mortality trigger females to conceive shortly afterwards (Rowell & Richards, 1979). As a result, infanticidal males increase their chances of fathering the next offspring. The benefits to the infanticidal male are even higher when considering that vervet females, at the very least, respond to the loss of an infant by increasing the level of care for the next infant (Fairbanks, 1988a).

Another form of male mate competition is male agonistic coalition, which partly explains the fact that high and low ranking males complete copulation at the same rates (Hausfater, 1975; Packer, 1977; Smuts, 1985, 1987 for savanna baboons). However, subordinate vervet males have never been reported as forming agonistic coalition against more dominant males.

Mate selection may also be a key component of male reproductive success (Altmann, *et al.* 1988), because of the effects of dominance on female reproductive success in some environmental conditions. It has been argued that mate competition should be greatest among females because they are the sex that invests more in offspring (Trivers, 1972; Dawkins, 1976 p.176; Huck & Banks, 1982; Jones, 1981). Seasonally breeding species may have more female-female mate competition (Altmann, *et al.* 1988).

It is common among some multi-male species to find that certain males associate with specific females for periods ranging from a few hours to days in what has been called 'sexual consortships' (for baboons: Hall & DeVore, 1965; Saayman, 1971; Hausfater, 1975; Seyfarth, 1978a; rhesus monkeys: Kaufmann, 1965; Chapais, 1983a; review in Ridley, 1986). These sexual consortships function as a mechanism which stops other males from copulating with potentially fertile females, and agonistic rank does not predict consort activity (review in Smuts, 1985, p.130). The members of a consort pair, apart from being involved in sexual interactions, groom, feed and rest next to each other, and more typically follow each other (Saayman, 1971). Unlike baboons and macaques, sexual consortships have not been described for vervet monkeys (Andelman, 1987).

Multi-male species such as baboons may also present special bonds which are not restricted to the period of female receptivity (Seyfarth, 1978b; Smuts, 1985). The advantages to the females and their offspring are that they benefit from male defence and have access to scarce resources (Hamilton, 1984; Altmann, *et al.* 1988). Males benefit by using their infants during agonistic interactions with other males (Packer, 1980; Dunbar, 1984; Strum, 1984), and male-female bonds are ultimately related to reproductive success (Smuts, 1985).

It is not yet understood why vervets do not form those male-female bonds, besides all their similarities with baboons and macaques (but see Keddy, cited in Cheney & Seyfarth, 1990 p.46). Melnick and Pearl (1987) argue that female vervets and talapoin may not need to form bonds with males because they are not as highly dimorphic as baboons. I suggest that vervet females rely on female coalition more than on male support, due to the highly differentiated network of female-female interactions.

## 1.6. AIMS OF THIS STUDY

After introducing the vervet monkey, reviewing some of the theoretical issues concerning the social structure of the species and the proximate mechanisms that regulate male sexual behaviour in closely related species, a detailed study on the implications of vervet monkey's multi-male social system will be carried out. The sampling methods, a description of the behavioural categories and of the study troops will also be given (chapter 2). The following points will be developed and original data from a caged environment and from a field study will be provided.

The problems of survival, that is time budgeting dedicated to maintenance activities and the effects these factors have on the way adult males and females allocate time for vigilance and social activities. Particular attention will be paid to constraints imposed by environmental conditions, the effects of the breeding season and rank-related on time spent feeding, resting and socialising. Differences between a caged and a free-ranging troop of vervets may provide good examples. Also to be discussed is the question do male vervets show the same diurnal rhythms as females? (chapter 3).

In order to investigate variation in vigilance among age-sex classes and the factors most responsible for this, the distribution of alarm calls in relation to time spent vigilant and the sex of the caller will be analysed. Special emphasis will be placed on time spent peripheral (away from other monkeys), exposed on top of the canopy and other risky positions such as at the head or tail of group progressions. The question of whether the dominant male participates to the same extent as additional males will also be looked at (chapter 4).

Whether there is asynchrony in male and female feeding activity that could be considered as a means of avoiding overt food competition or protection for other members of the troop from outside threat is discussed (chapter 4).

The social position of the adult males will be measured in terms of spatial, as well as interactive parameters with other adult members of the troop in relation to eventual mating opportunities and dominance rank. The analysis of the data will be more qualitative and directional than in the previous chapters (chapters 5 and 6).

It will also be necessary to determine quantitative and qualitative variations in male-male interaction (proximity, grooming and antagonistic behaviour) according to their respective dominance rank and the season (chapter 5).

An assessment of the strength and preferences in male social relationships with adult females during the birth, non birth-non mating and mating seasons as well as seasonal variation will be made. A second issue concerns responsibility for the initiation and maintenance of grooming between males and females (chapter 6).

A description and analysis of the distribution of sociosexual behaviour in order to determine the male and female short-term reproductive strategies employed to improve mating opportunities will follow. In order to determine the social constraints imposed in vervet male sexuality, an attempt is made to distinguish between male and female mate choice and mate competition. For predictive and comparative purposes it is necessary to determine short and long-term strategies employed by males and females to improve mating opportunities.

An attempt will also be made to test Henzi's (1981) prediction that the dominant adult male functionally castrates subordinate males. Although the exact reproductive state of the females could not be determined in this study, inferences can be made by backdating the time of conception in females who gave birth successfully (chapter 7).

The adaptiveness of vervet social structure will be discussed in terms of potential costs and benefits to the dominant and subordinate males who remain within a heterosexual group throughout the year. The male-female and inter-male differences in time budgeting for maintenance activities and the constraints imposed by those on social time may be good indicators of individual competition and degree of integration within the troop. A study of the mechanisms that exist to regulate male-male interactions, who does what to whom how often (see Rowell, 1988, p.439) will also be conducted (chapter 8).

Basically, the main questions in this study are directed towards understanding the multi-male nature of vervet social organisation. First, do unrelated adult vervet males coexist in multi-male multi-female troops outside the breeding season: i) for ecological reasons (*e.g.* obtaining food and avoiding predation), ii) to improve their mating opportunities in the next season (personal fitness) and/or iii) to increase the chances of survival of their offspring (collateral fitness)? Finally, to what extent vervet societies differ from other typically multi-male species.

## **2. METHODS AND STUDY ANIMALS**

This chapter describes the methods, the behavioural categories and the sampling procedures used to collect the data. Three troops of vervet monkeys were observed. First, the Cage Troop (CT) which was located in the Grounds Department at the University of Natal, Durban, and was established in 1975 (Tollman & Lucas, 1979). Observations were carried out from the 2nd September 1985 until the 28th November 1985, and from the 23rd January 1986 until the 28th November 1986. Second, the presence of a free ranging troop, Altre Troop (AT) in the same area where the Cage was, made it possible to study intertroop interactions on a daily basis. Sporadic sampling sessions continued until the 20th May 1987. Finally, a free living undisturbed troop at Windy Ridge Game Park (WT), Heatonville, was used to being followed, and studied from the 1st June 1987 to the 15th June 1988.

The location, environmental conditions and demographic changes of the three study troops are given. The demographic changes in troop composition are provided for a longer period than the duration of the intensive study, to give some idea of the females' reproductive success.

### **2.1 SAMPLING TECHNIQUES**

Although systematic sampling of the AT was not done, it provided some information on intertroop relationships, distribution of wounds, male transfer and troop composition. The following sampling methods were used (see Altmann, 1974):

#### **2.1.1 *Ad libitum* sampling**

Here no systematic constraints are placed on what is recorded or when it is recorded. This method was used throughout the study to record infrequent but important behaviours such as: alarm calls, intertroop and interspecific interactions, sexual behaviour, agonistic interactions, who led and who was at the tail of the troop during progressions, ecological notes and records of fresh wounds.

In summary, this method is useful in preliminary studies, for recording rare but important events, and for the study of the directionality of the interactions between pairs of individuals (Altmann, 1974).

Making observations according to some predetermined schedule is an important precaution against the bias that could arise if the observer merely records whenever something obvious or interesting happens. Avoidance of bias is best obtained using one of the sampling methods described below.

### **2.1.2 Focal-animal sampling**

In the present study, focal-animal samples (Altmann, 1974) consisted of 5 minutes of continuous recording of all occurrences of any of the behaviours described in the next section. Tables 2.1 and 2.2 give the monthly distribution of focal animal samples in the Cage and Windy Ridge respectively.

Table 2.1

Monthly distribution of focal animal samples in the Cage. FT, RN, FY, GO and LU were fully grown adult males. PA and PP were 3 years old when they were first used as focal animals and could be considered subadults from May 1986.

	FT	RN	FY	GO	LU	PP	PA
1985							
September	16	13	15	15	13	-	-
October	11	12	12	11	10	-	-
November	8	12	6	9	12	4	5
1986							
January	5	5	5	-	-	4	5
February	23	23	22	-	-	23	24
March	18	17	17	-	-	18	18
April	33	31	32	-	-	32	32
May	38	38	38	-	-	38	38
June	29	31	29	-	-	30	30
July	29	30	30	-	-	30	31
August	9	3	3	-	-	9	9
September	26	-	-	-	-	26	26
October	26	-	-	-	-	26	26
November	23	-	-	-	-	23	23
Total samples	294	215	209	35	35	263	267

Table 2.2

Monthly distribution of focal animal samples done on adult males (RO, LE, PE, CH, GR) subadult male (TI), and adult females (HI, SM, MO, BE, WE, TO, VE, ET) in Windy Ridge troop.

	RO	LE	PE	CH	GR	TI			
1988									
January	44	57	42	29	-	3			
February	58	67	68	-	-	7			
March	59	60	28	-	-	14			
April	72	69	-	-	-	12			
May	57	56	-	-	-	15			
June	41	42	-	-	6	22			

	HI	SM	MO	BE	WE	TO	VE	ET
1988								
January	1	0	3	0	3	7	1	8
February	9	5	14	10	4	15	6	19
March	16	13	10	21	12	16	13	14
April	17	14	8	17	19	16	9	14
May	13	23	12	15	16	21	14	16
June	16	9	16	12	13	17	12	25

The majority of interactions involved pairs of animals. However, when more animals were involved the interaction was split into its constituent dyads. The sample was terminated before the scheduled time when the animal was out of sight for more than 3 seconds or when it was not possible to observe the interactions in which it was engaged.

Adult and subadult males were sampled in both the Cage and in Windy Ridge. They were chosen randomly and focal-animal samples of each individual were not done more than once every hour to account for diurnal variability in behaviour. Focal samples were also carried out on adult females in Windy Ridge, however as male behaviour had preference in this study, samples on females were only carried out after the males had been sampled for that hour.

### 2.1.3 Instantaneous sampling

Here the observer records an individual's current activity at preselected moments in time. It is a sample of behaviours that are not instantaneous; that is of states and not of events (Altmann, 1974). Instantaneous samples of behaviour of all the adult and subadult males of Cage troop were done throughout the study period (Table 2.3). The activity the focal male was engaged in, the identity of his nearest neighbours (in contact, at less than 1 m, at 1-2 m, or the closest and at what distance) and whether they were on or off the ground, were noted. Samples were done on the focal male at the beginning and at the end of each continuous focal-animal sample.

Table 2.3.

Monthly distribution of instantaneous samples at the Cage for subadult males (PP and PA) and adult males (FT, RN, FY, GO, LU).

	FT	RN	FY	GO	LU	PP	PA
1985							
September	32	26	30	32	26	-	-
October	22	23	24	22	20	-	-
November	16	24	12	18	24	10	8
1986							
January	10	10	10	-	-	10	8
February	44	46	44	-	-	48	46
March	35	47	38	-	-	38	36
April	68	64	66	-	-	68	76
May	76	74	86	-	-	74	76
June	60	62	58	-	-	61	62
July	62	61	61	-	-	60	58
August	18	10	10	-	-	22	22
September	51	-	-	-	-	53	52
October	50	-	-	-	-	50	50
November	46	-	-	-	-	46	46
Total	612	451	449	90	86	538	534

If the behaviour of all visible group (or subgroup) members is sampled within a very short time period, the record approaches a simultaneous sample on all individuals and data can be obtained on the behavioural synchrony of the group. Altmann (1974) refers to such Instantaneous sampling on groups as **Scan sampling** and points out its advantages: i) a large number of animals can be sampled in a very short time, especially when using a tape recorder, ii) replicates are obtained in successive sessions, iii) animals need not be very well habituated and iv) it allows the estimation of the total percentage of time spent in specific states for different individuals and age/sex categories.



In the field study, from the 14th October 1987 until the 15th June 1988, scan samples were performed every 15 minutes on all age/sex classes (Table 2.4). Their activity, nearest neighbours (animals in contact, at less than 2 m, and between 2 and 10 m), level of the canopy (Table 2.5; Fig. 2.1), the location of the estimated centre of the troop in its home range and the general activity of the troop were recorded.

Table 2.4

Monthly distribution of scan samples in the Windy Ridge troop adult males (RO, LE, PE, CH, GR), subadult male (TI) and adult females.

	RO	LE	PE	CH	GR	TI		
1987								
October	72	50	67	37	-	49		
November	102	79	106	98	-	85		
1988								
January	178	181	150	95	-	66		
February	206	214	185	-	-	106		
March	178	179	84	-	-	101		
April	249	218	-	-	-	108		
May	284	215	-	-	-	119		
Jun	129	106	-	-	26	77		
Total	1398	1242	592	230	26	711		

	HI	SM	MO	BE	WE	TO	VE	ET
1987								
October	24	25	45	11	54	33	22	32
November	34	29	43	27	27	36	13	64
1988								
January	47	47	28	46	56	99	47	85
February	138	147	122	141	95	136	121	133
March	134	142	87	110	102	107	89	118
April	163	168	118	149	118	135	102	143
May	161	159	131	162	138	114	99	130
June	123	93	83	91	91	74	68	98
Total	824	810	657	737	681	734	561	803

Table 2.5

Levels above the ground that were distinguished during the study in Windy Ridge (see Fig. 2.1).

**T - Top level:** exposed on top of the canopy.

**M - Middle level:** in the canopy.

**G - On the ground:** not more than 0.5 m above the ground.

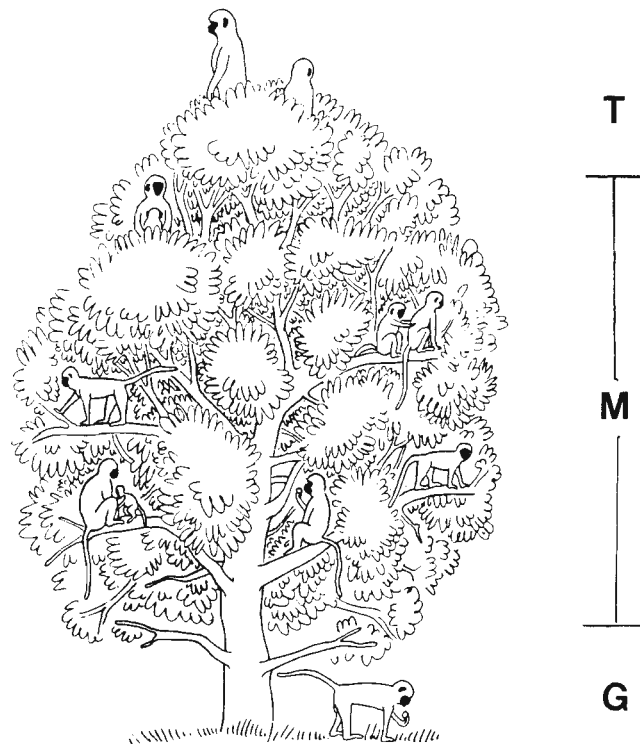


Figure 2.1. Vervet monkeys in different levels of the canopy (see Table 2.5).

## 2.2. BEHAVIOUR CATEGORIES

The behavioural categories (states) considered in this study for the instantaneous and scan samples are listed below. However, all the instances of sociosexual behaviours and sexual harassment were recorded using *ad libitum* sampling, when not included in another sampling method. These behaviours will be detailed in chapter 7.

The following behaviour categories were recorded during scan, instantaneous and continuous focal animal sampling: (\*indicates the categories that were only considered during the field study)

**AG - Aggression:** Chasing, hitting, grabbing or biting, which are normally accompanied by vocalisations. Threats that can easily lead to attack are also included in this category and these are: jerking of the forequarters either by i) sitting with hands on substrate, ii) sitting with hands on and off the substrate, iii) standing with hands on substrate or iv) standing with hands on and off the substrate. These variations are listed in order of increasing likelihood that they will be followed by attack by the actor (Struhsaker, 1967a).

**Al - Alarm:** Includes all the situations where the subject reveals tension and/or a high degree of alertness. i) Alarm vocalisations given towards possible predators, including man. ii) Intertroop agonistic interactions: retreat, agonistic vocalisations, territorial displays, and actual fighting. iii) Infant or mother distress calls. iv) During serious agonistic encounters when the recipient cannot flee, counterattack or when submissive displays no longer work. v) Standing on hind legs with trunk erect and forelimbs hanging by the sides of the body while looking intensely in one direction, when it is not directed to other members of the troop, or glancing about in different directions.

**CO - Coalition:** Collaboration during agonistic encounters with the actor or recipient of the aggression. The recipient may have solicited aid or not. It is equivalent to "alliance" (Seyfarth, 1980), but does not refer to the subject soliciting aid.

**CW (\*) - Confident walk:** Tail carried in such a way that male genitalia are clearly visible to most members of the troop. Struhsaker (1967a p.15) describes the confident walk as:

'A monkey walking in a confident manner appearing alert, but relaxed with an absence of extreme muscle tonus and an absence of rapid sideward glances of the head. The position of the tail was variable'.

Only performed by adult male vervets (cf. 'assertive walk' for male baboons, patas and drills: Bolwig, 1978).

**DP - Red-White and Blue Display (RWB Display):** All the behaviours included in this category can be considered variants of Struhsaker (1967a)'s Red-White-and-Blue Display directed to lower ranking males. It incorporates the 'Broadside' described by Henzi (1985) as a sustained posture, executed by walking or running up to another animal and then turning to stand 90° to it. In summary, any instance of an adult male displaying his genitalia towards another animal, while 'half circling', walking in front, or standing in front or above the recipient. It is normally accompanied by an extension or erection of the penis which may also jerk.

The recipient of the RWB Display either looks away avoiding eye contact with the actor or performs any of the submissive behaviours described below, accompanied by the *Woof*, *Woof*, *Woof-Waa* and *Waa* calls (Struhsaker, 1967c). Sometimes the RWB Display is terminated by the recipient giving a 'false-chase' at the displayer (Struhsaker, 1967a; also see **HO**).

**DR - Drinking:** Water intake from the pools or river. Although the licking of leaves in the early morning is common, it is not always possible to distinguish it from feeding.

**FE - Feeding:** Eating and food gathering which includes short locomotion (less than 10 sec), transporting and manipulation (rubbing with both hands or on the substrate, cleaning before ingestion, opening of *Acacia* or *Schotia* pods) of food items. Chewing behaviour, when the food from the 'cheek-pouches' is ingested is not classified in this category. During this chewing activity the animal is usually 'resting', 'resting /vigilant' or 'vigilant'.

**GR - Grooming:** Refers to 'alogrooming' that is grooming of an individual by another (Sparks, 1967). The groomer and the recipient are included in this category. It also incorporates characteristic body posturing for soliciting grooming.

**HR (\*) - Herding:** Mostly performed by dominant males towards adult females of their own troop. It can be very aggressive, often involving biting and attacking. It must be noted that Struhsaker (1967a) uses the term 'herding' for intertroop agonistic encounters, when the defending group spatially supplants the trespassing group.

**HO - Homage:** Refers to all agonistic encounters initiated by subordinates and directed at more dominant males, which includes submissive postures and/or vocalisations on the part of the actor (Henzi, 1985). It incorporates Struhsaker's (1967a) 'false chase' which differs from a truly aggressive chase in that the initiator gives fear vocalisations and never makes contact with the recipient who shows no signs of distress.

**IN (\*) - Agonistic interference:** There are two varieties and both have the effect of stopping ongoing agonism without any obvious coalition with the participants and without obviously directing the threat at a particular subject. First, the actor approaches an ongoing agonistic interaction and jerks its head while standing on its back legs in front of the interacting animals and/or 'shows the white of its chest' which is generally performed in a sitting posture with trunk erect and forelimbs hanging by the sides of the body. This may be accompanied by vocalisations -'grunt' (Struhsaker, 1967c)- or may not. Second, the actor approaches and simply sits or follows the animals (passive interference).

**LO - Locomotion:** Walking, running or galloping and climbing. Does not include looking for food when consisting of locomotion that does not last more than 10 sec.

**LP - Solitary play:** Jumping, leaping, tumbling or paddling without other members of the troop joining in. Playing with or investigating possible food or other items; a small animal (spider, insect or frog) or inanimate object is grabbed, thrown into the air, pushed or rolled while jumping back and forth.

**MA - Mild agonistic encounters or defensive threat:** Includes agonistic bouts in which one or more of the following patterns may occur: i) 'Staring' when both eyes are fixed on the recipient for a relatively long period of time. ii) 'Exposure of eyelids' - in vervet monkeys the eyelids and the area immediately above them are very light pink in colour and in sharp contrast to the black face (Struhsaker, 1967a), this makes both the intensity and the direction of the threat very clear (Gartlan & Brain, 1968). iii) 'Jerking of head' (Struhsaker, 1967a) combined with 'staring' function as a threat but it seems to develop into an attack less frequently than the 'jerking of the forequarters' (Struhsaker, 1967a) described in serious agonistic encounters. iv) 'Mild chases' not involving attack. v) Being avoided even when no threats are given. vi) Finally, this behavioural category also includes the actor of a spatial, food, partner or grooming displacement and the recipient of an avoidance.

If 'staring' and/or 'exposure of eyelids' are given in a crouched posture, they function as a defensive threat. If they are given from a confident posture they seem to be an aggressive threat (Struhsaker, 1967a).

For some analyses, displacements and avoidance interactions have been distinguished from other patterns included in this category.

**MF - Heterosexual behaviour:** Female presenting her hind quarters towards the male; male grabbing of hips, mounting, pelvic thrusting, penile intromission, ejaculation and any genital inspection (visual, tactile, olfactory or muzzling) of adult or adolescent female not exclusively related to grooming (for further detail see chapter 7). Sometimes the female can glance at the male and/or reach back with one hand and hold onto the male's body (Struhsaker, 1967a).

**MM - Homosexual behaviour:** Mounting or sexual presenting which involves only adult and subadult males and/or infants of either sex. When playing, a juvenile or subadult male can grab or muzzle his partners' genitalia and one or generally both of them develop an erection. The interaction is then classified as homosexual, as well as when infants mount or are mounted.

**MT - Masturbation:** Includes any self-manipulation of penis -oral or manual - which starts in or develops into an erection, with a duration of at least 5 seconds.

**RA - Redirected aggression:** It occurs spontaneously during intense intra- or intertroop agonism. Typically, the recipient of a threat or an aggression threatens or attacks a third animal -who can in turn threaten or attack a fourth animal. It is not necessarily against a member of the same species.

**RS - Resting:** Sitting or lying down completely relaxed or sleeping. The subject is not socially interacting in any active way.

**RV\*- Resting/Vigilant:** The subject is looking around quietly and adult males often adopt the "4 legs up" (Henzi, 1985). It differs from vigilant behaviour (VG) in a quantitative rather than qualitative way.

**SC - Self-Cleaning:** Auto-grooming, scratching or rubbing muzzle or eyes with hand.

**SF - Social Friendly:** Grooming and social play are considered separately. Included in this category are aunting behaviour; reaching to; protecting; seeking for protection; infants inspecting adults' genitalia; mouthing or smelling of other parts of the body between any pair of monkeys. Touching of another animal which does not include grasping, pulling or holding (see Bramblett, 1980). This incorporates the 'hand on head' and 'hand on shoulders' which Struhsaker (1967a) described as behaviours directed towards (the former), or done by (the last) potential groomers. Cohesion and/or progression grunt vocalisations are also classed as social friendly patterns because of their social implications.

**SM - Submission:** Includes the following behavioural patterns: i) Avoiding of another member of the troop -on many occasions one animal avoids another without the latter showing any aggressive behaviour. ii) Spatial, food or grooming displacements. iii) 'Lip-smacking' (Rowell & Hinde, 1963) and/or 'teeth-chattering' which accompany many submissive acts. iv) 'Rapid-glancing' toward and away from the aggressor while running away (Struhsaker, 1967a), which is also used to request coalition from other monkeys against the aggressor. v) 'Gaping' with open mouth without exposing teeth, normally accompanied by crouching and staring (Struhsaker, 1967a). vi) 'Grimacing', when the mouth is approximately one-half open and the lips are retracted exposing the unclenched teeth.

Submissive behaviour may or may not be accompanied by vocalisations: squeal, chatter-squeal, squeal-scream, *waa* or *wa-waa* calls or staring (Struhsaker, 1967c; Henzi, 1982). Finally, walking or running away, often in a crouched posture, and lip-smacking are typical of a submissive retreat.

**SP - Social play:** playing with other members of the same or different age/sex class. This category incorporates wrestling, grabbing at, hopping and jumping about, chasing and counter-chasing.

**TD - Tree Display:** (*sensu* Henzi, 1985) is only done by adult and subadult males. Performed by jumping through trees (or poles in the Cage) in a very confident manner and making a lot of noise. It is the equivalent to the 'bouncing on branches or bushes' (Hall & Gartlan, 1965), 'branch-shaking' (Struhsaker, 1967a) and the 'leaping and crashing' (Harrison, 1983a) that occurs during intertroop territorial displays.

**VG - Vigilant:** Scanning around, while sitting or standing on four legs. Characteristic postures adopted by vigilant males are '4 legs-up' and 'splayleg' in which their genitalia are clearly displayed (Henzi, 1985; see Fig. 2.2). 'Pacing the perimeter' (*sensu* Tollman & Lucas, 1979; see also Rowell & Hinde, 1963), that is running around the perimeter of the Cage while looking intensely outside, is also included in this category.

**WE (\*) - Weaning of Infant:** Varies from mother pushing her own infant away softly to slapping and biting infant away from nipples. It was recorded in the field study in focal animals and scan samples on adult females and in the Cage only in *ad libitum* sampling (no focal samples were done on females).

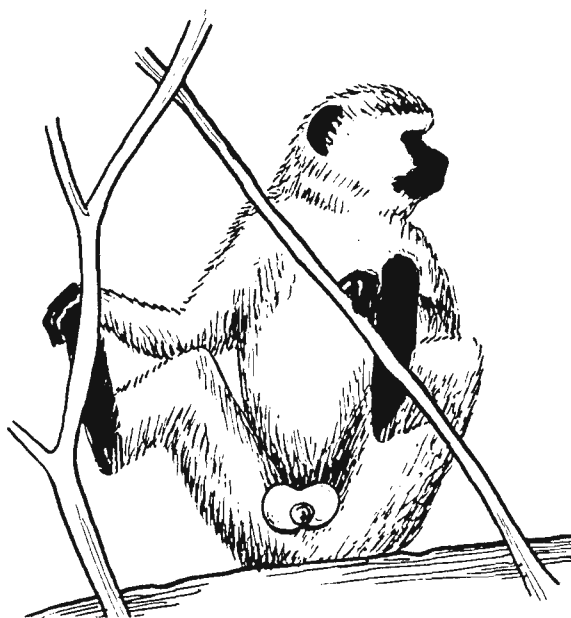


Figure 2.2. Vigilant male adopting the 'splayleg' posture.

### 2.3 DATA COLLECTION

During the study at the Cage troop, written descriptions were used for *ad libitum* sampling, and dictated verbal descriptions were used during continuous focal sampling. Instantaneous sampling was recorded directly onto check sheets (Hinde, 1973) whenever possible. Data collection in the Cage was limited to mornings and early afternoons (8:00 am - 4:00 pm). This was dictated by the times of cleaning and provisioning of food and the time when the gates of the Nursery were closed (Table 2.6; Fig. 2.3).

During the field study in Windy Ridge it was only possible to use verbal descriptions, and a tape recorder was required. In Windy Ridge data collection occurred mainly in the morning and late afternoon. The limitation in this case was the loss of concentration of the observer after a few hours of following the troop in dense vegetation and the difficulty in locating the troop again in the afternoon. The monthly distribution of field and observation time are given (Table 2.7; Fig. 2.3). A total of 1032:45 hours was spent searching for and observing the study troop. Of those, 653:58 hours (63.3%) were spent in visual contact.

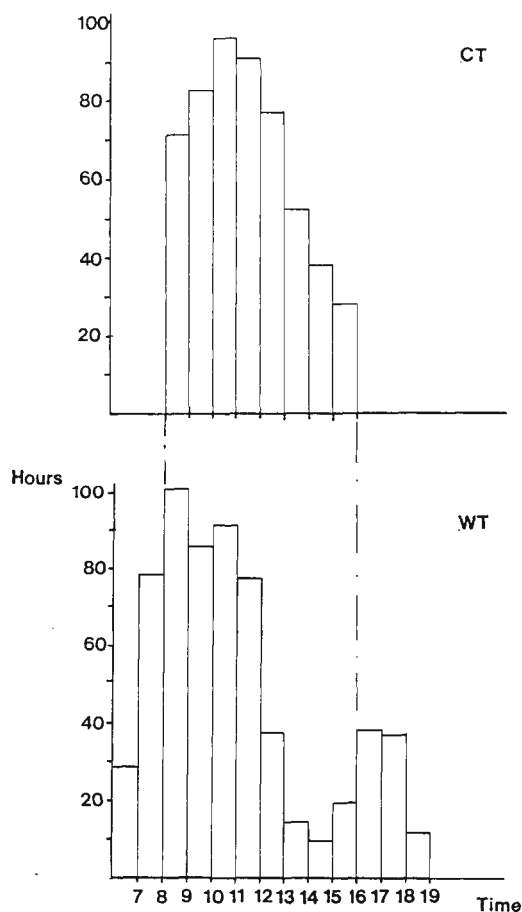


Figure 2.3. Hourly distribution of observation time in the Cage (CT) and Windy Ridge (WT).



Table 2.6. The distribution of total observation minutes in the Cage from which quantitative data has been obtained.

MONTH	HOURLY DISTRIBUTION OF OBSERVATION MINUTES							
	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-16
1985								
September	15	120	450	660	620	50	-	-
October	185	340	385	270	140	70	-	-
November	175	270	535	580	575	85	100	6
1986								
January	-	70	120	135	110	120	-	-
February	515	655	660	480	145	200	150	180
March	480	455	360	227	190	250	210	150
April	425	600	735	770	558	505	400	345
May	690	773	870	755	690	510	345	195
June	685	570	595	405	385	280	285	265
July	625	525	575	695	535	440	285	225
August	55	70	110	30	85	90	60	45
September	315	175	150	105	153	230	185	140
October	235	225	100	110	135	155	210	135
November	145	160	140	185	335	165	90	-
Total	4275	5008	5785	5407	4656	3150	2320	1686

Table 2.7. The distribution of total observation minutes in Windy Ridge Game Park (Zululand) from which quantitative data was obtained.

MONTH	HOURLY DISTRIBUTION OF OBSERVATION MINUTES						
	6-7	7-8	8-9	9-10	10-11	11-12	
1987							
October	170	515	538	690	705	470	
November	230	405	435	410	420	290	
1988							
January	205	555	765	990	1030	815	
February	390	815	680	810	835	735	
March	455	810	615	475	515	520	
April	165	425	850	630	675	555	
May	20	920	1385	655	775	745	
June	-	240	740	455	455	530	
Total	1635	4685	6008	5115	5410	4660	
	12-13	13-14	14-15	15-16	16-17	17-18	18-19
1987							
October	185	-	-	-	190	372	20
November	185	35	102	180	220	325	-
1988							
January	260	70	60	90	150	340	250
February	390	235	160	165	330	430	280
March	375	170	105	110	250	365	155
April	412	205	85	230	370	307	-
May	360	85	50	275	550	40	-
June	250	55	15	105	210	10	-
Total	2417	855	577	1155	2270	2189	705

The criteria used for obtaining data were the following. First, samples were initiated after a time lapse of 10 min after the first visual contact with the study troop. Second, the focal animal was chosen randomly beforehand. Finally, no animal was ever sampled when closer than 5 m. Due to field conditions in Windy Ridge, not all subjects could be sampled as scheduled, as was possible in the Cage.

### **2.3.1. Recognition of individuals**

After the first week of observations in the Cage, all the members were easily identified. This was facilitated by collars or tags on 4 individuals. Other members of the troop were recognisable from old wounds on their ears or by their facial features. After the birth season finished in January 1986, it was also possible to recognise all the newborn infants.

In the field individual adult males were recognised from an early stage of the study, although females and immatures were more wary and kept their distance. Infants were difficult to tell apart and many of the identifications were based on suckling behaviour and long lasting friendly interactions with particular adult females.

### **2.3.2. Seasons considered in this study**

The birth season (B) in Windy Ridge, lasted from the 11th October until the end of November 1987 and corresponded to a period of abundant food. The troop spent lots of time in areas where they were difficult to follow (see also Dunbar & Dunbar, 1988), so the quantity of data for this period is not as high as for the following periods. In the Cage the first birth of an infant was on the 14th of October 1985 and the birth season was considered finished after the 22th of January, 1986. On the following year, the birth season started on the 24th of October 1986 and ended on the 15th of January 1987.

The non-breeding/non-mating season or pre-mating season (N) extended from January until the end of March 1988 in Windy Ridge. Rain was abundant and temperatures were high (Fig. 2.4), food was plentiful except for January. In the Cage it included all the periods between birth and mating season.

The mating season (M) was defined as from the time the first complete heterosexual mounting was observed on the 1st April 1988 to the end of the study (15th June 1988) at Windy Ridge. At the Cage data collected from the 15th of February until the end of August 1986 was included. Food availability is lower than in the two previous seasons (de Moor & Steffens, 1972; Basckin & Krige, 1973) and corresponded to autumn with low temperatures and little rain (Fig. 2.4). As guenon foods are abundant during the wet season and last for 1 to 3 months thereafter (Butynski, 1988), the time when food scarcity is more apparent, corresponded to the months of habituation of the troop when focal and scan samples were not done in Windy Ridge.

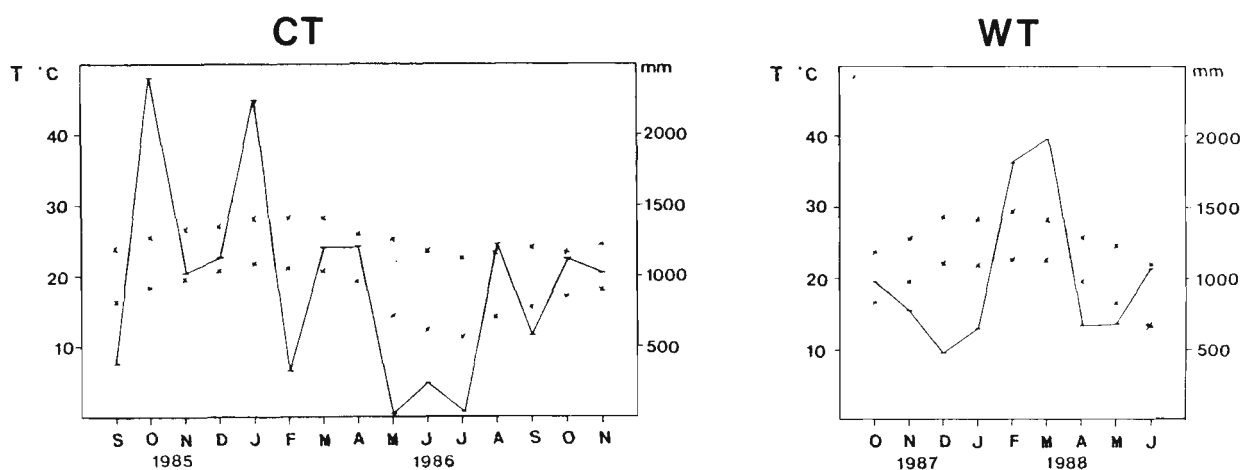


Figure 2.4. Rainfall, minimum and maximum temperature by month during the study period at the Cage (CT) and in Windy Ridge (WT). Data was generously provided by the South African Weather Bureau (Pretoria) and by the Municipality of Richards Bay.

## 2.4. STATISTICAL ANALYSIS

No quantitative analysis was done on the data collected during the habituation of the troop. Each chapter will contain a short reference to the statistics used.

Since the data mostly consisted of proportions or percentages, a chi-square test is used as often as possible. Although this test tends to under-exaggerate the significance of differences, it is better than using parametric tests when the distribution of the data does not follow a normal distribution.

Parametric tests (e.g. the Student's t test) are only applied when the distribution of the variables follow a normal distribution. Normality is tested using the Kolmogorov-Smirnov one-sample test. Otherwise non-parametric tests (Siegel & Castellan, 1988) are used. When scarcity of data prevents the use of any statistical method, plotting of the results facilitates visualising trends.

## 2.5. DESCRIPTION OF THE CAGE TROOP: CT

The Cage was a hemispheric dome (132 m<sup>2</sup> and maximum height of 6.5 m) located in a small man-made clearing in the gardens of the University of Natal. Tollman and Lucas (1979) give a detailed description of the Cage Troop (Fig. 2.5). Increased overt aggression, which is one of the greatest disadvantages of keeping animals in captivity was partly avoided by the geodesic shape of the enclosure and by providing hiding places where the monkeys could conceal themselves. The cement floor had two shallow pools which provided water *ad libitum*. Food was provided daily and consisted of brown bread, boiled eggs, fruits (grapefruit, oranges, apples, avocado pears) and vegetables (pumpkin, maize).

The Cage Troop was established in May 1975 by Tollman and Lucas (Tollman & Lucas, 1979; Tollman, 1981) who introduced eleven monkeys (1 adult male; 5 adult females and 5 immatures). Although the wire mesh of the Cage restricted physical contact with the members of the free-ranging troop inhabiting the surrounding area, intertroop grooming interactions, social play and agonistic interactions were often observed.

Troop composition and demographic changes for the Cage Troop and the free ranging troop which lived in the same area are given and group composition and demographic changes are detailed (Tables 2.8-2.9; Fig. 2.8).

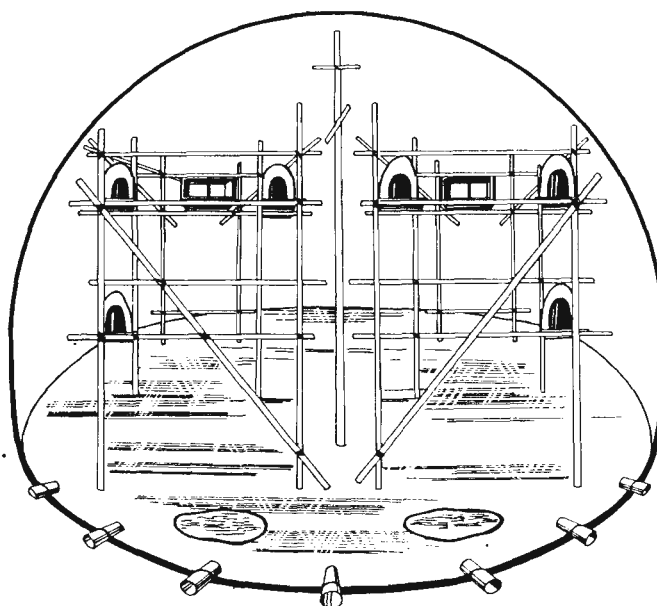


Figure 2.5. The Cage.

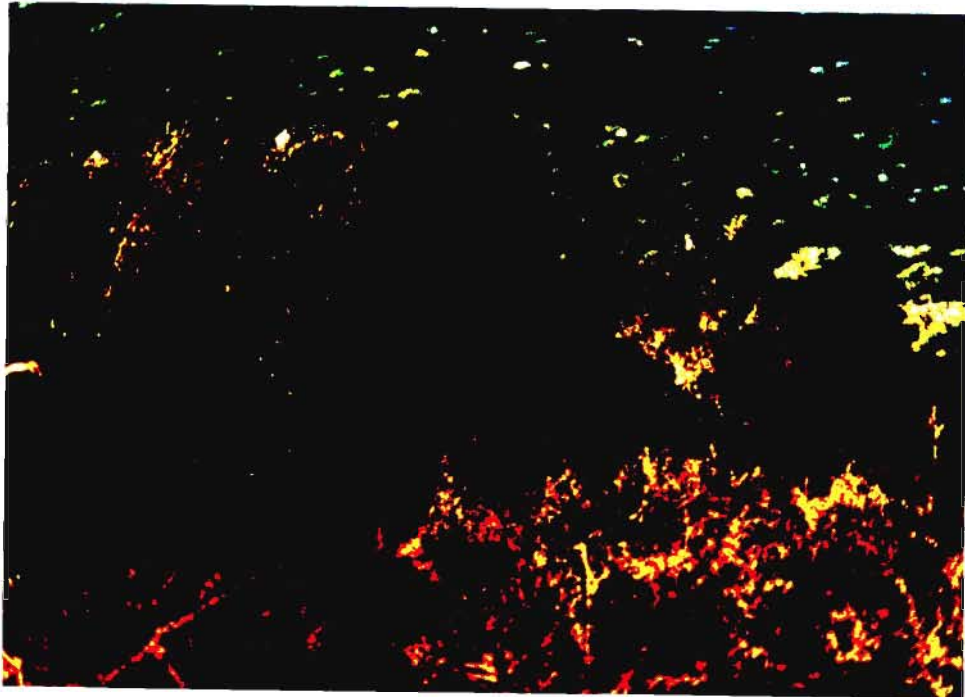


Plate 2.1. General view of the study area in Windy Ridge



Plate 2.2. Riverine bush in Windy Ridge Game Park.

Table 2.8. Membership of the Cage Troop (CT), a) at the beginning of the study period (4th August 1985) and b) at the end of the study (20th May 1987). Males: subadult (3.5-4.5 years old) and adult males (over 4.5 years old); Females: females 2.5 years old and over; Juveniles: females from 1-2.5 years and males from 1-2.5 years of age.

	MALES	FEMALES	JUVENILES	INFANTS
a)	FT GO RN FY LU	XA CE MC BA MY HH	PP PA	PT
	N=5	N=6	N=2	N=1
b)	FT PP PA	XA CE MC BA MY	PT CN MS BN PT	XT CL MG BY
	N=3	N=5	N=4	N=4

Table 2.9

Troop composition of the Altre Troop (AT) that lived in the same area surrounding the Cage at a) the beginning (4th August 1985) and b) the end of the study period (20th May 1987). The rest as for Table 2.8.

	MALES	FEMALES	JUVENILES	INFANTS
a)	MD MO	HT HC HQ HP	SH IZ PO	YY YY YY
	N=2	N=4	N=3	N=3
b)	MB ME MT	HT HC HQ HP IZ	SH PO YY YY YY IT IC IP	TT CC QQ
	N=3	N=5	N=8	N=3

Table 2-10. Demographic changes in the Cage Troop (CT). FF:adult female (>2.5 years); MM: adult male (>4.5 years); SA: subadult male (3.5-4.5 years); JM: juvenile male (1-3.5 years); JF:juvenile female (1-2.5 years); IM: male infant (< 1 year); IF: female infant (<1 year old) and II: infant with sex not determined (see Fig. 2.8).

DATE	EVENT	NAME	CLASS	TOTAL	COMMENTS
10-14-85	BORN	HZ	II	15	HH'S I
10-14-85	DIES	HH	FF	14	HZ'S M
10-14-85	DIES	HZ	II	13	HH'S I
10-28-85	BORN	MS	IM	14	MC'S I
11-11-85	"	XR	IF	15	XA'S I
11-24-85	"	BN	IF	16	BA'S I
11-28-85	"	CN	IF	17	CE'S I
01-22-86	ESCAPES	GO	MM	16	
01-22-86	"	RN	MM	15	
01-22-86	"	LU	MM	14	
01-22-86	"	CE+CN	FF+IF	12	STAYS BY CAGE
01-27-86	CAPTURED	RN	MM	13	WOUNDED
01-31-86	CAPTURED	CE+CN	FF+IF	15	CE WOUNDED
02-17-86	ESCAPES	PA	JM	14	(AT)CHASES
02-17-86	RUNS BACK	PA	JM	15	3' LATER
04-30-86	SUBADULT	PP	SA	15	
04-30-86	"	PA	SA	15	
08-25-86	ESCAPES	RN	MM	14	
08-25-86	"	FY	MM	13	
10-24-86	BORN	CL	IM	14	
10-26-86	"	BY	IM	15	
10-30-86	"	MG	IM	16	
07-01-87±	BORN	XT	IM	17	
05-01-87	MATURES	PP	MM	17	
05-01-87	"	PA	MM	17	

Table 2-11. Demographic changes for the free-ranging troop (AT) (See Table 2.10 and Fig. 2.8).

DATE	EVENT	NAME	CLASS	TOTAL	COMMENTS
10-13-85	BORN	IT	II	13	
10-20-85	"	IC	II	14	
10-03-85	"	IQ	II	15	
10-30-85	"	IP	II	16	
01-27-86	DEAD	IQ	II	15	TOP OF CAGE
02-14-86	SOLITARY	MO	MM	14	
04-23-86	IMMIGRATES	ME	MM	15	
06-18-86	"	MB	MM	16	
09-21-86	BORN	CC	II	17	
09-30-86	EMIGRATES	MD	MM	16	
10-07-86	IMMIGRATES	MT	MM	17	
10-16-86	BORN	TT	II	18	
10-18-86	"	QQ	II	19	
10-30-86	MATURES	IZ	FF	19	





The study group occupied a home range of 101 ha. The vegetation is a mosaic of which 47 ha consists of riverine forest and 54 ha of bushveld (Plates 2.1 and 2.2). Riverine forest borders most of the river and is replaced by bushveld as the gradient rises away from the river (Fig. 2.7a,b). The fact that over twenty ha of their home range was invaded by trifid weed (*Chromolaena odorata*) may have affected the feeding activity of the monkeys.

The Nseleni river, a seasonal river, crosses from south to north through the centre of the study area. In winter 1987 the river was never completely dry; a few pools remained, and in the following winter at least until the end of the study (15th June 1988), there was a permanent, but slight flow of water.

The study group varied in size from 18 to 22 animals, depending on births, deaths and the migration of adult males (Tables 2.12 and 2.13; Fig. 2.8). There were four neighbouring troops with whom they shared common boundaries (Fig. 2.7c).

Two sympatric species of diurnal, non-human primates occur in Windy Ridge Game Park: baboons (*Papio ursinus*) and vervet monkeys (*Cercopithecus aethiops pygerythrus*). The nocturnal thick-tailed bushbaby (*Galago crassicaudatus*) is also found here.

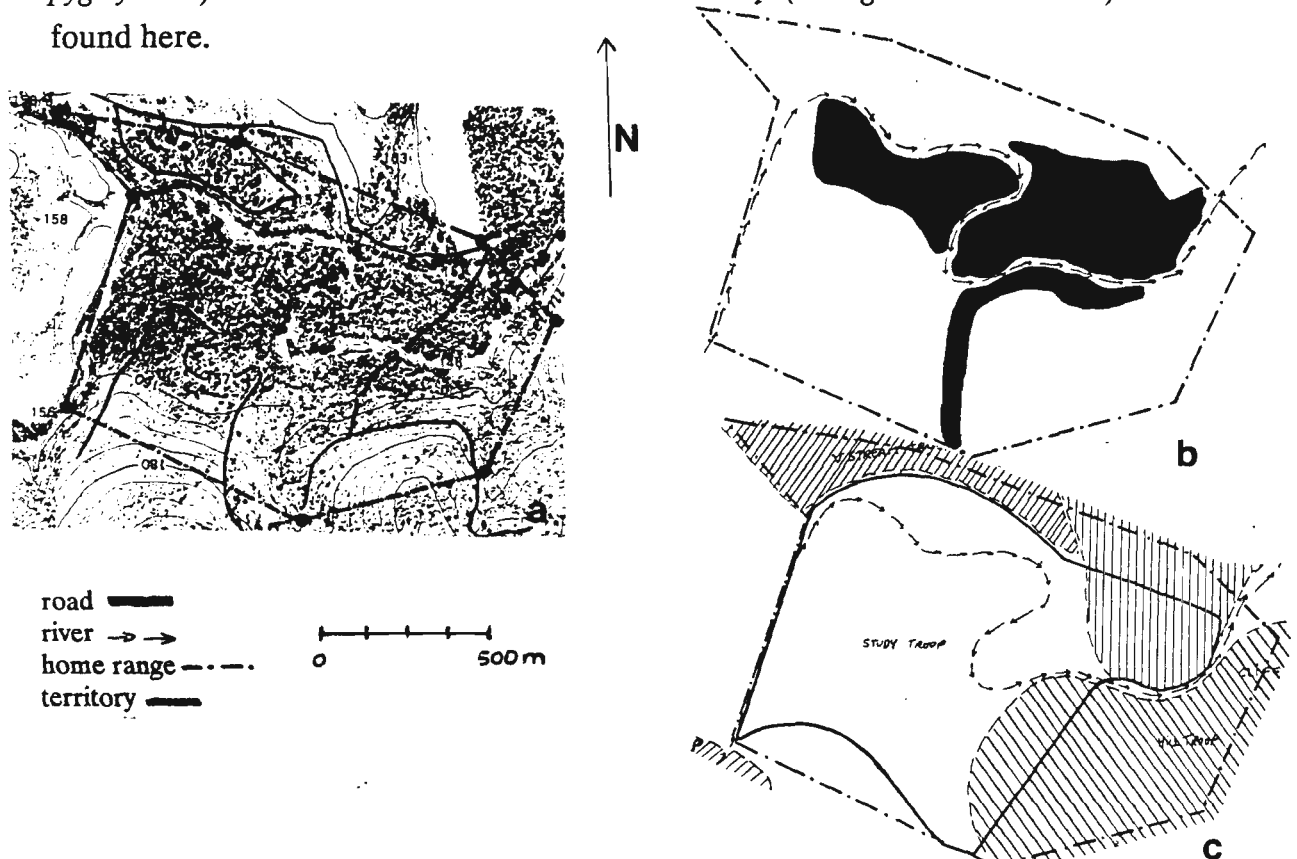


Figure 2.7. Area inhabited by the study troop in Windy Ridge: a) Aerial view, b) distribution of bushveld, and c) home range overlap with neighbouring troops.

Table 2-12.

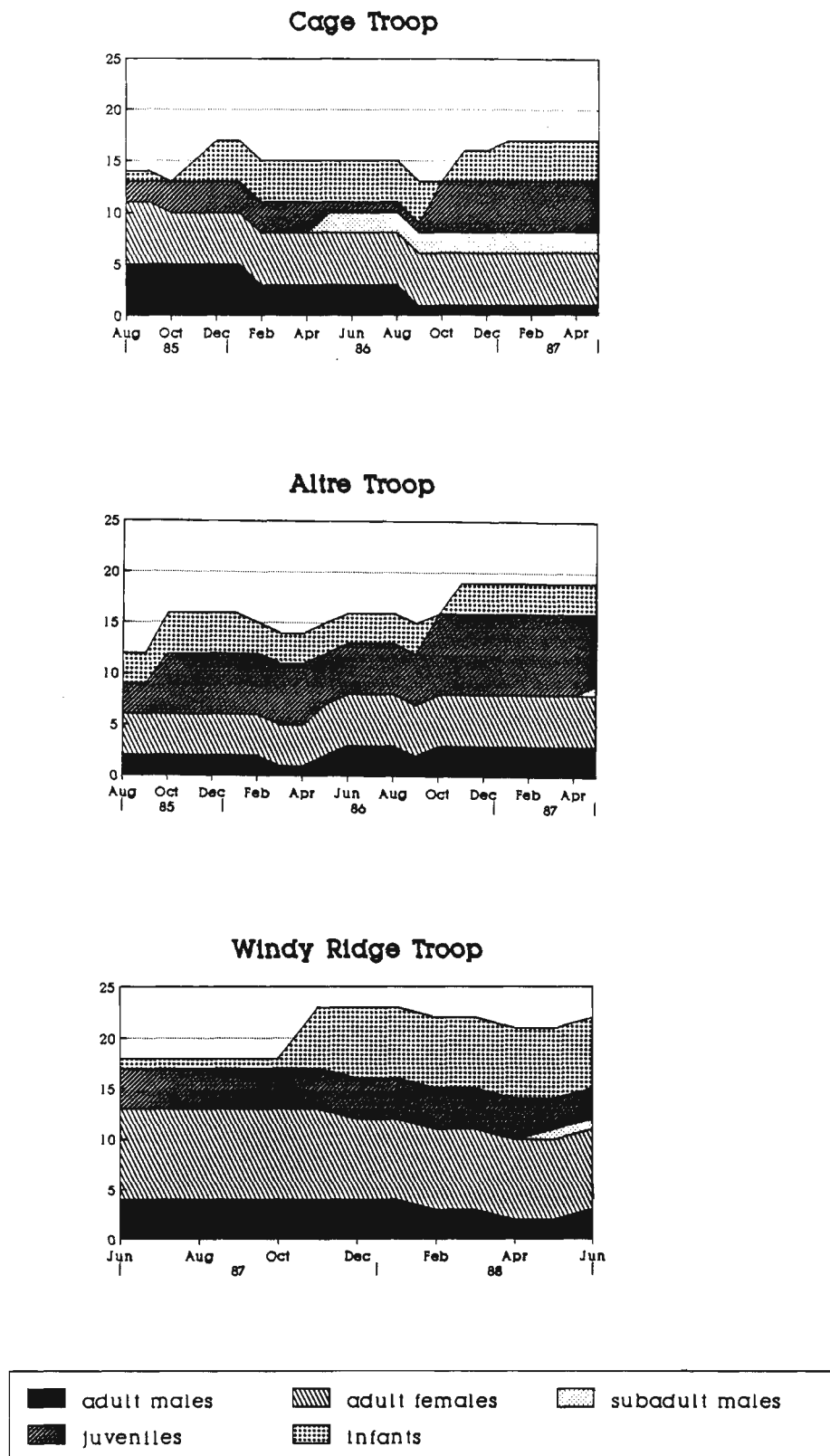
Membership of the study troop in Windy Ridge (WT) at a) the beginning of the study period (1st June 1987), and b) at the end of the study period (15th June 1988) (Note: as it was difficult to distinguish between two juvenile males, the same code was used).

	MALES	FEMALES	JUVENILES	INFANTS
a)	RO LE PE CH	HI MO WE BE ET VE TO SH	TI SM SE SE SI	FE
	N=4	N=8	N=5	N=1
b)	RO LE GR	HI SM MO WE BE ET VE TO	TI SE SE FE	IH IS IM IW IB IE IV
	N=3	N=8	N=4	N=7

Table 2.13

Demographic changes for the Windy Ridge troop (WT). FF: adult female (>2.5 years); MM: adult male (>4.5 years); SA: subadult male (3.5-4.5 years); JM: juvenile male (1-3.5 years); JF: juvenile female (1-2.5 years); and II: infant.

DATE	EVENT	NAME	CLASS	TOTAL	COMMENTS
10-17-87	KILLED	SI	JM	17	BY EAGLE
10-19-87	BORN	IM	II	18	MO'S I
10-30-87	"	IB	II	19	BE'S I
10-31-87	"	IW	II	20	WE'S I
11-03-87	"	IV	II	21	VE'S I
11-08-87	"	IE	II	22	ET'S I
11-15-87	"	IH	II	23	HI'S I
11-17-87	"	IS	II	24	SM'S I
11-17-87	KILLED	SH	FF	23	BY MAMMAL
01-26-88	EMIGRATES	CH	MM	22	
03-20-88	"	PE	MM	21	
04-30-88	SUBADULT	TI	SA	21	
05-06-88	IMMIGRATES	GR	MM	22	



**Figure 2.8**  
Demographic changes in the Cage Troop, Altre troop and Windy Ridge troop over the study period.

### 3. TIME BUDGETING

It has been argued that vervet monkeys behave more as uni-male or age-graded than as multi-male species (Henzi, 1985; Clutton-Brock, 1989). Taking into account that variables in the habitat may influence primate social structure more than single species traits (Lee, 1984), vervet society has to be understood as a result of environmental conditions that regulate social structure (see Eisenberg, *et al*, 1972).

Social structure must be understood in terms of social relationships, and those described in terms of social interactions (Hinde, 1983). As social behaviour is part of a larger time allocation problem, time spent in social interactions can therefore be dependent on the time available after completing other vital maintenance activities, i.e. feeding, resting and locomotion.

Altmann's (1980) model for yellow baboons predicts that an increase in time budget dedicated to feeding affects time spent socialising by females. This model assumes that female feeding activity increases with the age of the infant apart from a decrease in the quality of the food. However, Dunbar & Dunbar (1988) in their study on gelada baboons conclude that social time is conserved as far as possible and it is resting time that is mostly affected by an increase in time feeding when infants become more independent. When environmental conditions become severe, feeding time increases and time socialising is affected, though the 'most valuable grooming relationships' remain. As a corollary, the Dunbars suggest that lactation might be terminated because of the need to maintain social relationships which would increase the mother's future reproduction.

The importance of maintaining social time in geladas can be explained by the harsh environment they inhabit and by the importance of grooming as source of agonistic coalition from female relatives (Dunbar, 1984). Harrison (1983b) points out that green monkey females choose a low energy strategy during lactation, and a decrease in feeding time does not correspond to an increase in social time, but to more time resting.

Similarly, the importance of maintaining low metabolic levels during harsh conditions is emphasised by Lee's (1983) findings that vervets spend less time involved in energetically expensive forms of socialisation during the dry season.

Males and females tend to be more aggressive and receive more wounds during the breeding season, which may be explained as a consequence of mate competition rather than directly related to changes in hormonal levels (*e.g.* Walker, *et al.* 1983; Gordon *et al.* 1979) or to food shortages (Dittus, 1980).

The question that arises is whether males arrange their budgets to their advantage or whether their social activity and time spent in antagonistic behaviours have negative consequences in other areas. It is suggested that when male participation in vigilance and/or antagonistic behaviours increases, males should be more selective in their relationships, interacting with certain individuals that are more important to them and not with others, as has been suggested for female geladas (Dunbar & Dunbar, 1988).

On the one hand, male-female desynchronisation during feeding and locomotion could enhance the efficiency of resource utilisation, reduce food competition and provide other benefits (*e.g.* increased vigilance levels: see chapter 4). On the other hand, social desynchronisation could disturb social integration (see Regal & Connolly, 1980).

The frequency of friendly behaviours seems, *a priori*, more related to time available than do activities of an antagonistic nature. At the same time antagonistic interactions are related to food and mate competition, and are unavoidable in maintaining group structure. It is predicted that the activities of the males may reflect a higher investment in the acquisition and maintenance of social status than females, precisely because their dominance hierarchy is less stable (see chapter 1).

The main issues that will be considered in this chapter are summarised here. First, the differences in male and female time budgeting. Second, the influence of rank in male time budgeting. Third, the seasonal effects on maintenance and social activities. Fourth, the main constraints in the distribution of social time for males and females. Fifth, whether there is an overlap in male-female activity rhythms. Finally, as feeding in provisioned or captive troops is less time consuming, it is expected that the monkeys in the Cage Troop could socialise more than in free-ranging conditions.

In the group of antagonistic behaviours (AGO) it is possible to differentiate three subgroups:

1. Aggressive behaviours are those behaviours that involve: i) actual fighting or a high tendency to attack (AG), ii) spatial, food, partner and grooming displacements, and defensive threats (MA), iii) agonistic coalition of two or more animals against the focal animal including support to the aggressor or to the recipient of the aggression (CO), iv) redirected aggression (RA), v) interference during agonism (IN). This last category, which has the effect of neutralising ongoing agonism without apparent 'taking sides', leads to the next subgroup because it implies the power of the subject to stop an ongoing agonistic interaction without overt aggression. It is suggested that it works via visual signalling, as the posture adopted emphasises the white chest and displays the male's genitalia (see chapter 6).

2. Displays of dominance. Tree display (Henzi, 1985), herding behaviour (HR), confident walk (Struhsaker, 1967a) and Red-White and Blue display (Struhsaker, 1967a, also includes the broadside: Henzi, 1985). Only the first mentioned is not exclusively directed to members of the same group. As the actor in these displays is always a male, this subgroup will be studied in detail in chapter 5.

3. Displays of subordination. These can be classified in order of decreasing intensity. They can be initiated by the lower ranking animal (homage: Henzi, 1982; 1985); as a response to a displaying male or a threatening animal, or to its sole proximity (submission) or avoidance. The subordinate animal often lipsmacks while carrying out the above patterns of behaviour (Rowell, 1971).

### *Methods of analysis*

Individual activity budgets of the main maintenance activities (*i.e.* feeding, resting and locomotion), affiliative interactions and antagonistic behaviours (aggression, submission and dominance displays) are calculated as the percentage of scan samples in which a particular behaviour or group of behaviours were observed during each month.

To test for differences in monthly time budgeting (female *versus* male), Student's *t* test (two-tailed) is used when the distribution of the data was consistent with the fitted normal distribution. The distribution fitting is tested with the Kolmogorov-Smirnov one-sample test, with a limit set at  $p < 0.05$ .

When the variable does not follow a normal distribution, a less powerful non-parametric test, the Kolmogorov-Smirnov two-sample test is applied. In addition, sampling at set intervals gives an estimate of the total time spent in any given activity (Altmann, 1974).

Chi-square tests are applied to test for seasonal and individual differences in time budgeting, and to determine the effects of caging on the distribution of time (number of scans for a specific activity related to the number of scans when other activities were recorded). When significant differences are found in individual proportions of time spent performing a specific activity, the influence of rank is tested with the Spearman rank correlation test.

The rank order for the adult animals is determined by the outcome of agonistic interactions for each pair of the same sex. Both focal and *ad libitum* data are used to determine the direction of dominance, the advantage of this being that many dyads without any or with a few focal data are included in the sample.

The dominance order for adult males in Windy Ridge troop was in decreasing rank: RO>LE>PE>CH during the non-mating period and RO>LE>GR for the end of the mating season (Appendix A). For adult females it was: HI>SM>MO>BE>WE>TO>VE>ET (TO: post-reproductive and SM: nulliparous) (Appendix B). Reversals in the matrix obtained for adult males were uncommon and a clear linear hierarchy is reflected. For adult females the trend was the same. In the case of SM, the only primiparous female of the group, reversals were expected (Horrocks & Hunte, 1983b).

In the Cage Troop, dominance rank among males was not as stable as it was in the Windy Ridge troop (Appendix C); among males FT was dominant to both RN and FY. The subadult male PP was dominant to the other subadult PA and to some of the adult males during the mating season. Female rank order was: XA>CE>PT>MC>MY>BA (MY:post-reproductive and PT: nulliparous) (Appendix D).

Stepwise multiple regression analysis is used to assess the effects of variations in time budget dedicated to maintenance activities and social behaviours for adult males and females. The dependent variables are: the proportion of time spent in other maintenance activities, vigilant, social friendly, agonism, month number (1-9), time spent in marginal locations (peripheral or exposed on top of the canopy) and on the ground. All the variables that enter the model do so with a significance level of  $p < 0.05$ .

Sexual differences in the median values of the proportion of time adult males and females spent every month (within each season) in each activity, are tested with the Mann Whitney U-test (two-tailed with probability set at 0.05).

Diurnal rhythms of the major activities are plotted and confidence limits used to visualise sex differences. The presence of activity peaks for each activity during each season are determined using Chi-square tests.

### 3.1. DISTRIBUTION OF MAINTENANCE ACTIVITIES

In this section differences in the monthly proportion of scans for adult males and females of the Windy Ridge troop, involved in major maintenance activities such as feeding, resting and moving are analysed. A comparison with time budget dedicated to these activities by the adult males of the caged troop is included. Finally, differences between adult and subadult males in the Cage are reported.

#### 3.1.1. Gender differences in Windy Ridge troop

Table 3.1

Median values of the proportion of time free-ranging adult males (M) and females (F) spent every month in different activities during the birth (B), pre-mating (N) and mating (M) seasons. Significant differences are indicated by \* ( $p < 0.05$ ) and \*\* ( $p < 0.001$ ).

BEHAVIOUR	SEASON		
	B M/F	N M/F	M M/F
Feeding	25.3/25.5	19.8/29.1*	18.9/41.7**
Resting	26.3/32.3	19.3/23.4*	3.1/10.0
Locomotion	13.4/16.9	17.1/20.5	21.9/14.1*
Grooming	4.3/10.3*	2.3/10.2**	2.5/10.3**
Other social	7.8/16.2	3.6/11.0**	2.8/9.8*
Antagonism	3.1/3.0	4.0/2.4*	6.0/0.8**



### Feeding

Females spent significantly more time feeding than males ( $t=-3.692$ ;  $p<0.001$ ) (Fig. 3.1). However, during the birth season males and females fed for the same amount of time (Table 3.1). After performing the stepwise multiple regression analysis it was possible to conclude that a decrease in time feeding for males was correlated with a major participation in agonistic encounters ( $b=-1.26$ ;  $t=-2.85$ ) more than with any of the other dependent variables ( $F=8.127$ ; 23 df;  $p<0.001$ ). For females however, resting ( $b=-0.60$ ;  $t=-12.05$ ), social friendly ( $b=-0.61$ ;  $t=-8.3$ ) and locomotion ( $b=-0.60$ ;  $t=-7.3$ ) affected feeding time the most ( $F=93.99$ ; 60 df;  $p<0.001$ ).

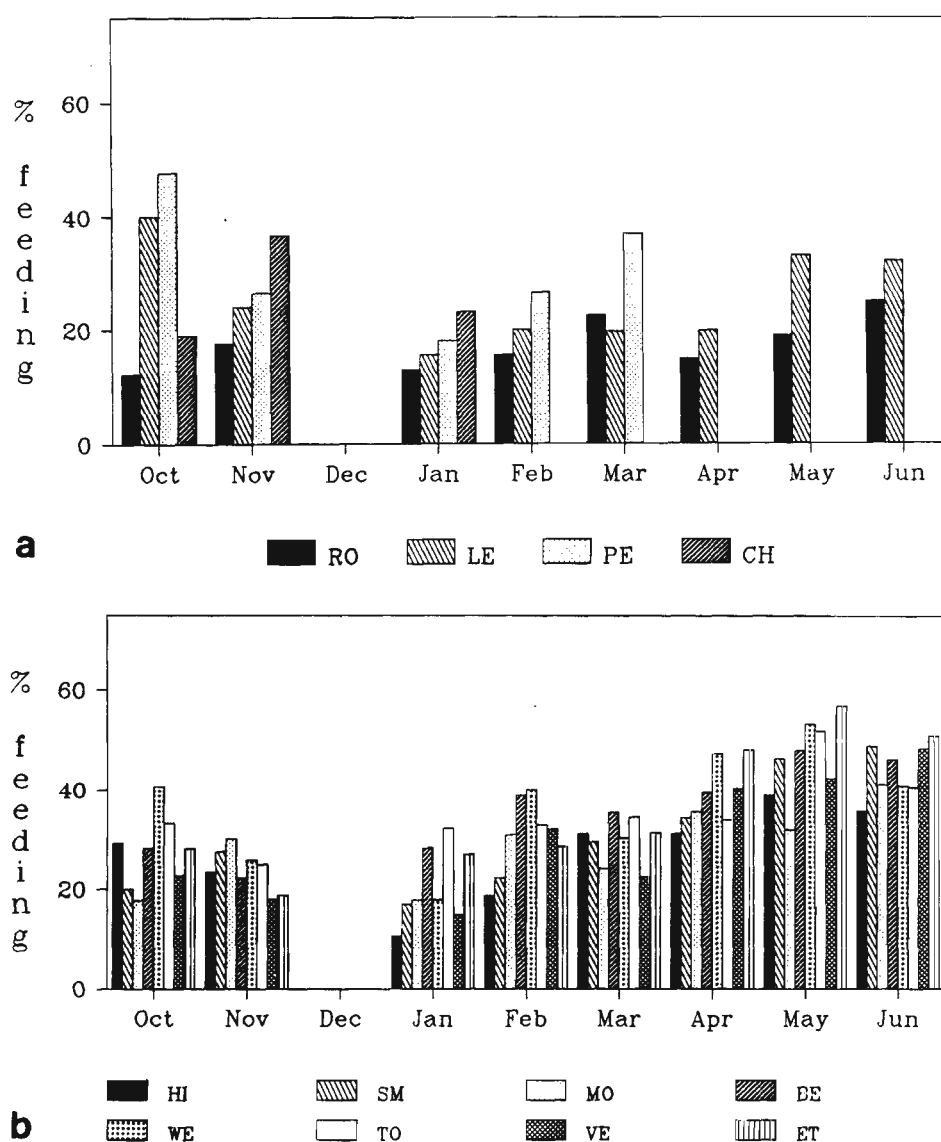


Figure 3.1. Monthly time budget spent feeding by: a) adult males and b) adult females of the Windy Ridge troop. No data were collected in December.

### Resting

In general, males and females spent comparable times resting ( $t=-0.839$ ;  $p=0.4$ ) (Fig. 3.2). It was only during the pre-mating season that females rested significantly more than males (Table 3.1). For males, locomotion ( $b=-1.14$ ;  $t=-6.65$ ), vigilance ( $b=-0.66$ ;  $t=-6.17$ ) and feeding ( $b=-0.69$ ;  $t=-6.78$ ) activities increased when males rested less, and a tendency to rest less became apparent as the study progressed, that is from the birth into the mating season ( $b=-1.21$ ;  $t=-3.9$ ) ( $F=35.332$ ; 19 df;  $p<0.001$ ). By contrast, for females, friendly behaviours correlated with resting ( $b=-0.67$ ;  $t=-6.71$ ), month number ( $b=-1.78$ ;  $t=-5.33$ ) and time spent peripheral ( $b=-1.1$ ;  $t=-2.84$ ) ( $F=57.897$ ; 58 df;  $p<0.001$ ).

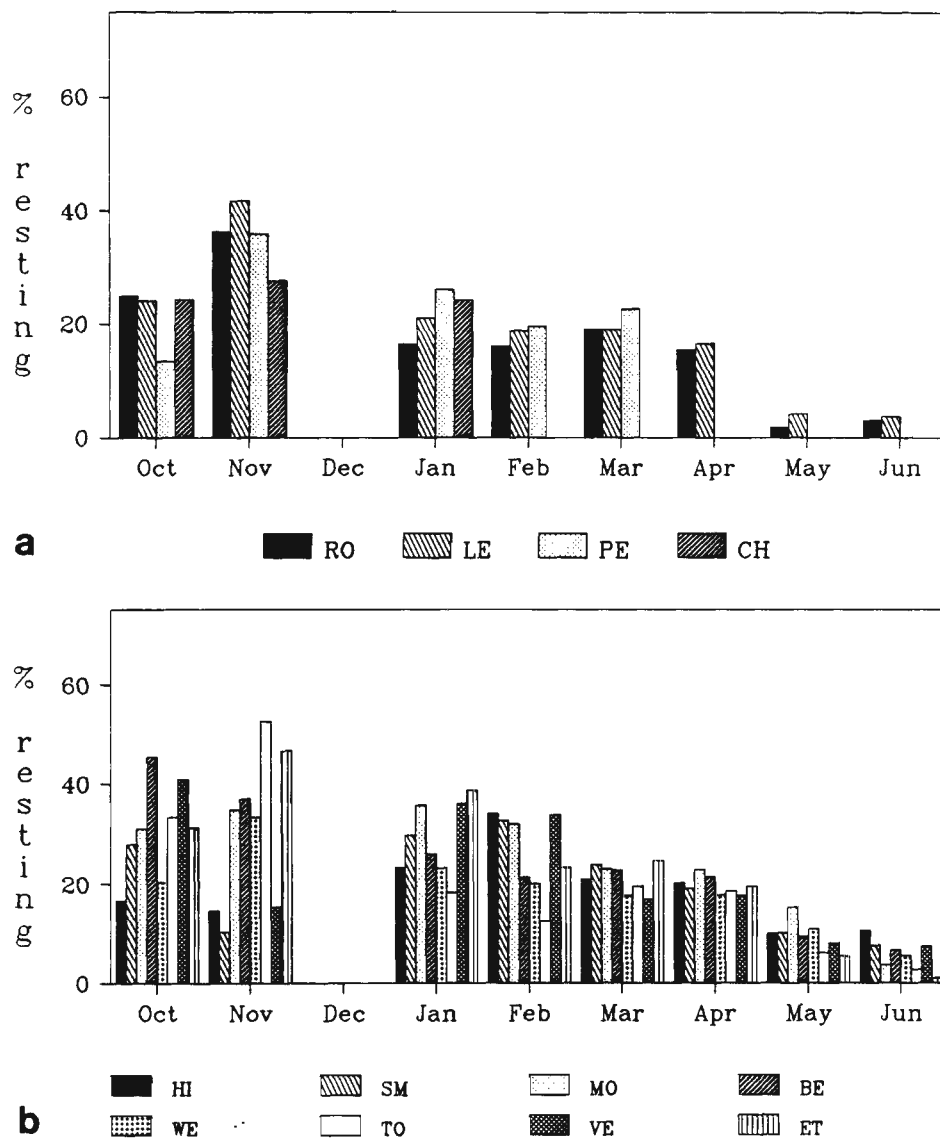


Figure 3.2. Monthly time budget spent resting by: a) adult males and b) adult females of the Windy Ridge troop.

### Locomotion

In general, locomotor activity did not differ for males and females ( $t=0.772$ ;  $p=0.44$ ), although during the mating season, males were more mobile than females (Table 3.1; Fig. 3.3).

For males only, resting ( $b=-0.45$ ;  $t=-4.83$ ), feeding ( $b=-0.38$ ;  $t=-4.27$ ) and vigilance ( $b=-0.42$ ;  $t=-3.49$ ) affected time moving ( $F=9.890$ ; 21 df;  $p<0.001$ ). For females, higher levels of locomotion occurred when they rested ( $b=-0.67$ ;  $t=-7.77$ ) and fed ( $b=-0.70$ ;  $t=-7.00$ ) less. They moved less during the birth season and more as the mating season approached ( $b=-1.18$ ;  $t=-3.37$ ). Moreover, time spent peripheral ( $b=-0.86$ ;  $t=-2.31$ ) was also negatively correlated with locomotion ( $F=17.128$ ; 58 df;

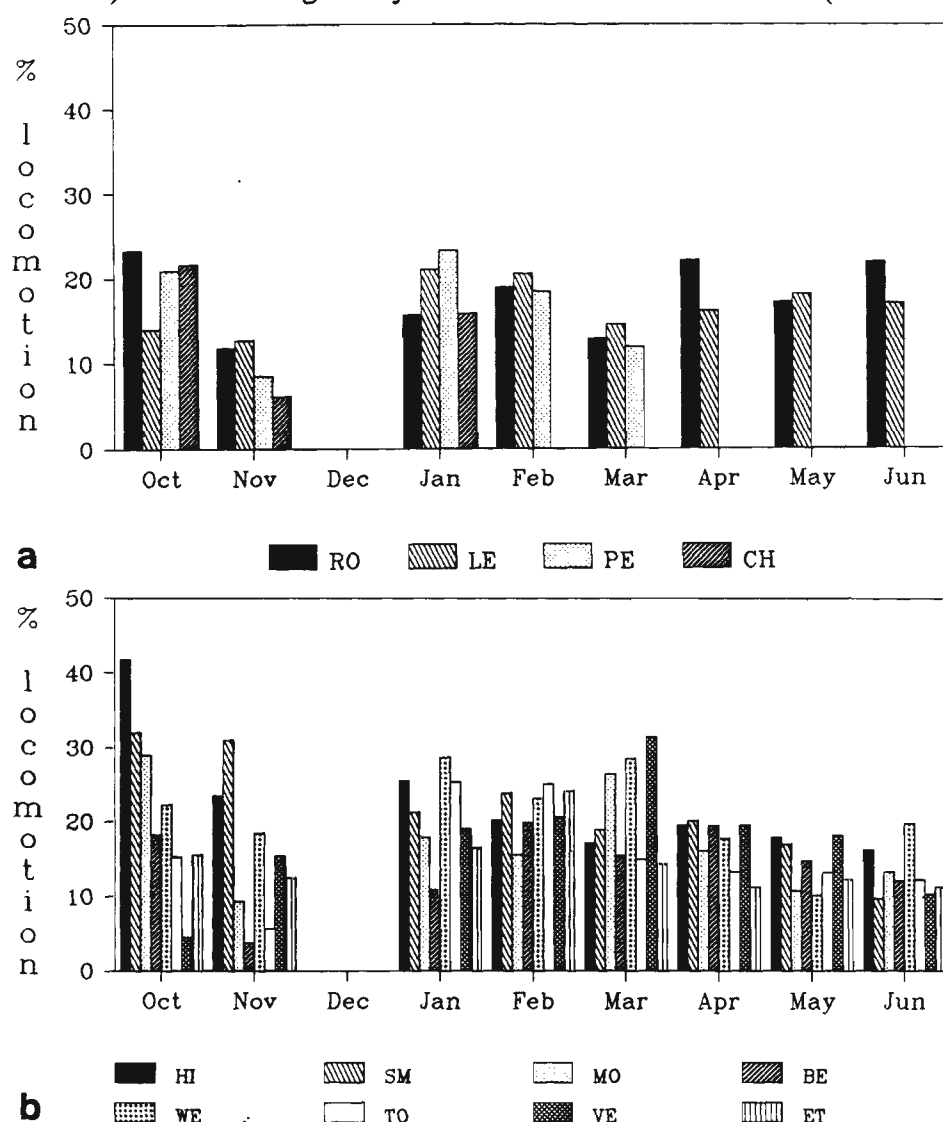


Figure 3.3. Monthly proportion of time spent in locomotion by: a) adult males and b) adult females of the Windy Ridge troop.

### **3.1.2. The influence of caging on maintenance activities**

The proportion of time males spent feeding ( $X^2=72.24$ ; 1 df;  $p<0.001$ ) and moving ( $X^2=75.82$ ; 1 df;  $p<0.001$ ) was significantly higher for the Windy Ridge troop (22.1% and 17.2% respectively) than for the Cage troop (11.8% and 7.7% respectively) as expected.

Alternatively, resting ( $X^2=109.32$ ; 1df;  $p<0.001$ ) and vigilance ( $X^2=18.40$ ; 1 df;  $p<0.001$ ) occupied a higher proportion of time budget for the captive troop (30.6% and 25.1% respectively) than for the wild troop (17.3% and 19.6% respectively).

### **3.1.3. Adult and sub-adult male differences in the Cage**

Age differences affected the amount of time captive males spent feeding during the pre-mating and mating seasons. During these seasons subadult males fed for longer periods than adult males. It was only during the mating season that adult males showed higher values for resting than subadults. Adult males were always more mobile than younger males in the cage troop. Higher levels of vigilance were only shown by adults during the mating season (Table 3.2).

For social behaviours, during the non-mating and mating period the subadults were more involved than adult males in other affiliative behaviour (SP+SF). However, grooming did not differ between age classes. Adult males were more aggressive than subadult males during the non-mating season. Submissive behaviours (homage included) were more common for adult than subadult males during the entire study (Table 3.2). Subadult males were only observed paying homage during *ad libitum* sampling.

**Table 3.2**

Proportion of time spent in different activities by adult (M) and subadult (SA) males of the Cage Troop. Age differences were calculated using Chi-squared tests with Yates correction (the rest as for Table 3.1).

BEHAVIOUR	B M/SA	N M/SA	M M/SA
Feeding	12.9/15.6	10.7/20.0**	12.2/20.0**
Resting	37.1/34.1	35.5/28.7	26.5/21.0 *
Locomotion	8.2/4.4**	8.2/4.3**	7.3/3.3 *
Grooming	4.7/2.2	8.0/7.0	4.3/6.4
Other social		(B+N) 3.8/8.0**	2.7/8.7**
Submission		(B+N) 2.4/0.5 *	2.9/1.0 *
Aggression		(B+N) 2.7/0.3 *	0.7/0.9

### **3.1.4. Seasonal changes for free-ranging males**

Seasonal effects in male time budget in the Windy Ridge troop are presented in this section.

#### *Feeding*

The top ranking male (RO) did not show any seasonal changes in time spent feeding ( $X^2 = 1.467$ ; 2 df; NS). The subordinate (LE) spent less time feeding during the pre-mating season (B/N/M:  $X^2 = 15.932$ ; 2df;  $p < 0.001$ ; see Table 3.3 and Fig. 3.1). This was a period when LE's time budget dedicated to feeding did not differ from RO's ( $X^2 = 0.46$ ; 1 df; NS). Like LE, the subordinate male PE spent less time feeding during the pre-mating season ( $X^2 = 4.690$ ; 1df;  $p < 0.001$ ), although PE showed a peak before he left the troop (Fig. 3.1a). The young male who emigrated at the end of January failed to show any significant differences during the time he was in the troop ( $X^2 = 1.672$ ; 1df; NS). Overall, males did not show seasonal differences in time feeding. In contrast, female feeding activity increased from birth through to the mating season (Table 3.4).

#### *Resting*

A significant reduction in resting time for both RO ( $X^2 = 73.630$ ; 2df;  $p < 0.001$ ) and LE ( $X^2 = 55.980$ ; 2df;  $p < 0.001$ ) between the birth and the mating season was partly correlated with an increase in time spent vigilant for the same period (see chapter 4). However, no differences in time spent resting between the birth and the pre-mating season were found for the other two males that emigrated, PE ( $X^2 = 1.296$ ; 1df; NS) and CH ( $X^2 = 0.07$ ; 1df; NS).

Males in general spent more time resting during the birth season than during any other season, while females showed a progressive reduction in resting activity from the birth season to the mating season (see Table 3.4).

#### *Locomotion*

Time spent locomoting remained roughly the same throughout the study period for the two resident males RO ( $X^2 = 3.973$ ; 2df; NS) and LE ( $X^2 = 3.155$ ; 2df; NS) and for the migrant males PE ( $X^2 = 2.800$ ; 1df; NS) and CH ( $X^2 = 1.035$ ; 1df; NS) (Table 3.1).

The significance obtained when the total number of observations for males was grouped together shows that males were more mobile during the mating than during the birth season. This cannot be explained in terms of searching for food because female locomotor activity during the breeding season was: i) lowest for most of the subordinate females (Spearman rank correlation test:  $r_s = -0.29$ ; 8 df;  $p = 0.02$ ) and ii) less common during the mating season (see Table 3.4). The possibility that males were searching for a specific kind of food could not be excluded. However an alternative explanation might be that they were patrolling their territory; possibly searching for, or preventing other males from approaching receptive females.

For females, seasonal differences in locomotion could result from the presence of young infants moving away from their mothers, and females maintaining proximity to them; that is during the non birth-non mating season (see Table 3.4).

Table 3.3

Total number of scans for each season (B:birth; N:pre-mating and M:mating) and the proportion of time the different adult males (RO, LE, PE, CH, GR) of the Windy Ridge troop (WT) were either feeding (FE), resting (RS) or locomoting (LO). When significant seasonal differences in a particular activity by a male could be tested, they were calculated using the Chi-square test and significant differences are indicated by \* ( $p < 0.05$ ) and \*\* ( $p < 0.001$ ) or NS when not significant. The degrees of freedom ranged from 1 (Yates correction was applied) to 2 (for RO, LE).

MALE	SEASON	SCANS	ACTIVITY		
			FE	RS	LO
RO	B	176	15.3	31.3	15.3
	N	562	16.7	17.1	16.0
	M	663	18.7	7.1	19.9
			NS	**	NS
LE	B	130	30.0	34.6	12.3
	N	575	18.4	19.5	18.8
	M	539	27.5	9.1	17.1
			**	**	NS
PE	B	173	34.7	27.2	12.7
	N	420	25.5	22.4	18.8
			*	NS	
CH	B	135	31.9	26.7	10.4
	N	95	23.2	24.2	15.8
			NS	NS	
GR	M	26	15.4	7.7	19.2

Table 3.4.

Median and standard deviation for the adult males and adult females of the free-ranging troop during the birth (B), pre-mating (N) and mating season (M) for the proportion of time spent feeding, resting and locomotion. Significant seasonal differences were determined using the Wilcoxon signed rank test (z) with a probability set at  $p < 0.05$ . Significant differences are indicated.

		Feeding	Resting	Locomotion
Males	B	25.3 $\pm$ 12.3	26.3 $\pm$ 9.0	13.4 $\pm$ 6.4
	N	19.8 $\pm$ 6.9	19.3 $\pm$ 3.2	17.1 $\pm$ 3.7
	M	18.9 $\pm$ 5.1	3.1 $\pm$ 7.4	21.9 $\pm$ 2.8
		B = N = M	B > N = M	B < M
Females	B	25.5 $\pm$ 6.1	32.3 $\pm$ 12.5	16.9 $\pm$ 10.8
	N	29.1 $\pm$ 7.8	23.4 $\pm$ 7.1	20.5 $\pm$ 5.2
	M	41.7 $\pm$ 7.1	10.0 $\pm$ 6.6	14.1 $\pm$ 3.6
		B < N < M	B > N > M	N > M

### 3.1.5. Seasonal changes for captive males

The only seasonal effects observed in time budgeting of maintenance activities for the caged males were for the lowest (FY) and the middle (RN) ranking (Table 3.5). FY spent less time resting during the mating season (B/N:  $X^2 = 0.35$ ; 1 df; NS and N/M:  $X^2 = 5.36$ ; 1 df;  $p < 0.05$ ). This decrease in time resting for the mating season, seems related to the higher levels of 'pacing the perimeter' which was considered as vigilance (B/N/M:  $X^2 = 13.99$ ; 2df;  $p = 0.001$ ; and N/M:  $X^2 = 13.00$ ; 1df;  $p < 0.001$ ) (see chapter 4).

### 3.1.6. Male individual differences

#### *Feeding*

An analysis of individual differences reveals on the one hand, that the alpha male of the Windy Ridge troop was the male who always spent less time feeding (B: all males  $X^2 = 19.21$ ; 3 df;  $p < 0.001$ ; N:  $X^2 = 13.144$ ; 3 df;  $p < 0.05$  and M:  $X^2 = 13.846$ ; 2 df;  $p < 0.001$ ). On the other hand, no differences among additional males were found (B:  $X^2 = 0.77$ ; 2 df; NS; during M: LE/GR:  $X^2 = 1.276$ ; 1 df; NS), the exception was again during the pre-mating season, when LE fed less often than the other two subordinate males who left the troop at that time.

In the captive troop, all the males spent a similar time feeding (B:  $X^2=1.679$ ; 4 df; NS; N:  $X^2=7.537$ ; 4 df; NS and for M:  $X^2=1.032$ ; 2 df; NS).

### *Resting*

In Windy Ridge all the males spent a similar proportion of time budget resting (B:  $X^2=2.824$ ; 3 df; NS; N:  $X^2=5.528$ ; 3 df; NS; and for M:  $X^2=1.626$ ; 2 df; NS).

However, the two highest ranking males (FT and GO) of the captive group rested less than the subordinate males (FT+GO/RN+FY+LU:  $X^2=4.484$ ; 1 df;  $p<0.05$ ) during the pre-mating season, *i.e.* during the period of greatest social instability.

Table 3.5

Total number of scans for each season (B:birth; N:non-birth/non-mating and M:mating) and proportion of scans in which the different adult males (FT, RN, FY, GO, LU) of the Cage troop (CT) were found involved in any of the major maintenance activities (FE: feeding; RS: resting; or LO: locomotion) (see Table 3.3).

NAME	SEASON	SCANS	ACTIVITY		
			FE	RS	LO
FT	B	78	15.4	34.6	3.8
	N	170	11.9	28.2	7.1
	M	294	11.9	28.2	7.1
			NS	NS	NS
RN	B	26	15.4	38.5	19.2
	N	92	7.6	38.0	9.8
	M	267	10.9	27.3	9.4
			NS	NS	NS
FY	B	16	12.5	25.0	18.8
	N	105	16.2	36.2	4.8
	M	278	13.7	23.7	5.4
			NS	*	
GO	B	22	9.1	31.8	4.5
	N	64	15.6	26.6	7.8
			NS	NS	
LU	B	28	7.1	53.6	7.1
	N	54	7.4	51.9	18.5



### *Locomotion*

In the free-ranging troop locomotion figures were the same for all the males irrespective of season (B:  $X^2=1.751$ ; 3 df; NS; N:  $X^2=2.154$ ; 3 df; NS and for M:  $X^2=1.588$ ; 2 df; NS). In the cage troop, subordinate males were more mobile than the two higher ranking males during the birth season (FT+GO/RN+FY+LU:  $X^2=4.484$ ; 1 df;  $p<0.05$  when those two males who remained a short period in the troop were excluded, FT/RN+FY:  $X^2=5.861$ ; 1df; $p<0.05$ ). However, no differences were found for the pre-mating (FT+GO/RN+FY+LU for N:  $X^2=0.228$ ; 1 df; NS) and for the mating season ( $X^2=3.190$ ; 2 df; NS).

## **3.2. SOCIAL BEHAVIOUR**

A stepwise multiple regression analysis was used to assess the relative influence of time dedicated to maintenance activities, time spent in marginal positions (exposed on top of the canopy; no other monkeys within 50 m) and month number (1 for October and 9 for June) to explain an individual's level of socialisation and agonism. All the data presented in this section, as in the previous ones, was collected using scan (at WT) or instantaneous (at CT) sampling.

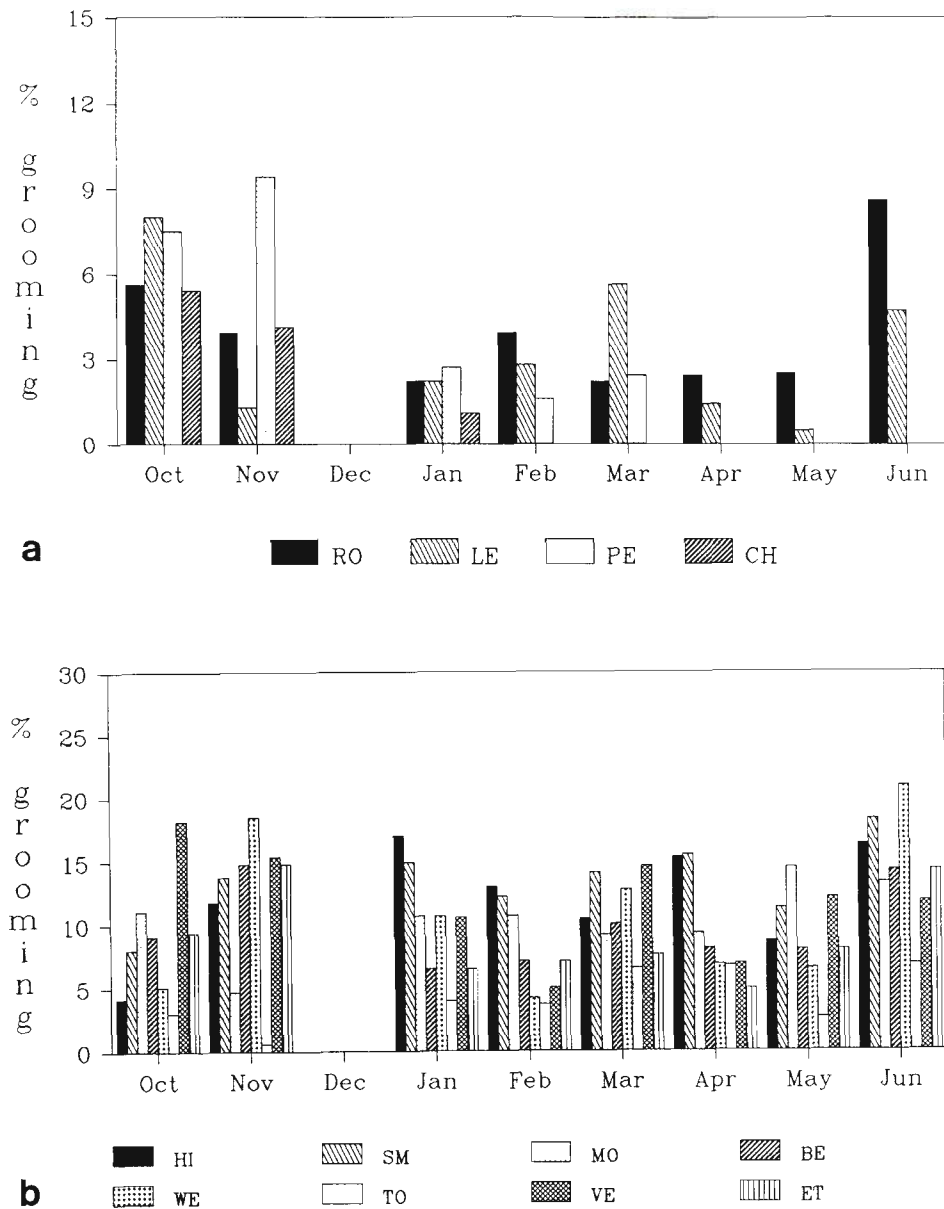
### **3.2.1. Male and female participation in affiliative behaviours**

When referring to social time hereafter, grooming (GR), social play (SP) and social friendly (SF) will be included (see chapter 2) if not otherwise stated.

#### *Grooming*

Males spent significantly less time involved in grooming per month than females ( $t=-6.87$ ;  $p<0.001$ ) (Fig. 3.4). This was true during the three seasons (Table 3.1 p. ).

Stepwise regression analysis showed that male participation in agonistic encounters ( $b=-0.28$ ;  $t=-2.18$ ) reduces the chances of participating in grooming interactions ( $F=4.738$ ; 23 df;  $p<0.05$ ). Whereas time spent meeting metabolic requirements did not affect grooming for males.



**Figure 3.4**  
Proportion of time that a) every adult male and b) adult female spent grooming in Windy Ridge Troop.

In contrast, female grooming was inversely correlated to time spent on the main maintenance activities, that is feeding ( $b = -0.36$ ;  $t = -5.36$ ), resting ( $b = -0.23$ ;  $t = -3.40$ ) and locomotion ( $b = -0.23$ ;  $t = -2.9$ ); and to time spent more than 50 m from other members of the troop ( $b = -0.93$ ;  $t = -3.58$ ) ( $F = 9.738$ ; 58;  $p < 0.001$ ). Therefore, as low ranking females spend more time away from others than high ranking females ( $\rho = 0.465$ ;  $p < 0.001$ ), they were also involved in less grooming ( $\rho = -0.279$ ;  $p < 0.05$ ).

### *Other friendly interactions*

Social play was common among immature monkeys, but was rare among adults. Only in 28 (0.8%) scans were males observed playing; most of these records were from the younger adult males (PE and CH). For females, social play was even less common, with only 5 observations during scan sampling (0.1%) ( $X^2=31.60$ ; 1 df;  $p<0.001$ ).

Social play (SP) and other friendly (SF) activities can be considered as having equal value for the reinforcement of social ties among its adult participants. When considering only these social interactions -excluding grooming- there were clear sex differences ( $X^2=8.119$ ; 1 df;  $P<0.01$ ), accounting for 1.4% of male and 2.2% of female time budget. However, during the birth season males and females did not differ in time spent in these activities (Table 3.1).

Males were more involved in play and females in aunting behaviours (see above) than *vice versa*. Thus it is conclusive that other friendly behaviours (SF) were more common among females than among males.

The same results as those for grooming interactions were found for females; low ranking individuals participating in less SF and SP than higher ranking females ( $\rho=-0.35$ ;  $p<0.05$ ).

### *All affiliative behaviours*

When considering the time spent on any kind of affiliative behaviour (grooming, social play, other friendly activities), sex differences still remained significant ( $t=-4.935$ ;  $p<0.001$ ). Females in general were more involved in social activities than males.

For males, vigilance ( $b=-0.23$ ;  $t=-3.80$ ) and time spent at the periphery of the troop ( $b=-0.30$ ;  $t=-2.3$ ) were the factors that affected social time the most ( $F=11.531$ ; 22 df;  $p<0.001$ ).

On the other hand, for females the maintenance activities: feeding ( $b=-0.81$ ;  $t=-8.59$ ), resting ( $b=-0.58$ ;  $t=-7.03$ ), locomotion ( $b=-0.56$ ;  $t=-5.32$ ) and less vigilance ( $b=-0.33$ ;  $t=-2.41$ ), and time spent peripheral ( $b=-1.14$ ;  $t=-3.02$ ) affected social time ( $F=21.728$ ; 58 df;  $p<0.001$ ).

### 3.2.2. Seasonal effects in social time

To reach any conclusions on the degree of importance each social activity had for each adult class, a more detailed study of time budgeting in relation to the presence of receptive females was necessary.

The extent to which grooming, social play and other social behaviour vary between seasons, for the free-ranging males and females as a group, within and between males, will be investigated in this subsection.

Males as a group participated in grooming interactions more often during the birth season than during any other season. In contrast, females showed the same levels of grooming throughout the study (see Table 3.6).

However, the proportion of time spent grooming did not show any significant seasonal differences for those adult males who remained in WT for the entire study; that is, for RO ( $X^2=1.311$ ; 2 df; NS) or LE ( $X^2=4.100$ ; 2 df; NS). Differing results for the seasonal effects on grooming for adult males as a group can be explained by the dramatic reduction in grooming PE showed before he left the troop ( $X^2=11.820$ ; 1 df;  $p<0.001$ ) and by the same tendency shown by CH (see Table 3.7).

Table 3.6

Median and standard deviation for the adult males and adult females of the free-ranging troop during the birth (B), non birth-non mating (N) and mating (M) seasons. For proportion of time spent grooming (GR), involved in other social friendly interactions (SP+SF); or in antagonistic behaviours (AGO). Significant seasonal differences were determined using the Wilcoxon signed rank test (z) with probability set at  $p<0.05$ . Significant differences are indicated.

	Season	GR	SP+SF	AGO
Males	B	5.5 ± 2.6	7.8 ± 3.7	3.1 ± 2.0
	N	2.3 ± 1.3	3.6 ± 2.5	4.0 ± 2.5
	M	2.5 ± 3.6	2.8 ± 3.3	6.0 ± 0.8
		B > N = M	B > N = M	B < M
Females	B	10.3 ± 5.6	16.2 ± 11.7	3.0 ± 4.2
	N	10.2 ± 3.7	11.0 ± 6.9	2.4 ± 2.3
	M	10.3 ± 4.5	9.8 ± 4.4	0.8 ± 1.1
		NS		*

(\*) Female antagonistic behaviours did not fit a normal distribution, therefore this test could not be used (arc-sine transformation was not possible for the presence of 0 in some months).

### *Seasonal differences in male socialisation*

Overall, adult males were more involved in social behaviour (other than grooming) more often during the birth season (see Table 3.6). This was true for the second ranking male (LE:  $X^2=7.070$ ; 2df;  $p<0.05$ ) but not for the two younger males (PE:  $X^2=0.06$ ; 1 df; NS and CH:  $X^2=0$ ; 1 df; NS). The seasonal effects on the alpha male's social activities (SP+SF) could not be tested due to the very low number of observations, although there did not appear to be any increase during the mating season (Table 3.7).

For both males and females, social activities that did not consist of grooming or sociosexual behaviours (see chapter 8) were more common during the birth than during the mating season (Table 3.6). The seasonal differences obtained for males as a group can be better explained by considering that younger males spent more time involved in social play than older males, as was the case for grooming.

### **3.2.3. Intra-gender differences in affiliative behaviours**

#### *Grooming*

During the non-mating period, the males of the Windy Ridge troop did not differ in participation in grooming interactions (B:  $X^2=4.597$ ; 3 df; NS; for N:  $X^2=2.720$ ; 3 df; NS). In contrast, during the mating season the dominant male tended to be more involved in grooming than the subordinate male, although this difference was not significant ( $X^2=3.53$ ; 1 df;  $p=0.06$ ) (see Table 3.7).

Similar results were found in the Cage: i) during the non-mating period the two dominant males were involved in grooming as often as the three most subordinate males (FT+GO/RN+FY+LU for B:  $X^2=0.340$ ; 1 df; NS; for N:  $X^2=3.430$ ; 1 df; NS) and ii) the same results were found for the mating season ( $X^2=14.300$ ; 2 df;  $p<0.001$ ) with the lowest ranking male (FY) grooming less than other males (RN/FY:  $X^2=13.365$ ; 1 df;  $p<0.001$  while FT/RO:  $X^2=1.008$ ; 1 df; NS) (Table 3.8).

Table 3.7

Proportion of scans in Windy Ridge in which the different adult males (RO, LE, PE, CH, GR) were involved in some form of social interaction (GR: grooming; SF: friendly; SP: social play; SM: submission; HO: Homage; AGO: attack, threat, redirected aggression and agonistic coalition) and DP: Red-White and Blue Display. Number of total scans per season and significance level of the Chi-square test as for Table 3.3 (p. 60).

NAME	SEASON	GR	SF+SP	SM+HO	AGO	DP
RO	B	4.5	0.6	0	3.4	1.7
	N	2.8	0	0	1.1	2.0
	M	3.6	0.3	0	1.2	2.5
		NS			NS	NS
LE	B	3.8	3.1	1.5	0.8	0
	N	3.5	0.9	3.7	1.6	0.3
	M	1.7	0.6	5.4	0.4	0
		NS	*	NS	NS	
PE	B	8.7	2.9	1.2	2.3	0
	N	2.1	2.1	1.7	0.5	0
		**	NS	NS		
CH	B	4.4	8.1	1.5	0.7	0
	N	1.1	8.4	3.2	0	0
			NS			NS
GR	M	0	0	15.4	3.8	0

Table 3.8

Proportion of scans in which the adult males (FT,RN,FY,GO,LU) were involved in some form of social interaction (GR:grooming; SF:social friendly; SP:social play; SM:submission; HO:Homage; AGO:attack, threat, redirected aggression and agonistic coalition) (see Table 3.5 p.65).

NAME	SEASON	GR	SF+SP	SM+HO	AGO	DP
FT	B	2.6		1.3	1.3	3.8
	N	8.8	+1.2	0.6	3.5	0.6
	M	4.8	5.4	0	1.4	2.4
		NS	*		NS	NS
RN	B	7.7		0	3.8	0
	N	10.9	+4.3	7.6	1.1	0
	M	7.1	2.2	4.9	0.7	0
		NS	NS	NS		
FY	B	0		0	0	0
	N	5.7	+2.9	5.7	1.9	0
	M	0.7	2.5	4.0	0	0
		*	NS	NS		
GO	B	18.2		0	4.5	0
	N	9.4	+3.3	0	6.3	6.3
LU	B	0		0	7.1	0
	N	3.7	+5.8	1.9	0	0

### *Individual differences in friendly behaviours (SF+SP)*

During the birth season the two younger adult males of the Windy Ridge troop participated more often in social activities (grooming excluded) than the older more dominant adult males for the time they were in the troop (birth season:  $X^2=13.660$ ; 3 df;  $p<0.05$  and pre-mating season:  $X^2=23.560$ ; 2 df;  $p<0.001$  -RO excluded-) (see Table 3.7).

During the mating season - when the two young males had left the troop - no individual differences were found among the males of the Windy Ridge troop ( $X^2=0.590$ ; 2 df; NS), the same was true for the two long-term resident males ( $X^2=0.05$ ; 1 df; NS).

In the Cage Troop, no male individual differences were found for friendly behaviours when all males were considered ( $X^2=7.189$ ; 4 df; NS). However, RN (middle ranking male) seemed to spend more time than FT (alpha male) interacting in a friendly way (grooming excluded) during the non-reproductive season ( $X^2=3.697$ ; 1 df;  $p=0.055$ ) (Table 3.8). In contrast, during the mating season the dominant FT participated in other social behaviours more often than the other two subordinate males (FT/RN+FY:  $X^2=4.471$ ; 1 df;  $p<0.05$ ).

### **3.2.4. Effects of caging on male social behaviour**

Males at the Cage participated in grooming interactions more often than their free-ranging counterparts ( $X^2=14.50$ ; 1 df;  $p<0.001$ ). Similarly, other social behaviours (SP+SF) were more common in adult males living in a protected environment ( $X^2=18.870$ ; 1 df;  $p<0.001$ ).

## **3.3. ANTAGONISTIC BEHAVIOURS**

### **3.3.1. Gender differences in agonism**

Concerning antagonistic interactions, males were more often involved than females except during the birth season (Table 3.1, p. 60). There were 70 instances (2.0% of activity budget) of submission (including homage) for males and 62 (1.0%) for females. Even though homage is not included in the analysis, males can be seen to have used submissive behaviours more often than females ( $X^2=4.337$ ; 1df;  $P<0.05$ ).

The Red-White and Blue Display (DP) was almost exclusively performed by the alpha male (N=30; 94% of all occurrences) and occupied a mere 2.1% of his time budget. The remaining occurrences of DP (N=2), when the actor was the second ranking male, were directed towards the next lower ranking male (see chapter 6). Herding behaviour (HR), tree display (TD) and confident walk (CW) were also rank-related and were quite uncommon (2.7% of RO's scans and 1.1% of the total samples done on males).

There was a clear sex difference in the overall number of scans in which agonism, either aggressive, submissive or expressed in the form of displays of dominance, were recorded. Data from scans regrouped by monthly individual values (Kolmogorov-Smirnov two-sample test:  $D_N=0.529$ ;  $P<0.001$ ) reinforce the results reported in the literature which claim that males are involved in more agonistic interactions than females.

As the frequency of agonistic encounters was not very high, the stepwise regression analysis was carried out on the monthly individual proportion of time spent in any kind of negative interaction. The independent variables were the proportion of time spent in the main maintenance activities, vigilant, social friendly (SP + SF), grooming, time peripheral, on top of canopy, on the ground, month number and dominance rank (highest ranking = 1) for males and females.

For males, apart from the proportion of time spent feeding ( $b=-0.22$ ;  $t=-3.2$ ), resting ( $b=-0.14$ ;  $t=-2.27$ ) also entered the model ( $F=7.377$ ; 22 df;  $p<0.01$ ). For females, the analysis could not be run because agonism did not follow a normal distribution (see above). These results suggest that when males interacted agonistically more often, their feeding and resting time were impaired.

### **3.3.2. Seasonal changes in agonism in Windy Ridge troop**

The proportion of time males at Windy Ridge spent involved in any kind of agonism is depicted in Figure 3.5. RO, the dominant adult male was not involved in more aggressive acts during the mating season ( $X^2=5.658$ ; 2 df;  $p=0.06$ ). The same results were found for LE, the second ranking male ( $X^2=2.497$ ; 2 df;  $p=0.11$ ) (see Table 3.7; Fig. 3.5).



The free-ranging adult males did not show any significant difference in submissive behaviours between the mating and non-mating seasons (Table 3.7). This applied to LE's self-initiated displays of subordination (homage:  $X^2=0.026$ ; 1 df;  $p=0.9$ ) but not to other submissive behaviours ( $X^2=6.500$ ; 1 df;  $p<0.05$ ) which were more common during the mating season (4.6%) than during either the birth (0.8%) or pre-mating (2.6%) seasons. The lowest ranking male CH was never recorded doing homage during his scan samples, and PE only once in 173 scans done during the birth season (0.6% of his time budget) and 5 times in 420 scans during the pre-mating season (1.2%).

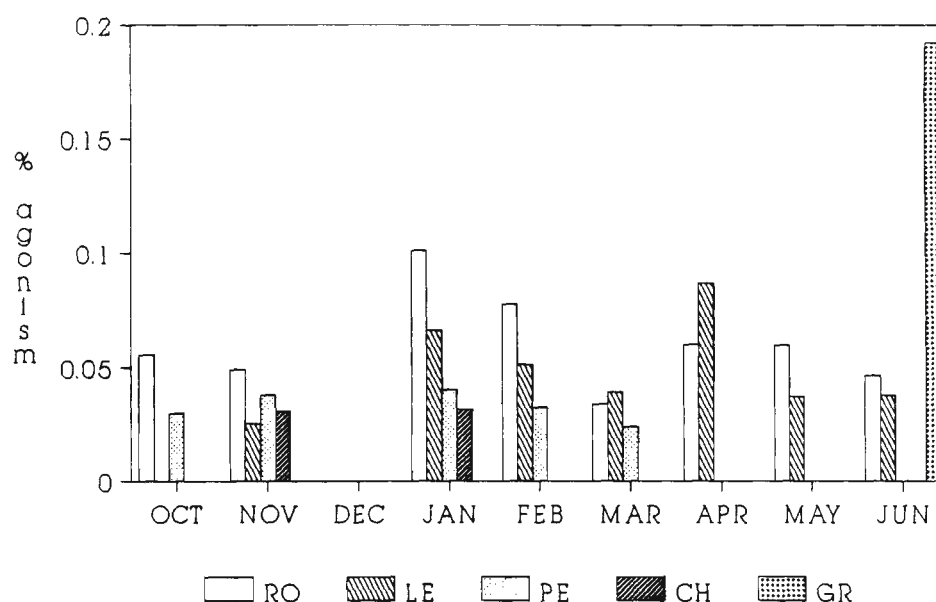


Figure 3.5

Proportion of male time budget spent in agonistic interactions in Windy Ridge.

Contrary to expectations, RO did not show any increase in displaying his genitalia to other males of the troop (DP) during the mating season ( $X^2=0.49$ ; 2 df; NS). However, when all the displays of dominance are considered (DP+HR+CW+TD), RO showed an increase for the pre-mating (35 of 562 scans) and mating (30 of 663 scans) periods in relation to the birth season (3 of 176) (B/N/M:  $X^2=6.23$ ; 2df;  $p<0.05$  and B/N:  $X^2=4.727$ ; 1df;  $p<0.05$  and N/M:  $X^2=1.433$ ; 1 df; NS).

In summary, the dominant male performed tree-display, herded other members of the troop and used confident walk more often during the pre-mating and mating than during the birth season. However, there was no seasonal effect on his Red-White and Blue display.

### **3.3.3. Male individual differences in agonism**

#### *Aggression*

The dominant male of the free ranging troop did not spend more time taking part in aggressive encounters than the lower ranking males (B:  $X^2=1.760$ ; 1 df; NS; N:  $X^2=0$ ; 1 df; NS and for M:  $X^2=0.899$ ; 1 df; NS). The same results were found for the two highest ranking males of the caged troop (B+N:  $X^2=1.230$ ; 1 df; NS and for M:  $X^2=1.440$ ; 1 df; NS). It seems therefore, that aggression was not completely related to male rank for either of the study troops.

#### *Submission*

The top ranking male of the Windy Ridge troop did not perform any submissive behaviour during his scan samples, therefore he was excluded from the analyses. During the birth season, LE showed submission to another animal only once in 129 scans, PE also once in 172 scans and CH twice in 133 scans. During the pre-mating season, additional males did not differ in time spent behaving submissively ( $X^2=2.011$ ; 2 df; NS). However, during the mating season the newly immigrated male (GR) was more involved in submissive actions than the long term subordinate male (25 instances in 514 scans for LE and 4 out of 22 for GR:  $X^2=4.941$ ; 1 df;  $p<0.05$ ) (see Table 3.6).

In agreement with the above results, the higher ranking males of the caged troop (FT and GO) participated in fewer submissive interactions than the other males ( $X^2=4.45$ ; 1 df;  $p<0.05$ ), even though they were sorting out their rank relationships. Similarly, individual differences between the two subordinates left in the Cage during the mating season were not detected ( $X^2=0.81$ ; 1 df; NS).

#### *Homage or self-initiated displays of subordination*

The youngest and lowest ranking male of the Windy Ridge troop (CH) was never observed doing homage using this sampling method. The subordinate males LE and PE did homage at comparable rates (B+N:  $X^2=0$ ; 1 df; NS). The newly immigrated male GR was never observed doing homage during his limited number of samples.

Similar results were obtained for the adult males in the Cage; during the non-reproductive season the lowest ranking male (LU) did not perform homage while RN and FY did so at comparable frequencies ( $X^2=0.26$ ; 1 df; NS). Comparable results were found for the mating season; the lowest ranking male at that time (FY) was never involved in homage throughout his 278 scan samples, while the middle ranking (RN) participated in 7 displays of subordination during his 260 scans.

#### *Displays of dominance*

Red-White and Blue Display: The alpha male RO (N=30) was the main performer of these displays. On two occasions, the subordinate LE was seen to display his genitalia at PE.

In the cage, both higher ranking males were found displaying their genitalia towards other males (4 times in 244 instantaneous samples for FT and 4 out of 82 for GO:  $X^2=1.507$ ; 1 df; NS).

#### **3.3.4. Effects of caging on male antagonism**

Do male agonistic interactions increase in a caged environment? Interestingly, the only activities which did not vary between the males of the two study troops were those of an agonistic nature. Submission and homage accounted for the same proportion of time (CT: 2.7%; WT: 2.0%;  $X^2=1.95$ ; 1df;  $p=0.16$ ) as did overt aggression, threats and supplants (CT: 1.6%; WT: 1.14;  $X^2=1.44$ ; 1df;  $p=0.23$ ). Finally, displays of dominance were as common for the caged males as for the free-ranging ones (CT:0.9%; WT: 1.0%;  $X^2=0.02$ ; 1 df;  $p=0.88$ ).

#### *Does agonism by caged males increase during the mating season?*

The male dominance rank of the Cage Troop was more unstable than that of the Windy Ridge troop (see Appendices A and C). The rank dominance order among the adult males that remained in the troop during the mating season was (FT>RN>FY) and for the subadult males it was (PP>PA). However, PP was clearly dominant to some of the adult males at the end of the study. The subordinate males' submissive behaviours did not vary between the non-mating and mating periods (RN:  $X^2=0.022$ ; 1 df; NS and FY:  $X^2=0.035$ ; 1 df; NS). Similarly, the highest ranking male's participation in aggression ( $X^2=0.804$ ; 1 df; NS) and displays of dominance ( $X^2=0.106$ ; 1 df; NS) were not higher during the mating season (Table 3.7).

### **3.3.5. Agonism during feeding**

To test the hypothesis that feeding activity increases the possibility of agonistic interaction, I analysed the proportion of submissive acts that occurred when the general context was feeding in relation to the total number of submissive episodes observed in other general contexts.

Submission was expressed either as avoidance or other specific patterns of subordination (e.g. lipsmacking, crouching low). These occurred more often during feeding among females (32.0%) than among males (20.9%) ( $X^2=3.705$ ; 1 df;  $p=0.05$ ). This last result agrees with the hypothesis that females' limiting resource is food (Wrangham, 1979) and water (Wrangham, 1981).

If the rate of submissive acts is related to food shortage, seasonal differences ought to be found. Surprisingly, there were no seasonal effects on the proportion of submissive behaviour that occurred during feeding; either for males ( $X^2=0.554$ ; 2 df;  $p=0.8$ ) or for females ( $X^2=4.145$ ; 2 df;  $p=0.13$ ). If avoidance episodes are treated separately, records of females approach significant seasonal differences ( $X^2=3.65$ ; 2 df;  $p=0.056$ ). During the non-mating season 49.3% of female avoidance interactions occurred during feeding against 27.8% during the mating season. Therefore, there was a tendency for females to avoid other members of the troop for reasons other than food competition more often during the mating season than at any other times.

## **3.4. CONSTRAINTS IN MALE TIME BUDGET DURING THE MATING SEASON**

To detect whether or not constraints in time budget differed between the mating and the non-mating season, time spent feeding, resting and vigilant were plotted against other non-social and social behaviours.

It seems that a reduction in time males spent feeding and resting during the mating season were prompted by an increase in time spent in vigilance (Fig. 3.6a,b). Time spent feeding did not seem to affect grooming activities during the mating season (Fig. 3.6c). The same was found for social behaviour and feeding. In addition, the higher values for feeding and socialising applied to the two young adult males that migrated during the study (ranks 3 and 4). That is, the younger and lowest ranking males fed and played more than the other two older, more dominant males (Fig. 3.6d).

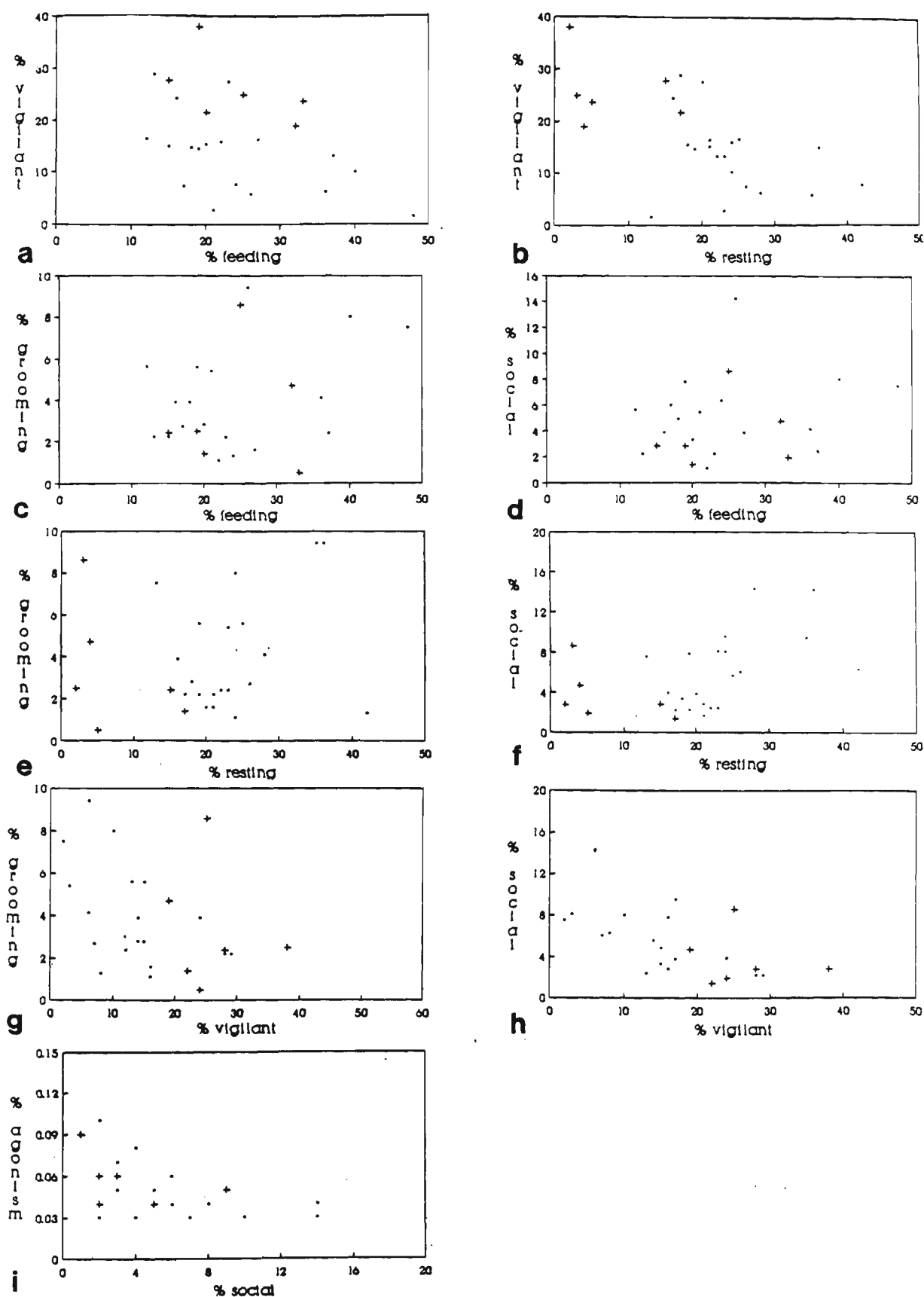


Figure 3.6. Constraints imposed by some maintenance and agonistic activities on time socialising, resting and/or feeding. The numbers indicate male rank (rank=1 for the alpha male) and circles indicate that the data were collected during the mating season.

There is no clear indication of a relationship between time spent resting and time grooming (Fig. 3.6e) or with time socialising (Fig. 3.6f) during the mating season. No correlation between grooming or other social activities and vigilance was found during the mating season, as was the case when considering all months of the study (Fig. 3.6 g,h). However, high levels of agonism corresponded to a reduction in time socialising when considering the entire study period or the mating season alone (Fig. 3.6i).

### 3.5. DIURNAL RHYTHMS

This section is chiefly concerned with analysing male-female diurnal rhythms for each season. The confidence limits and proportion of time spent on feeding, resting, locomotion, vigilant and grooming are shown for both males and females.

Feeding peaks were found for both males (B:  $X^2=37.99$ ; 8 df;  $p<0.001$  and M:  $X^2=22.72$ ; 9 df;  $p<0.05$ ) and females (B:  $X^2=18.42$ ; 8 df;  $p<0.05$ ; N:  $X^2=33.08$ ; 12 df;  $p<0.001$  and M:  $X^2=31.89$ ; 9 df;  $p<0.001$ ). The exception was for males during the non-birth/non-mating season (N:  $X^2=12.714$ ; 12 df; NS) (Fig. 3.7), when no clear peaks in daily feeding were apparent.

Resting periods were common among males (B:  $X^2=17.615$ ; 9 df;  $p<0.05$ ; N:  $X^2=69.773$ ; 10 df;  $p<0.001$  and M:  $X^2=24.363$ ; 6 df;  $p<0.001$ ), while female resting time was spread equally throughout the day during the birth season ( $X^2=14.363$ ; 9 df; NS), but showed clear peaks during other seasons (N:  $X^2=76.882$ ; 12 df;  $p<0.001$  and M:  $X^2=63.041$ ; 10 df;  $p<0.001$ ) (Fig. 3.8).

Locomotion by males did not vary during the hours they were observed in the birth season ( $X^2=7.858$ ; 7 df; NS), but was higher in the early mornings and late afternoons during the other two seasons (N:  $X^2=23.151$ ; 10 df;  $p<0.05$  and M:  $X^2=15.836$ ; 8 df;  $p<0.05$ ). Conversely, females showed peaks of locomotion during all seasons (B:  $X^2=29.953$ ; 8 df;  $p<0.001$ ; N:  $X^2=84.355$ ; 12 df;  $p<0.001$  and M:  $X^2=35.129$ ; 9 df;  $p<0.001$ ) (Fig. 3.9).

Male vigilance was spread throughout the day during the birth season (males:  $X^2=4.03$ ; 6 df; NS) while clear peaks existed during the pre-mating and mating seasons (N:  $X^2=54.525$ ; 12 df;  $p<0.001$  and for M:  $X^2=28.206$ ; 9 df;  $p<0.001$ ). For females, similar levels of vigilance occurred for the hours data were collected during the non-birth/non-mating season ( $X^2=15.914$ ; 12 df; NS), but not for the mating period ( $X^2=19.605$ ; 10 df;  $p<0.05$ ) (see Fig. 3.10).

Due to the low levels of vigilance and the limited number of samples for females during the birth season, the daily distribution of vigilance could not be determined.

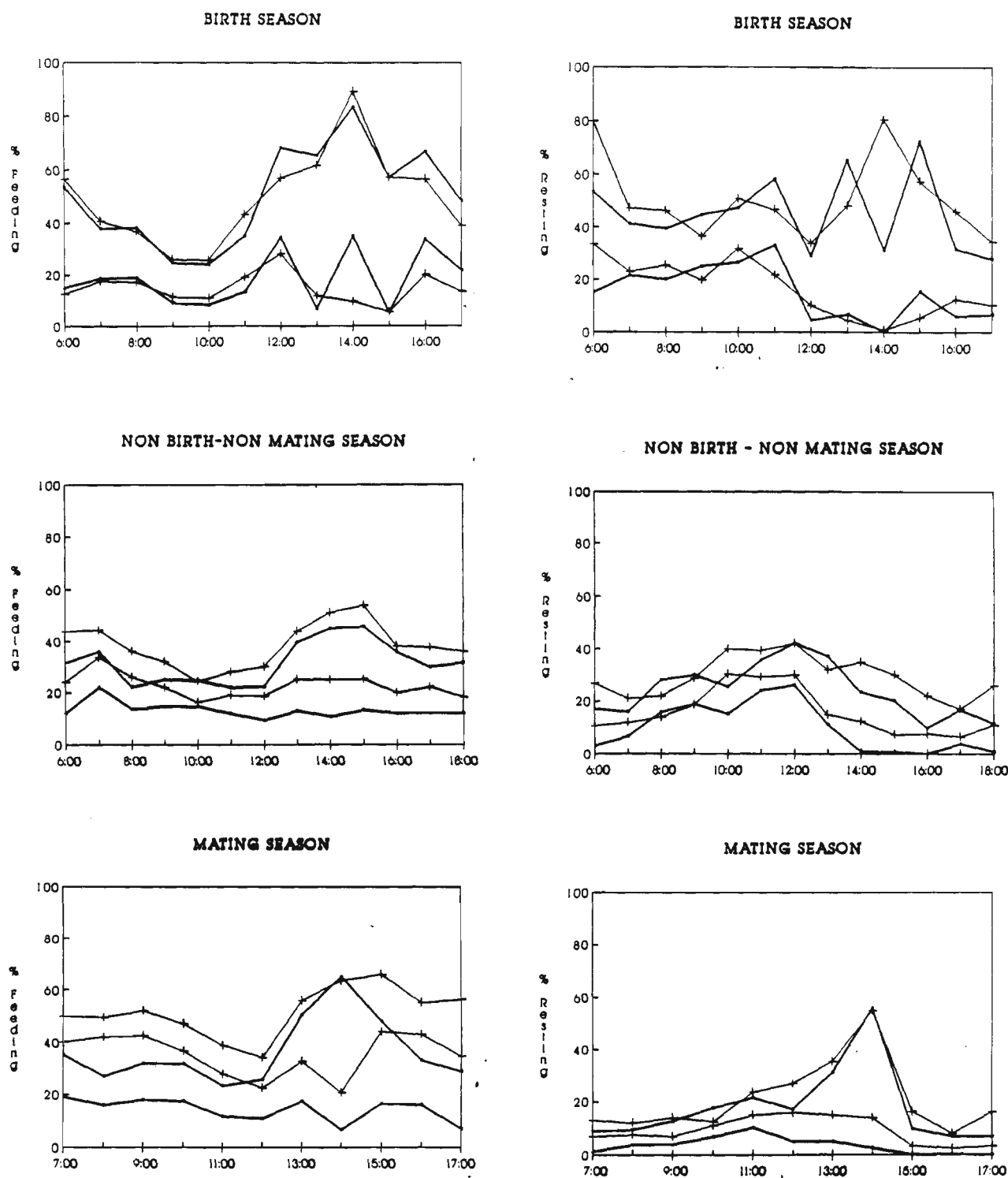


Figure 3.7. Diurnal patterns of feeding. The horizontal axis represents the hour, the vertical axis the confidence limits for adult males (thicker lines) and adult females (thinner lines) of proportion of time spent feeding.

Figure 3.8. Diurnal patterns of resting (see Fig. 3.7).

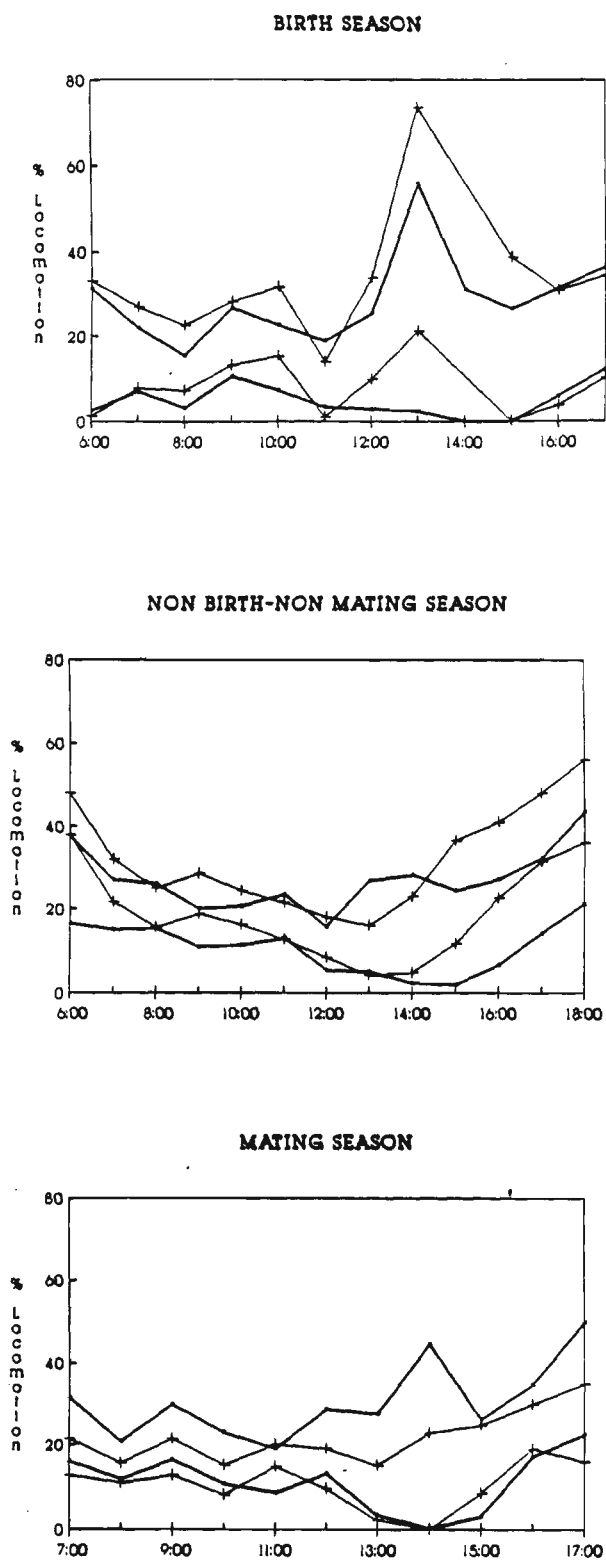


Figure 3.9. Diurnal patterns of locomotor activity (see Fig. 3.7).

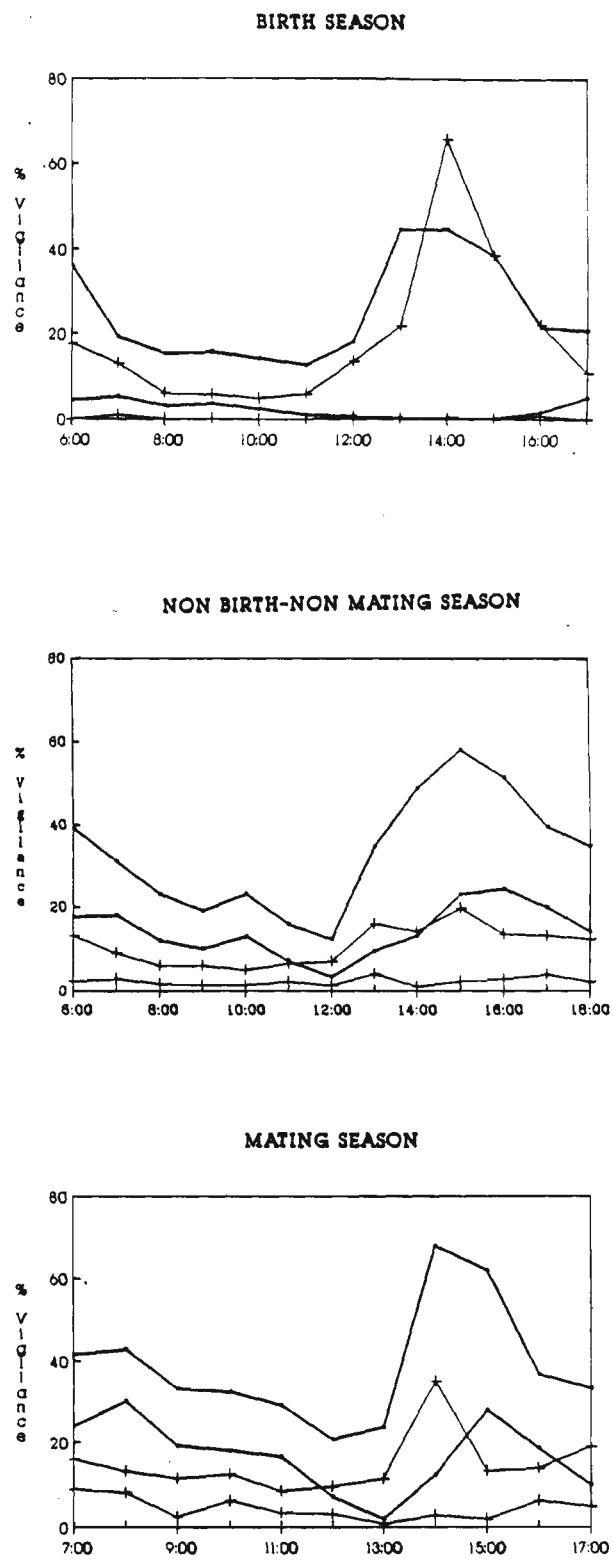
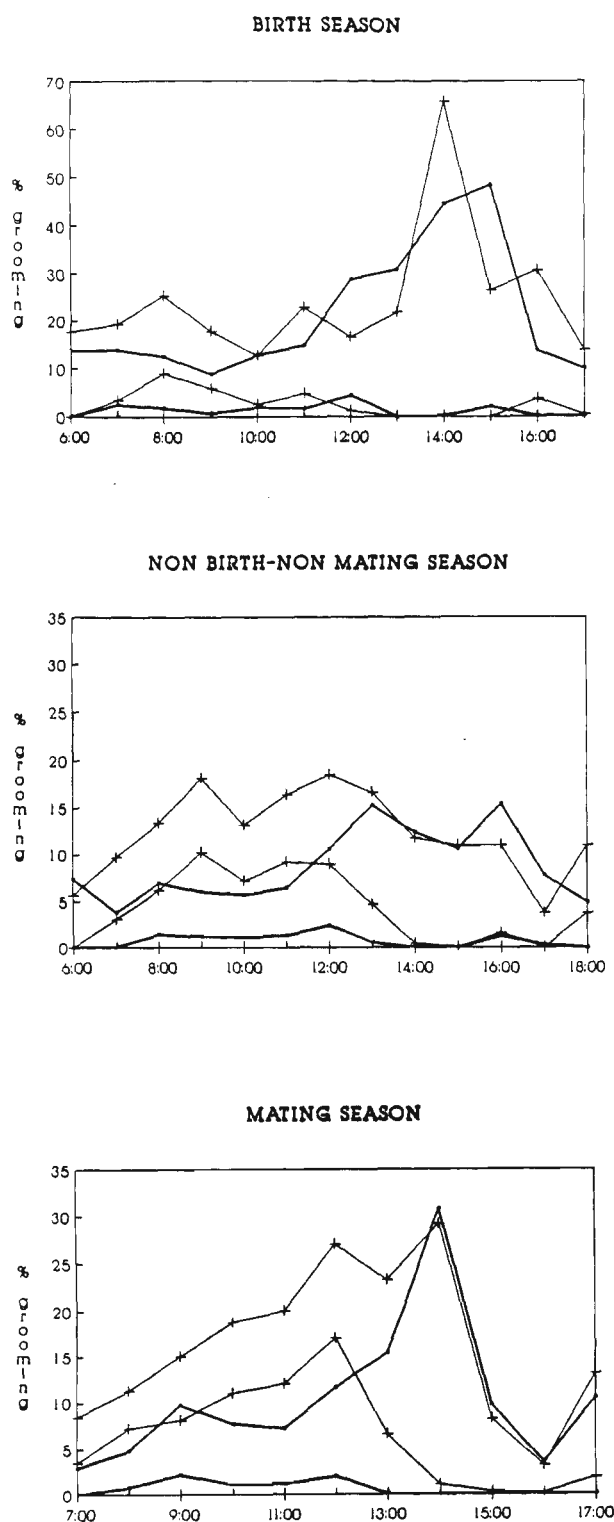


Figure 3.10. Diurnal patterns of vigilance (see Fig. 3.7).





Grooming peaks for adult males were only found during the mating season ( $X^2=10.23$ ; 5 df;  $p<0.05$ ), but not at other times (B: $X^2=1.725$ ; 4 df; NS and N: $X^2=11.690$ ; 6 df; NS). Females were found grooming at comparable rates throughout the day during the birth season ( $X^2=5.58$ ; 4 df; NS), but not during the pre-mating ( $X^2=41.85$ ; 6 df;  $p<0.001$ ) or mating ( $X^2=71.44$ ; 5 df;  $p<0.001$ ) seasons (Fig. 3.11). It is suggested that peaks in grooming activity correspond to periods of decreased feeding activity for both the males and females (compare Fig. 3.7 and 3.11 for N and M when more data were available).

Figure 3.11. Diurnal patterns of grooming (see Fig. 3.7).

### 3.6. DISCUSSION

Although time budgeting in feral monkeys is undoubtedly the result of many converging factors, analysis of seasonal and individual differences as a function of both female reproductive condition and sex/social status respectively offer fundamental insights into how free ranging vervet monkeys distribute their time.

#### 3.6.1. Metabolic requirements

The only significant sex differences in monthly time spent performing major maintenance activities were for feeding and vigilance. Feeding was more time-consuming for females (see review Clutton-Brock, 1977b, p. 545-555) and vigilance for males (chapter 4).

The amount of time spent feeding is primarily determined by metabolic demands and food availability (Rose, 1977). Females' nutritional costs are higher than males' because of the costs imposed by pregnancy and lactation (Clutton-Brock, 1977, p.545). Dominant animals have access to favourable food resources (Wilson, 1975) which allows them to spend the minimal time feeding (see Dittus, 1977; Rose, 1977). As vervet males are slightly bigger than females (Bramblett & Coelho, 1987 p.76) and their canines more effective, female competitive abilities are generally lower than males' (Clutton-Brock, 1977 p.545).

The priority of higher ranking animals for preferred food resources (*e.g.* sycamore figs) was evident when looking at the order in which they entered these feeding trees. The dominant male would arrive first, go to the very top of the canopy, scan around and he would then proceed to feed. The highest ranking females followed and at times it was evident that one of them would 'guard' the entrance route to the tree. Meanwhile, lower ranking individuals would remain waiting in the lower levels of the canopy in the surrounding area, resting or feeding on other foods.

Females generally spent more time feeding than males (Dittus, 1979 for *Macaca sinica*; but see Harrison, 1983b for *C.(a.) sabaues*). The fact that no sex differences in the amount of time spent feeding existed for the birth season in Windy Ridge, is in partial agreement with Poirier's (1970) statement that langur mothers feed less than other group members during the birth season (see also Rose, 1977). Females fed more during the mating season possibly to offset the nutritional demands of the lactation period (Iwamoto, 1982) and to attain a minimum body condition in order to ovulate (Lee, 1984a; Dunbar & Dunbar, 1988 chapter 4).

The increase in time spent feeding for females was taken primarily from: i) time spent resting (cf. Dunbar & Dunbar, 1988), ii) time spent in social interactions (see also Altmann, 1980) and was inversely correlated to locomotor activity. Therefore, to spend more time feeding does not imply moving over longer distances. In contrast, male feeding activity was mainly impaired by the time spent interacting agonistically.

During the mating season environmental conditions in Natal (Basckin & Krige, 1973) are such that one would expect an increase in feeding. This was true for the subordinate male and the adult females, but the alpha male proved to be an exception. Unfortunately, the hardest time for vervets (Butynski, 1988) was the period for which data was not available at Windy Ridge.

The seasonal variation of the second and third ranking males in feeding behaviour could be explained by the fact that they fed more when the temperatures were lower (that is during the mating season and beginning of the birth season) and conditions were drier. The proximate causes might be that: i) an increase in quantity or quality of food is required by homeotherms when the temperature drops (Dunbar, 1988, p. 18), ii) adult males and subordinate animals in general suffer from loss of temperature to a greater extent because they do not maintain as high a level of body contact as high ranking females and juveniles (see Pulliam & Caraco, 1984 for a review; Tollman, 1984 for caged female vervets), and iii) during drier conditions animals are expected to dedicate more time to feeding (Clutton-Brock, 1977, p. 556; Lee, 1983, p.226).

Clear inter-male differences were found for each season, with the alpha male always spending less time feeding than other members of the troop. This result is in accordance with Wilson's theory (1975) that high ranking animals have greater access to limited resources. Subordinate males fed for comparable periods of time except during the pre-mating season when LE foraged for the same amount of time as RO, while both migrating males fed more. It is possible that there is an increase in feeding activity by males just before they leave the troop. It is during the mating season that more male transfers between groups occur (Henzi & Lucas, 1980; Cambefort, 1981; Cheney & Seyfarth, 1983) and there is intense competition to mate with estrus females (see Hausfater, 1975 for baboons). Consequently, males are expected to spend less time feeding and switch to feeding in very high quality patches ('time minimizers' Richard, 1985, p.204 for baboons). Although the dominant male of Windy Ridge could have followed the same strategy, his physical condition appeared to have deteriorated.

Males were expected to spend more time resting because of their lower nutritional requirements and higher basic rank when compared to adult females. This expectation was proven true for the free-ranging individuals with the exception of the birth season.

It can be concluded that male involvement in vigilance and mate competition affect their resting time during the pre-mating and mating seasons (cf. Watson, 1985). Among females the increase in feeding was related to a reduction in time resting and socializing (see Lee 1983, p. 227; 1984a). In addition, when females were more peripheral their resting time was also reduced. Some low ranking females were forced to feed away from other monkeys, and did so when the rest of the troop was resting.

Furthermore, free-living males did not differ in time spent resting during any of the seasons. In contrast, the two higher ranking captive males (FT and GO) showed the highest levels of agonism during the non-mating season which impaired their resting activity. The lowest ranking male (FY) of the Cage troop rested more than the two higher ranking males during the mating season. FY also failed to participate in homage during the mating season and remained very isolated from the rest of the animals. It can therefore be deduced that FY's strategy was to remain unnoticed so as to avoid any involvement in agonistic encounters.

In conclusion, resting time was reduced for free-ranging males and females during the pre-mating and mating seasons. For males, this was mainly due to increased levels of vigilance, feeding and locomotion, while for females the main factor was an increase in time socialising.

Males tended to be more mobile during or prior to the mating season, although no statistical significance was reached when considering the two individual males that remained in the troop during the entire study period. For females, locomotor activity was higher during the pre-mating season. This could have been related to the infants becoming more independent of the mother and females being forced to keep up with them, possibly to prevent predation and infanticide.

Therefore, increased locomotion due to lower food quality (see review in Dunbar & Dunbar, 1988, p.49) has not been found in this study (cf. Lee, 1983 p.227; 1984a; reviewed by Fedigan & Fedigan, 1988, p.400-401). It cannot be concluded that this was the case for the entire year, because no data were available for the driest season (July-early September).

Resting and feeding activities affected locomotor behaviour by males and females, in addition time spent vigilant also restricted their locomotion. During the mating season the free-ranging males were more mobile than the females. Finally, low ranking animals (males and females) were not necessarily more mobile than high ranking in free-ranging conditions but the caging situation augmented the mobility of lower ranking animals for the period of higher instability, which reflected the tendency of low ranking animals to become peripheral.

It is proposed that differences in locomotor activity found in this study are not primarily related to food quality, but to social reasons (e.g. high levels of the stress hormone serotonin: see Raleigh *et al.* 1980) and mate competition.

In general, the total time budgets obtained for the study troop in Windy Ridge were similar to those reported by Watson (1985) for vervets in Hluhluwe, a nearby reserve (see Fig. 2.6).

### **3.6.2. Affiliative behaviours**

Apart from the removal of ectoparasites (e.g. Struhsaker, 1967b), allogrooming is known to be important for the reinforcement of friendly relationships (e.g. Seyfarth, 1980). The fact that females spent more time grooming than males (see also Harrison, 1983b) is related to their living in female bonded groups in which grooming is related to the formation of agonistic coalition and access to high quality or patchy food resources (see chapter 1).

It was predicted that male participation in social interactions would change as the mating season approached, in order to improve mating opportunities.

First, the seasonal differences in grooming interactions found for the Windy Ridge troop when considering all the adult males together could be the result of the high participation shown by one of the adult males that migrated. Just before emigrating, both males (PE and CH) showed a clear reduction in participation in grooming interactions. The top ranking male tended to be more involved in grooming interactions than the second ranking male during the mating season. In addition, the subordinate male's involvement in social activities other than grooming decreased during the mating season.

Similar results were obtained for the Cage Troop. During the mating season, the lowest ranking male (FY) showed a significant drop in participation in grooming. In addition, males in general participated in grooming more often during the pre-mating season. This may be attributed to the higher levels of stress during this period among males and the use of grooming as an appeasement activity (see chapter 5).

Second, among free-ranging males, grooming activity was negatively correlated with time spent interacting agonistically, which means that grooming peaked at the time when agonism was low (*i.e.* during the birth season). Meanwhile, monthly time spent grooming by individual females was affected by time spent feeding, resting, vigilant and peripheral. The general increase in feeding activity during the mating season did not produce significant changes in time spent grooming (see chapter 7 for qualitative changes). Lee (1983 p.228) pointed out that grooming is an inexpensive activity worth conserving, at least for females. High ranking females participated more in grooming and other social interactions than lower ranking females (see also Seyfarth, 1980 for vervets; Sade, 1972 for rhesus monkeys).

It was found that social play, although rare among adult vervet monkeys, was more common for males than for females (see also Bramblett, 1978), a common pattern among non-human primates (Loizos, 1967; Loy *et al.* 1978) and peaked during the birth season (see also Rostal *et al.* 1986). This last result could also be a consequence of younger males participating in play more often and emigrating before the mating season started. Additionally, it has been suggested that when resources are not plentiful, *C. aethiops* spends proportionately more time involved in cheaper forms of socialising (Lee, 1983).

On the other hand, females were more involved than males in friendly behaviours such as cuddling, aunting behaviour, and intratroup friendly vocalisations (*grunts*: Cheney & Seyfarth, 1982a or *progression grunt* or *woof*: Struhsaker, 1967c). These behaviours tended to be less frequent as the mating season approached and were obviously related to a loss of interest in the infants. The adaptive significance of this sexual difference may well be in terms of preparation for the most important roles in life (Lancaster, 1971).

As the lowest levels of social play and other friendly behaviours occurred during the mating season, no sex differences were apparent at that time.

In both troops the top ranking males (RO and FT) showed fewer friendly behaviour than additional males during the non-mating period, while the tendency was the opposite for the mating season. The very low levels of affiliative behaviour for RO during the mating season might be interpreted as a consequence of his high levels of vigilance for that period (see chapter 4).

In general, affiliative behaviour among males is impaired by time spent vigilant and peripheral. In contrast, for females, time spent in all the major maintenance activities affects their time socialising. In addition, participation in social behaviour for females was related to dominance rank, while for males it was more related to age than to agonistic rank, at least during the non-mating season.

### **3.6.3. Agonistic behaviours**

Male and female vervet hierarchies seem to function separately, however, sometimes females are dominant to adult males (Lancaster, 1971; see chapter 6).

Adult males participated in agonistic behaviour more often than females (Bramblett & Coelho, 1987 for vervets) except during the birth season (see chapter 6 and 7 for qualitative changes). This was expected as females living in female-bonded groups present a stable and long lasting linear dominance hierarchy (vervets: Seyfarth, 1980; gelada baboons: Dunbar, 1983d p. 307). As a result, males used submissive patterns more often than females and in general, additional long-term resident males did not differ in the frequency of participation in submissive behaviours. However, the newly immigrated male (GR) presented more instances of submissive behaviour than the long-term resident subordinate male (LE). These results agree with Wrangham's (1980) hypothesis that unrelated subordinate males are the recipients of more aggression than dominant males and are expected to be able to counteract this agonism with submissive acts.

Male participation in agonism increased from the birth through the mating seasons (see also Slobodchikoff & Schulz, 1988, p.18) and was parallel to a decrease in time feeding and resting. These results agree with the theory that the mating season is characterised by a high degree of instability, because the presence of adult estrus females increases fighting among males (rats: Albert, *et al.*, 1990; *Papio anubis*: Packer, 1979 b; *Papio cynocephalus*: Hausfater, 1975, but see Dunbar, 1983d p.305 for *Theropithecus gelada*).

On the other hand, female agonistic interactions seemed to decrease from the birth into the mating season and were more related to food competition than was the case for males. During the mating season however, females avoided other individuals more often when not feeding (see also Dittus, 1977).

Within-male variations in aggression, submissive behaviour and displays of dominance did not show any quantitative seasonal component for males of either troop (for qualitative changes see chapter 5 and 6). The exception was for the subordinate adult male LE, who showed more submission (homage excluded) during the mating season.

The fact that the lowest ranking male of each troop was never seen paying homage, while no differences among the other subordinate males were observed suggests that only males which rank immediately below the higher ranking males are the actors of homage. The strategy employed by the lowest ranking males to avoid conflict is to keep well away from their counterparts; that is, to become peripheral to the troop.

Displays of dominance were typically performed by the top ranking males (RO in Windy Ridge and both FT and GO in the Cage). When the second ranking male (LE) was found displaying his genitalia towards PE, RO manipulated his penis until he reached erection; he then ejaculated and approached the interacting pair aggressively, performing a full display around LE and threatening the 'insubordinate'.

The findings that the Red-White and Blue display occurs equally often during the mating and non-mating season disagrees with Struhsaker's (1967a) suggestion that the RWB-display mainly serves to assert rank during the mating season. It is hypothesised that during periods of instability or when there are receptive females, more effort is put into overt aggression and less into displaying. Displays of dominance only work when the participating animals have assumed their relative rank, and this occurs throughout the year. Difference in agonism between the mating and non-mating season which have been reported for other species does not necessarily occur in vervets due to the vervet male visual signalling system

In conclusion, one of the advantages adult vervet males achieve by remaining in the troop is to assert their relative rank before the females become receptive. This is an important argument as to why the alpha male might accept other males in the troop.



### **3.6.4. Variation in diurnal rhythms**

Social desynchronisation could either enhance fitness by reducing direct competition for resources or reduce fitness first, by impairing the efficiency of resource utilisation and second, by disturbing social organisation, because:

'A strong selective advantage exists for the individual organism that can maximize its chances for survival by synchronizing its behaviour and physiology with daily or yearly events' (Regal & Connolly, 1980).

Diurnal feeding peaks have been widely reported in the literature on Old World monkeys (Hall & Gartlan, 1965; Poirier, 1970; Harcourt, 1978; Iwamoto, 1982). The common trend is to find a peak in feeding activity in the first half of the morning and the second half of the afternoon (Clutton-Brock, 1977, p.548-549). A differential utilisation of the levels of the canopy (Hall & Gartlan, 1965) and food choice may occur during the day (Clutton-Brock, 1977b).

When looking at the distribution of maintenance behaviour throughout the day for adult males and females in Windy Ridge, it was found that male feeding, resting, locomotor and vigilant activities showed clear peaks except for: i) male feeding activity during the pre-mating season; ii) male locomotor activity during the birth season and iii) male vigilance during the birth season. These exceptions corresponded to the lowest levels of the above mentioned activities. For females however, resting activity was equally spread throughout the day during the birth season, while the same was found for vigilance during the pre-mating season; which were also the times when these activities were less common.

The distribution of social behaviour have been found to change during the day and to be regulated by peaks of feeding and/or resting activity (see Hall, 1962; Hall & Gartlan, 1965; Iwamoto, 1982). It is questionable whether grooming peaks are related to temperature changes during the day (cf. Troisi & Schino, 1986).

In Windy Ridge diurnal peaks of grooming were found for males during the mating season and for females during both the pre-mating and the mating seasons. The mating season was the time when male-female grooming was more common (see chapter 7), and female grooming periods may have affected the distribution of male grooming. Those peaks in grooming occurred at times when feeding activity was at its lowest. The fact that females failed to show peaks of grooming activity within the day during the birth season may be explained by the following: i) most female grooming was directed to new born infants and ii) feeding activity was at its lowest, though not equally distributed during the day.

### **3.6.5. Cage versus free-ranging**

When considering the total percentage of time dedicated to maintenance activities, the caged males spent more time resting and vigilant while free-ranging males fed and moved more.

FT, the top ranking male of the Cage troop failed to show any significant seasonal variation in the proportion of his time budget dedicated to maintenance activities or vigilance. This could be explained by the high levels of arousal shown by this particular male during the first birth season. At that time, frequent serious agonistic encounters with GO (the adult male that escaped on the 22 of January 1986) were common; thus it could be classified as a period of social instability. For the pre-mating season, GO was still in the surrounds of the cage and a few intertroop agonistic encounters involving the Cage Troop, the free-ranging troop (AT) and GO were witnessed.

The high levels of vigilance shown by FY (the lowest ranking male), increased when the mating season started and when there were only 3 adult males in the troop. Most of his vigilance behaviour consisted of walking/running around the perimeter of the cage, while looking intensely outside. This male was under considerable stress during this season. I suggest that his behaviour was an expression of his desire to become peripheral, reflected by him hiding away when any internal or external disturbance affected the troop. The question of why caged vervet males spend more time socialising can be explained by: i) their having less pressures on their time budgeting, ii) being more related and/or iii) more 'special relationships' might have developed.

### **3.6.6. Subadult-adult male comparison**

Caged subadult males fed more during the pre-mating and mating seasons and rested less during the mating season than did the adult males. The decrease found for resting did not correspond to an increase in vigilance behaviour, but to the high levels of sexual motivation expressed by the two subadult males (see chapter 7).

Locomotor activity was more common among adult than among subadult males at all times. This might be explained by the fact that subadult males were more involved in social play and other social friendly behaviour than adults, although no difference in grooming activity was found (cf. Bramblett & Coelho, 1987)

In the Cage, subadult males participated in grooming as often as adult males though they were more involved in social play and friendly behaviour than adult males. The post-pubertal decrease in social play has been related to an increase in levels of testosterone (Loy, *et al.* 1978).

It is argued that subadult males are 'socially protected'. This was reflected in their showing less submissive behaviour (including homage) than adult males, except during the birth season, and being as aggressive as adult males during the mating season.

In summary, considering that the most important resource for females is food and water (Wrangham, 1979; 1981) which are most scarce towards the end of the mating season (at least in Natal), the presence of more than one adult male in the troop during the non-mating season did not impose serious constraints on female foraging. It is also suggested that male temporal segregation in feeding benefits females and other members of the troop (chapter 4).

On the other hand, for males the most important resource is females (Emlen & Oring, 1977). Access to females can be facilitated if males are known to females and more so if 'special friendly' relations have been established before the female starts cycling (Smuts, 1985). The fact that subordinate males socialise more than the alpha male during the non-mating season suggests that this is the case (see also chapter 6). A lower participation of males in grooming interactions was mostly explained by an increase in participation in agonistic bouts. However, as male participation in play was uncommon and restricted to the younger animals, the argument that aggression reduces playing activity more than any other social behaviour (Symons, 1978) could not be corroborated in this study.

The most dominant male may benefit from coexistence with unrelated males by establishing their relative dominance rank well before the mating season starts. This is mostly accomplished through displays of dominance and subordination which are less costly than open aggression to both the dominant and the subordinate males. In addition, as demonstrated by vervets, a wide range of foods allows monkeys to coexist better (Chapman, 1990).

#### **4. PREDATION, VIGILANCE AND THE QUESTION OF SUPERNUMERARY MALES IN VERVET MONKEYS**

It has been argued that non-human primates live in social groups in order to improve their ability to locate and defend food resources (Wrangham, 1980, Robinson, 1982) and increase the possibility of detecting and avoiding predators (Struhsaker, 1967b; Gartlan & Brain, 1968; Alexander, 1974; van Schaik, 1983, Pulliam & Caraco, 1984) at the expense of greater intraspecific competition for food and mates.

The presence of additional adult males in multi-male troops has been explained by the inability of the dominant male to preclude access to a group of females by other males (see chapter 1). This is more apparent when the number of adult females and the degree of estrus synchrony increases (Ridley, 1986). However, the above proximate explanation does not explain the presence of more than one adult male in troops of vervet monkeys outside the mating season when no receptive females are available (Henzi, 1988). Some of the arguments relating to this issue will be reviewed here.

First, predation avoidance is one of the determinants of the adult sex ratio in primate groups (van Schaik & van Noordwijk, 1989). The balance between food competition and the risk of predation determines interspecific and intraspecific differences in group size in any particular situation (van Schaik & van Hooff, 1983). In addition, polyspecific associations found in some species of arboreal monkeys are regarded as having evolved primarily under the pressure of predation (Gautier & Gautier-Hion, 1983; Gautier-Hion & Tutin, 1988; cf. Cords, 1990) and are advantageous because of lower levels of food competition and the absence of competition for mates between species.

Second, according to Wrangham's ecological model (1980), in female bonded primates the female's biggest concern is to protect limited resources from other female groups. Therefore, females might accept the presence of more than one adult male in the troop in order to protect these food resources, or if males provide them with other benefits.

Taking into account that time allocated to vigilance for predators conflicts with other major maintenance activities such as feeding (see Krebs & McCleery, 1984, p.109), resting and locomotion or with other everyday social interactions (for example grooming and social play), females still benefit by sharing the costs of vigilance with males. In summary, vervet females and their offspring may enjoy a lower risk of predation when males remain in the troop because males: i) provide a dilution effect, ii) increase the levels of vigilance, iii) serve as cannon fodder or iv) they directly attack predators.

Third, why do supernumerary unrelated adult males stay in a non-natal troop in spite of harassment by the dominant male and food competition with unrelated adult females?

Finally, terrestrial and semi-terrestrial non-human primates have evolved different strategies to outweigh the increased risk of predation in open habitats (some of them only possible because of the distribution of food resources in those environments): i) they attain a bigger body size than their forest counterparts (Clutton-Brock & Harvey, 1977b p. 567; Pulliam & Caraco, 1984); ii) they live in large groups (Eisenberg *et al.* 1972; van Schaik, 1983; see also Anderson, 1986); iii) there is a marked sexual dimorphism and males possess large canines for group defence (*e.g.* for baboons: DeVore, 1963) even though these characters may have evolved by sexual selection in polygamous species (Crook & Gartlan, 1966; Struhsaker, 1969; Clutton-Brock, 1977 546); iv) multi-male groups are found (DeVore, 1963; Struhsaker, 1969; Eisenberg, *et al.* 1972; van Schaik & van Noordwijk, 1989) when well defined hierarchical organisations predominate (Chance, 1959) and solitary individuals are rare (Anderson, 1986).

As is common, certain exceptions contradict the above hypotheses. One is the large, highly dimorphic (in weight) mandrill and drill, which live in dense forests, forage mainly on the ground and live in multi-male groups (Napier & Napier, 1985 p.135). Another is the patas monkey *Erythrocebus patas*, a small, terrestrial, very dimorphic in weight monkey that lives in uni-male groups. Patas are seasonal breeders, females can potentially reproduce every year and extranumerary males leave the troop at the end of the breeding season (Harding & Olson, 1986). That additional male patas leave the troop when there are no receptive females might be prompted by the harsh environment where patas live (Crook & Gartlan, 1966). The colouration, the behaviour and social organisation of patas monkeys allows them to blend into their environment, so as to conceal them from potential predators (Hall, 1967).

If a predator detects a patas troop, the adult male diverts its attention towards himself while the rest of the troop remains out of sight in tall grass (Crook & Gartlan, 1966). In addition, Hall (1967) found that the adult male of a patas group remained vigilant while the others were foraging in the presence of humans. Male patas behaviour is similar to the 'sentinel' behaviour of *C.a.sabaeus* in Barbados while raiding crops (Horrocks & Hunte, 1986). These two last study troops had in common the open spaces where they ranged and the presence of a single adult male.

Therefore, it can be hypothesised that the slightly dimorphic, semi-terrestrial vervet monkey behaves in a similar way to outweigh its body size and relatively small troop size. The fact that there is more than one adult male in the troop may also prove to be an important issue in contributing to the reduced risk of predation, possibly increasing the general level of vigilance of the troop.

The suggestion that predation plays a major role in regulating vervet populations (in Amboseli: Struhsaker, 1967 b) is given added weight by the fact that vervets have evolved an auditory signalling system that reduces the risk of predation by using highly specific alarm vocalisations when they sight potential predators (Struhsaker, 1967c; Seyfarth *et al.* 1980; for ringtailed lemurs: Pereira & Macedonia, 1991) which can be regarded as rudimentary semantic signals (Seyfarth & Cheney, 1982). The ability to distinguish between classes of predators, *e.g.* terrestrial mammal *versus* flying bird, is already found in very young animals (Seyfarth & Cheney, 1982) and improves during ontogeny due to reinforcement from adult reactions (Cheney, 1984 p.66).

In summary, the above hypotheses strongly suggest that one of the ultimate cause of vervet monkeys living in multi-male groups is to reduce the risk of predation.

The following issues will be investigated in this chapter in order to understand the benefits in terms of increased fitness for males remaining in the troop throughout the year. First, whether there are differences in time spent vigilant by adult and subadult males, and females. Second, if these differences exist, whether they are rank-related or show a seasonal effect. Third, are there sex and/or rank differences in responses to predators *e.g.* alarm calls and actual defence? Fourth, can time spent in potentially dangerous positions be related to sex and dominance rank and levels of vigilance?

#### 4.1. VIGILANCE

Vigilance is defined as a state of high awareness towards the environment surrounding the subject (Plate 4.1-4.2). During the field study, certain behaviours were difficult to categorise as either resting or strictly vigilant, consequently a composite behaviour category 'Resting-Vigilant' (RV) was defined. When writing about vigilant states hereafter, I will refer to the behaviour category 'Vigilant' (VG) (see chapter 2) if not otherwise stated.



Plates 4.1 and 4.2. Vigilant adult male (alpha male of the Windy Ridge troop).

Reasons for vigilance may differ; unfortunately it was not possible to determine what these were for each sample. A vigilant monkey could be wary for various reasons: i) the activities of other monkeys in the troop, ii) the proximity of extragroup vervets, iii) the proximity of a potential predator or iv) signs of distress are shown by other species. The data presented in this section were obtained from scan samples and the values correspond to the monthly and total percentage of samples in which the focal animal was vigilant.

I hypothesise that adult male vervets spend more time vigilant than other members of the troop: i) to offset nutritional costs, specially additional males as expected from Wrangham's (1980) predictions, ii) because they have more time available due to their lower metabolic demands, iii) as they tend to be more peripheral, particularly subordinate individuals (Hall & Gartlan, 1965) they are more at risk than others.

#### **4.1.1. Vigilance rates for the Windy Ridge troop**

In general, adult males spent more time vigilant every month than adult females ( $t=6.283$ ;  $p<0.01$ ) (Fig. 4.1). This was true for the pre-mating and mating seasons but not for the birth season (Table 4.1). This occurred because although both males and females increased their levels of vigilance as the mating season approached ( $y=5.39+2.41x$ ;  $t_{\text{slope}}=5.07$ ; 24 df;  $p<0.001$  and  $y=1.99+0.96x$ ;  $t_{\text{slope}}=4.29$ ; 63 df;  $p<0.001$  respectively), males did so more rapidly than females (Zar, 1974,  $t=8.68$ ; 85 df;  $p<0.001$ ).

Seasonal differences in time spent vigilant were found for all the adult males of the free-ranging troop. Those reflected an increase in vigilant behaviour as the mating season approached (Table 4.2). TI, a three year old juvenile male at the beginning of the study, also exhibited a steady increase in the time allocated to vigilance during the course of the study (Table 4.2). It was intermediate between that shown by adult males and the mean value for reproductive females (Fig. 4.1).

It is uncertain whether the increased levels of vigilance were due to a reduction in the number of adult males or were directly related to the mating season, when the influx of extra-troop males increases (Henzi & Lucas, 1980). The dominant RO showed higher levels of scanning for May, just before another adult male (GR) joined the troop and a secondary peak in January that corresponded to the time one of the subordinate males (CH) left the troop in January (Fig. 4.1). PE showed an increase just after CH had left and so did LE. LE also increased his vigilance when PE migrated in March (Fig. 4.1).



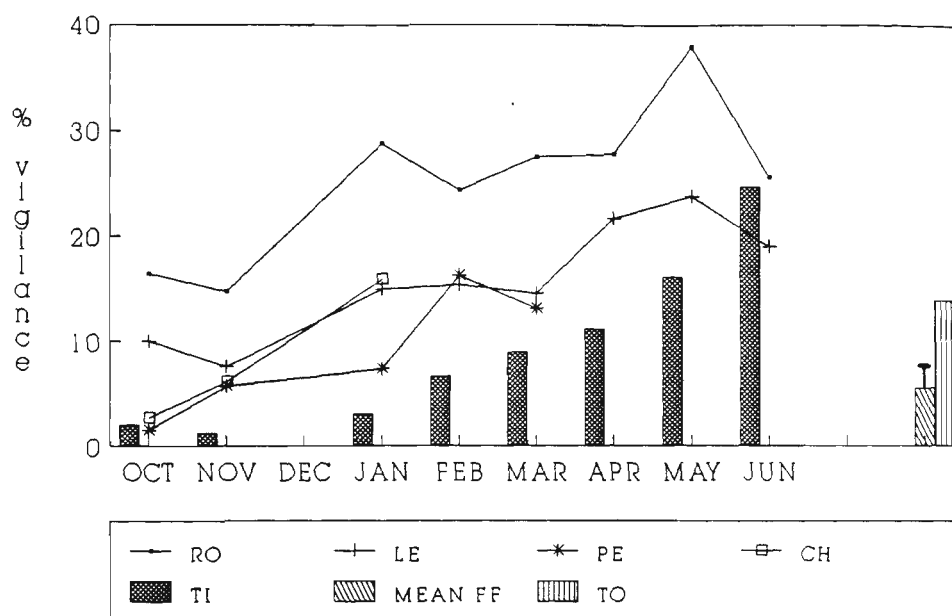


Figure 4.1. Monthly time budget adult males (RO,LE,PE,CH,GR) and subadult male (TI) spent vigilant, mean and standard deviation for reproductive females over all the study period and total vigilance by the post-reproductive female (TO).

Table 4.1.

Median and standard deviation for the adult males and females of the free-ranging troop (WT) during the birth (B), pre-mating (N) and mating (M) seasons for time spent vigilant. Within class seasonal differences were tested using the Wilcoxon signed rank test ( $z$ ) and are detailed ( $\leq$  when  $p=0.06$ ). inter-gender differences were assessed using the Mann-Whitney U-test (two-tailed and significance level set at 0.001).

	SEASON			
	B	N	M	
males	6.9 ± 5.3	15.6 ± 6.8	27.7 ± 6.8	B < N ≤ M
females	4.0 ± 3.4	4.3 ± 3.9	8.2 ± 6.1	B = N < M
	NS	p < 0.001	p < 0.001	

Table 4.2.

Proportion of time budget dedicated to vigilance by adult and subadult males during the birth (B), pre-mating (N) and mating (M) seasons. Seasonal differences were tested using the Chi-square test and the level of significance was set at  $p < 0.05$  (\*) and  $p < 0.001$  (\*\*). Males are ordered in decreasing dominance rank order.

SEASON				
	B	N	M	X <sup>2</sup>
Adult males				
RO	15.3	26.7	31.4	18.230 **
LE	7.7	15.0	21.9	18.610 **
PE	4.0	12.4	---	8.593 *
CH	5.2	15.8	---	6.075 *
GR	---	---	23.1	
Subadult male				
TI	1.0	6.6	16.5	31.060 **

#### *Intra-gender differences in vigilance*

In order to investigate rank differences among males and females individual differences were sought with the Chi-square test. The rank order was determined by the outcome of agonistic encounters for both adult males and females (see chapter 3). For the adult males of the Windy Ridge troop it was  $RO > LE > PE > CH$ ; and for the adult females  $HI > SM > MO > BE > WE > TO > VE > ET$  from highest to lowest ranking individual.

RO, the dominant adult male during the entire study period, showed the highest levels of vigilance for males (birth:  $X^2 = 17.35$ ; 3 df;  $p < 0.001$ ; pre-mating:  $X^2 = 40.93$ ; 3 df;  $p < 0.001$  and mating season:  $X^2 = 13.756$ ; 2 df;  $p < 0.001$ ). LE, the other adult male who remained in the troop for the entire study period and adopted a subordinate role, showed lower levels of vigilance when compared to the dominant male. This was true during the pre-mating ( $X^2 = 23.08$ ; 1 df;  $p < 0.001$ ) and mating ( $X^2 = 13.04$ ; 1 df;  $p < 0.001$ ) seasons but the differences in vigilance during the birth season were just above the level of significance ( $X^2 = 3.427$ ; 1 df;  $p = 0.06$ ).

It is interesting to note that subordinate (additional) males did not differ among themselves in proportion of time dedicated to vigilance among themselves (birth:  $X^2 = 1.938$ ; 2 df; NS; pre-mating:  $X^2 = 1.599$ ; 2 df; NS and mating season:  $X^2 = 0$ ; 1 df; NS). It is concluded that the highest ranking adult male in Windy Ridge spent more time vigilant than additional males (Fig. 4.2).

## RANK/VIGILANCE ADULT MALES (WT)

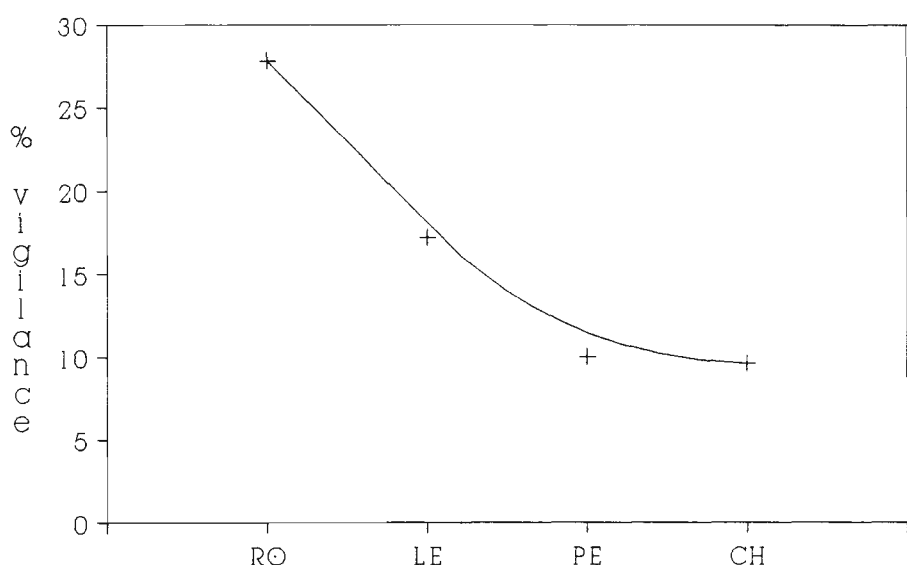


Figure 4.2. Time spent vigilant by (RO>LE>PE>CH) in Windy Ridge troop.

The free-ranging adult female who spent the most time vigilant was TO (Fig. 4.1), one of the lower ranking females. TO was the only female who did not have a dependent infant during the study period, neither from the previous breeding season (because of the appearance of her nipples) nor in the following two breeding seasons. Her level of vigilance was comparable to that of an additional adult or subadult male, possibly because of the reduction in time necessary for activities such as nursing and caring for the young. TO was also more vigilant during May and June.

The two other females who showed higher levels of vigilance were the top ranking HI and third ranking MO. It is also necessary to take into account the fact that the second ranking female SM was very young which could explain why she did not show the same trend. Spearman rank correlation coefficient showed that there was no relationship between dominance rank and vigilance among females ( $r_s = -0.28$ ; 7 df;  $p = 0.44$ ), not even when excluding TO, the post-reproductive female ( $r_s = -0.50$ ; 6 df;  $p = 0.22$ ). It is speculated that female vigilance is more related to age than to rank, unfortunately the age of the females was not known.

At this point, it can be concluded that time spent vigilant by adults in Windy Ridge was higher for adult males, especially the top ranking male, that there were no differences between the post-reproductive female and additional males, and finally, that the reproductive females that were more vigilant were the first and third ranking individuals. In addition, the general levels of vigilance increased as the mating season approached, either because of seasonal effects or because the number of males decreased from January onwards (Figs. 4.1 and 4.2).

Stepwise multiple regression analysis was used to assess the relative importance of month (1-9), time spent feeding, resting, grooming, on the ground, exposed on top of the canopy and peripheral, on time spent vigilant every month. When all the adult members of the troop were analysed together, it was found that time spent on top of the canopy ( $b=1.48$ ;  $t=11.42$ ), month number ( $b=0.75$ ;  $t=6.0$ ) and time peripheral ( $b=0.63$ ;  $t=3.44$ ) were the variables more correlated with time spent vigilant ( $F=194.05$ ; 86 df;  $p<0.001$ ).

The proportion of time spent vigilant every month by an adult male was affected mainly by time spent on top of the canopy ( $b=1.2$ ;  $t=6.29$ ) and increased during the study period, that is from the birth through the mating season ( $b=2.08$ ;  $t=8.19$ ). Those were the only variables that entered the regression model ( $F=165.5$ ; 25 df;  $p<0.001$ ). In agreement with what was found for adult males, the female's increase in time dedicated to vigilance was mainly explained by a greater time exposed on top of the canopy ( $b=1.26$ ;  $t=3.28$ ) and month number ( $b=0.69$ ;  $t=3.07$ ) ( $F=16.071$ ; 61 df;  $p<0.001$ ).

#### **4.1.2. Vigilance rates for the Cage Troop**

The total level of awareness towards the surroundings is expected to be related to the risk of predation and to the proximity of extratroup monkeys. The caged monkeys had been born in captivity or had been trapped at least 10 years earlier. Even though the risk of predation was drastically reduced, the typical reactions to predators remained; they alarm called when eagles or hawks flew over the cage or when strangers approached the area. When snakes approached or entered the enclosure they showed the same curiosity as the wild troop and alarm called.

Taking into account that the behaviour resting/vigilant was included as vigilance during the study in the Cage, and as a different category during the field study, total vigilance was comparable for males of both troops (25% VG+RV and 20% VG + 7.6% RV respectively).

In the Cage troop 'pacing the perimeter' (Tollman & Lucas, 1979) was also considered as vigilance. The reason for doing so was because of the intensity shown by the animals while looking outside the enclosure when performing this behaviour. Tollman and Lucas found that this was more common among high ranking males and suggested that it could represent the initiation of troop movements. However, my impression was that it was a stereotype or tension-related behaviour and it could better reflect the tendency of low ranking males to become peripheral. The lowest ranking male (FY) showed the highest frequency of this behaviour followed by the middle ranking male (RN). 'Pacing the perimeter' explains the high level of vigilance found for FY and RN. Cage escapees GO and LU were only recorded as vigilant in 10 and 7 samples respectively, so it was appropriate to ignore them for statistical purposes.

In the Cage, adult males were also more vigilant than subadult males (Fig. 4.3 and Table 4.3). The subadult males also showed a progressive rise in vigilance throughout the study (see also Fig. 4.1 for TI, the subadult male of WT). The middle ranking (RN) and the low ranking male's (FY) levels of vigilance were higher during the mating season (Table 4.3), due to an increase in the frequency of 'pacing of the perimeter'. However, the top ranking adult male and the subadult males did not show any seasonal change in time spent vigilant (Table 4.3). The high levels of vigilance maintained by FT once the mating season had ended, compared to the previous year, could have been related to a reduction in the number of adult males in the troop (Fig. 4.3).

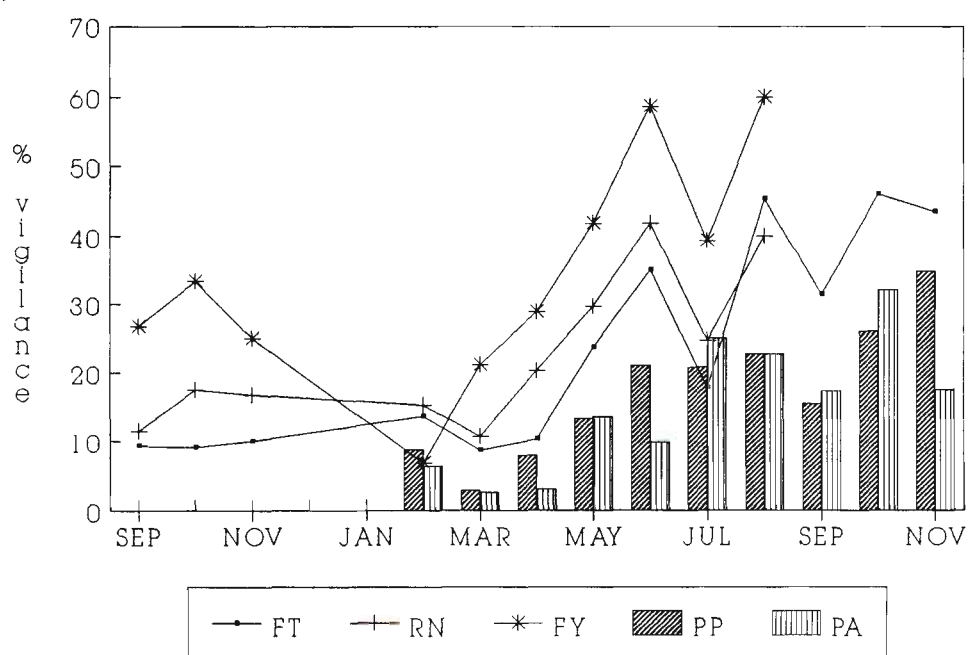


Figure 4.3.

Proportion of time spent vigilant every month by adult (FT>RN>FY) and subadult males (PP>PA) in the Cage Troop.

Table 4.3.

Proportion of time budget dedicated to vigilance by adult males of the Cage Troop during the birth (B), pre-mating (N) and mating (M) seasons. Seasonal differences were tested using the Chi-square test and the level of significance ( $p$ ) was set at  $<0.05$  (\*) and  $<0.001$  (\*\*). Males are ordered in decreasing dominance rank order.

	SEASON			
	B	N	M	$\chi^2$
<b>Adult males</b>				
FT	29.5	22.1	22.1	1.990 NS
RN	15.4	12.0	29.2	12.200 *
FY	31.3	21.0	41.4	13.990 **
<b>Subadult males</b>				
PP	(B+N) 19.8		14.1	2.679 NS
PA	(B+N) 16.6		12.3	1.702 NS

#### *Male differences in vigilant behaviour in the Cage Troop*

In the Cage the results obtained for male differences in vigilant behaviour were opposed to those found for the free-ranging troop. The three adult males for which enough samples on vigilance had been collected did not differ in time spent vigilant during the non-mating periods (B:  $\chi^2=2.181$ ; 2 df; NS and N:  $\chi^2=4.378$ ; 2 df; NS), but did so during the mating season ( $\chi^2=25.320$ ; 2 df;  $p<0.001$ ). These differences are explained by the lowest ranking male (FY) being more vigilant than either the dominant male FT ( $\chi^2=23.628$ ; 1 df;  $p<0.001$ ) or the middle ranking male RN ( $\chi^2=8.272$ ; 1 df;  $p<0.05$ ). The differences in vigilance between the middle and top ranking male were above significance ( $\chi^2=3.350$ ; 1 df;  $p=0.07$ ). Finally, both subadult males of the Cage showed a similarity in amount of time spent vigilant during the non-mating ( $\chi^2=0.587$ ; 1 df; NS) and mating seasons ( $\chi^2=0.315$ ; 1 df; NS).

Even though subadult males were significantly less vigilant than adult males during the mating season, no differences were found for the non-mating period (Table 4.4). However, differences were apparent for the subadult free-ranging male, possibly due to the fact that in Windy Ridge the study progressed from the birth onto the mating season which was not the case for the study in the Cage. It was true that the subadult males in both troops showed a tendency to increase their levels of vigilance with age (Figs. 4.1 and 4.3).

Table 4.4.

Differences in time spent vigilant by the adult and subadult males of the Cage troop during the birth (B), pre-mating (N) and mating seasons (M) (see Table 4.3 for level of significance obtained using the Chi-square test).

	SEASON		
	B	N	M
Adult males	21.2	16.7	30.8
Subadult males	20.0	17.0	13.6
	NS	NS	p < 0.001

#### **4.1.3. Synchronisation during feeding and locomotion**

It is advantageous to have vigilant animals when the activity of most members of the troop requires a high level of attention (Krebs & McCleery, 1984 p.114). This section will provide data obtained from the Windy Ridge troop.

The aim of this section is to investigate sexual and intra-gender differences in synchronisation during feeding and locomotion. These activities require more concentration and movement, which make monkeys more vulnerable to predation, consequently, a certain asynchrony due to the presence of vigilant animals or 'sentinels' is expected. In other words, one or more animals would remain vigilant while the rest of the troop forages.

The degree of synchronisation is reflected in the percentage of scans in which the behaviour of the focal animal was the same as the general activity. This was described as the most common behaviour occurring at the time of each scan sample (more than half of the observed animals were carrying out this particular activity). Student's t tests have been used to test for sex differences, after having first ensured that the variables fitted a normal distribution; this was done using a Kolmogorov-Smirnov one sample test.

Stepwise multiple regression analyses determined the most common activities for adult females (for males alone there were not enough samples to undertake this analysis) when they were not feeding or moving with the rest of the troop. The influence of rank in the degree of synchronisation is also analysed.

### *Feeding periods*

Females fed with others ( $75.9 \pm 4.8$ ) more often than males did ( $61.6 \pm 13$ ) ( $t = -2.847$ ;  $p < 0.05$ ). This result could also be explained as a strategy to reduce or avoid direct male-female food competition. Male synchronisation in feeding with others presented significant individual differences ( $X^2 = 32.23$ ; 3 df;  $p < 0.001$ ) and the same occurred among females ( $X^2 = 16.186$ ; 7 df;  $p < 0.05$ ).

The expectation that low ranking animals feed at different times to avoid food competition was not corroborated in this study (females:  $\rho = -0.347$ ;  $n = 8$ ;  $p = 0.36$ ). Conversely, feeding with other members of the troop was more common amongst the two lowest ranking and the subadult males than it was for the higher ranking males ( $r_s = -0.900$ ,  $n = 5$ ,  $p < 0.05$ , one-tailed). Moreover, subordinate males fed ( $67.0 \pm 9.0$ ) as often as females when the general context was feeding (see below).

Table 4.5.

Total number of scan samples for adult and subadult males, and adult females ordered in decreasing rank when the general context was 'feeding' and the percentage of these samples when the behaviour of the focal animal was Resting/Vigilant (RV), Feeding (FE), Locomotion (LO) or Vigilant (VG).

		<u>RS/RV</u>	<u>FE</u>	<u>LO</u>	<u>VG</u>
<b>Adult males</b>					
RO	332	11.7	45.5	10.8	30.1
LE	281	14.9	56.9	8.9	16.4
PE	143	7.7	74.1	5.6	7.7
CH	50	8.0	70.0	4.0	8.0
<b>Subadult male</b>					
TI	218	6.4	76.6	6.4	7.8
<b>Adult females</b>					
HI	232	12.9	72.4	6.9	5.6
SM	245	6.9	81.6	7.8	0.8
MO	182	9.3	76.4	6.6	4.9
BE	244	8.6	79.1	6.6	3.3
WE	216	5.5	81.9	6.9	3.7
TO	179	5.6	72.6	9.5	8.9
VE	140	12.1	75.0	9.3	0.0
ET	220	17.7	68.2	9.1	2.7



Resting ( $b=-0.94; t=-19.13$ ) followed by vigilance ( $b=-0.97; t=-13.61$ ) and locomotion ( $b=-1.34; t=-8.59$ ) were the most common activities adult females were involved in when not feeding with the rest of the troop ( $F=209.55; 4 \text{ df}; p<0.001$ ). For males, vigilance was the most common behaviour when not feeding with other members of the troop, especially for the top ranking male (RO) (Table 4.5 and Fig. 4.4 a).

It can be hypothesised that any mechanisms which reduce direct male-female competition for food resources may have been selected in multi-male species. This includes any advantages males may provide to females during foraging. Adult males fed at different times to females, thereby reducing intersexual food competition. Additionally, high levels of alertness were possible as the males remained vigilant when the rest of the troop was foraging. The ultimate cause of feeding asynchrony between males and females could therefore be to reduce predation.

#### *General locomotion*

During general locomotion the female's degree of synchronisation with the rest of the troop ( $51.9 \pm 11.6$ ) was equivalent to the male's ( $40.6 \pm 5.6$ ) ( $t=-1.80; p=0.10$ ). There were significant differences in individual values amongst females ( $X^2=61.975; 7 \text{ df}; p<0.001$ ) but not amongst males during locomotion ( $X^2=0.26; 3 \text{ df}; p=0.26$ ) (Table 4.6). Males moved ( $r_s=0.818; n=5; p=0.10$  one-tailed) and fed ( $r_s=1.224; n=5; \text{NS}$ ) with the troop independently of their rank (Fig. 4.4b). On the other hand, a negative correlation with rank on the degree of synchronisation of females with the rest of troop was found ( $b=-4.03; t=-3.91$ ) which was significant ( $F=15.265; 6 \text{ df}; p<0.01$ ) (Table 4.6). For adult females in general, the degree of synchronisation was correlated with rank ( $r_s=-0.881, n=8, P<0.05$ , one-tailed), with high ranking females moving more often with other members of the troop than with lower ranking females. Meanwhile, low ranking females spent more time resting than high ranking females ( $r_s=0.905; n=8; p<0.05$ ).

#### *Is de-synchronisation prompted by vigilance?*

During feeding, males were more vigilant ( $15.6 \pm 10.5$ ) than females ( $3.7 \pm 2.8$ ) ( $t=3.10; p<0.05$ ). The same results were found during general locomotion ( $t=3.34; p<0.05$ ) with males being more vigilant ( $18.5 \pm 6.6$ ) than females ( $6.8 \pm 5.2$ ). This was especially true for RO, the most dominant male (Tables 4.5 and 4.6). In addition, RO was vigilant in a strategic position (at the top of the canopy) more often than expected ( $X^2=6.832; 1 \text{ df}; p<0.01$ ).

### *Sex differences without the alpha male*

When the top ranking male is removed from this analysis, sex differences in degree of male synchronisation during feeding ( $t=-2.19$ ;  $p=0.056$ ) and locomotion ( $t=-1.87$ ;  $p=0.09$ ) were not significant. However, additional males are still more vigilant than females during feeding periods ( $10.7 \pm 4.9$ ) ( $t=3.02$ ;  $p<0.05$ ) and general locomotion ( $15.5 \pm 3.3$ ) ( $t=2.6$ ;  $p<0.05$ ).

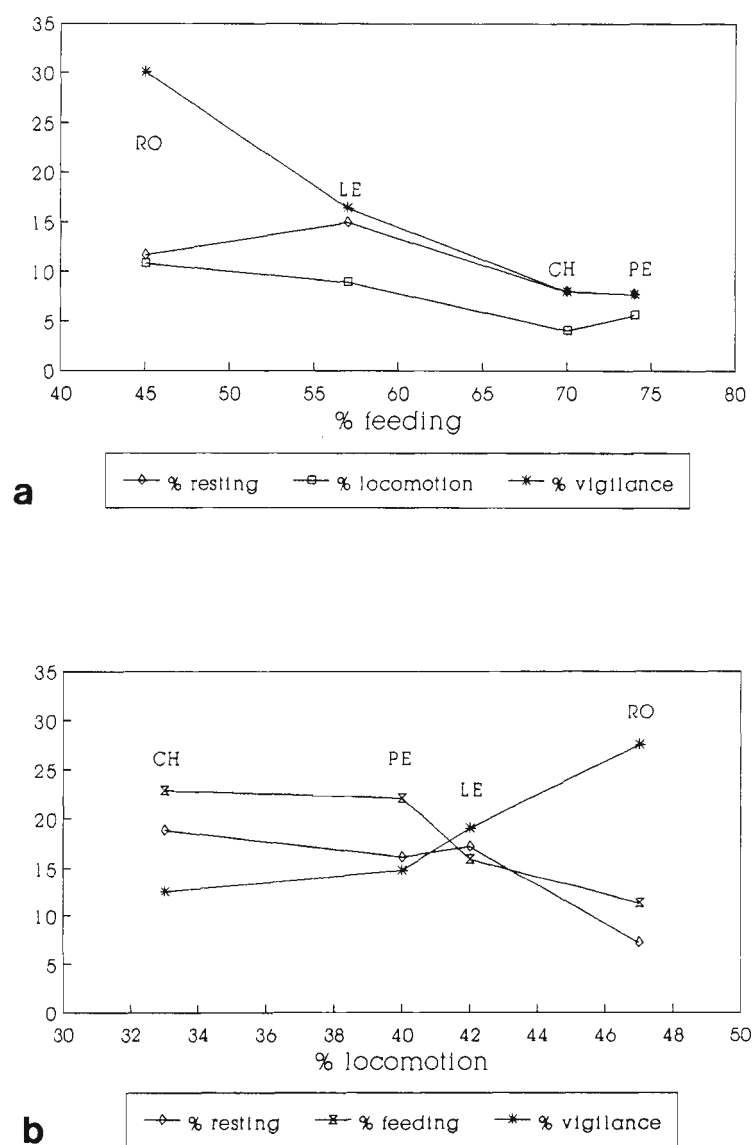


Figure 4.4. Male activity when most of the members of the troop were: a) feeding or b) during general progressions.

Table 4.6.

Total number of scan samples for adult males and adult females ordered in decreasing rank when the general context was 'locomotion' and the percentage of these samples when the behaviour of the focal animal was Resting/Vigilant (RV), Feeding (FE), Locomotion (LO) or Vigilant (VG).

		<u>RS/RV</u>	<u>FE</u>	<u>LO</u>	<u>VG</u>
<b>Adult males</b>					
RO	291	7.2	11.3	46.7	27.5
LE	232	17.2	15.9	42.2	19.0
PE	149	16.1	22.1	40.3	14.8
CH	48	18.8	22.9	33.3	12.5
<b>Subadult male</b>					
TI	146	15.1	23.3	49.3	7.5
<b>Adult females</b>					
HI	174	8.0	19.0	62.6	6.9
SM	160	8.8	16.3	68.1	4.4
MO	125	13.6	16.8	57.6	4.8
WE	136	12.5	22.1	57.4	5.1
BE	146	16.4	26.0	49.3	4.1
TO	168	16.7	27.4	35.1	19.0
ET	171	22.8	32.2	38.0	2.3
VE	124	23.4	18.5	46.8	8.1

In summary, additional males are also advantageous to the troop during locomotion and feeding periods, as they act as 'sentinels'. These results emphasise the importance of the behavioural strategies vervet monkeys use that avoid direct food competition. Apart from this temporal strategy which may act to reduce intersexual agonism during feeding periods, other proposed strategies which compensate for rank differences are those of ecological segregation.

## 4.2. RESPONSES TO PREDATORS

In this section I will discuss: i) alarm vocalisations specifically prompted by the presence of a potential predator; ii) alarm situations when no alarm vocalisations were heard; iii) context during which alarm vocalisations were given; iv) behaviour prior and after alarm vocalising and finally, description of actual encounters with predators. Alarm vocalisations given at the proximity or when sighting extra-group monkeys, will not be considered here.

#### 4.2.1. Distribution of alarm vocalisations

Adult males gave 84 alarm calls (51%), the post-reproductive female 22 (13%), the seven reproductive females 47 (28%), and immature monkeys only 14 (8%). That is, a total of 167 alarm vocalisations were recorded during the field study. Of these 117 were first alarms, 44 subsequent alarms and on 26 occasions it was not possible to identify if the vocalisation was the first alarm given in the troop or a subsequent alarm.

In general, the number of 1st alarm vocalisations given by an individual was highly correlated with time spent vigilant ( $r_s = 0.63$ ; 12 df;  $p < 0.05$ ); the same was true for males (GR excluded:  $r_s = 0.99$ ; 3 df;  $p < 0.05$ ) and females ( $r_s = 0.79$ ; 7 df;  $p < 0.05$ )(Fig. 4.5). If males were investing more time in vigilance than females in order to detect predators, we might predict that they were more efficient at doing so, but this was not the case ( $t_{\text{elevation}} = 1.8$ ; 10df; NS).

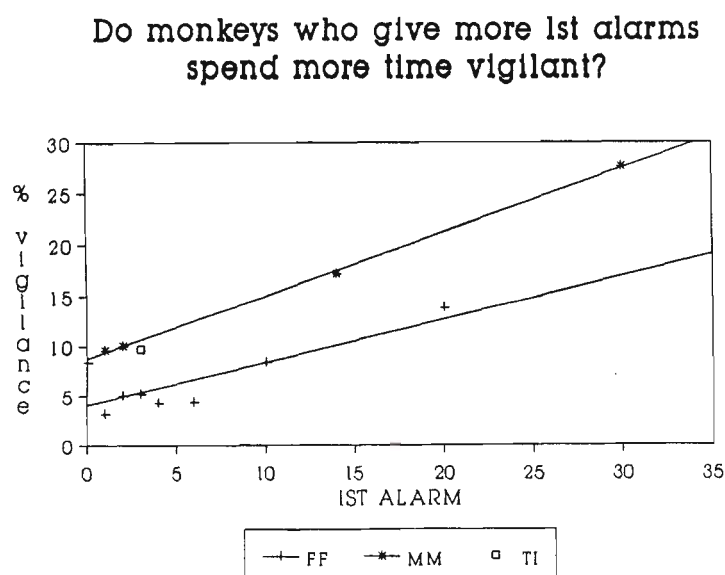


Figure 4.5. Relationship between time spent vigilant and number of first alarm calls given by adult females (FF), adult males (MM) and the subadult male (TI).

The first alarm vocalisation given can be assumed to serve as a warning for the rest of the troop, while the subsequent alarm vocalisations can function as a threat towards potential predators. The total number of 1st alarm vocalisations given by each adult monkey was significantly correlated to the number of subsequent alarm calls ( $r_s = 0.915$ ,  $N = 11$ ,  $P < 0.001$  two-tailed).

The relation between the number of times an individual gives a 1st alarm *versus* the number of times he gives non-first alarm vocalisation is as follows (with a minimum of 5 first alarms recorded): adult males RO (60.0%) and LE (66.7%); adult females HI (83.3); TO (90.0%) and ET (100%). These results show that adult females were primarily first vocalisers while adult males tended to vocalise more often when the troop had already been warned of the danger.

#### **4.2.2. First alarm vocalisations**

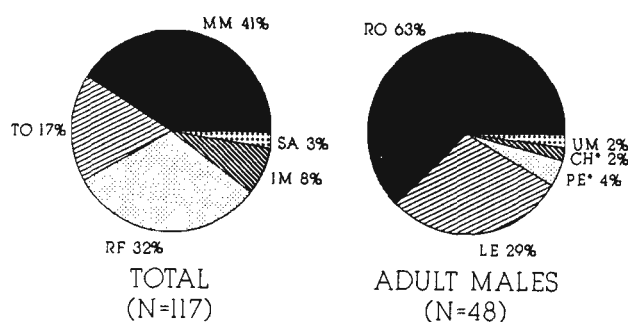
In the following analysis, the number of calls have been corrected according to the time each individual spent in the troop.

In general, adult males gave more first alarm calls than adult females ( $X^2 = 26.4$ ; 1 df;  $p < 0.001$ ). However, individual males did not vocalise more often than individual females (Mann-Whitney U-test;  $U = 8$ ;  $p = 0.14$ ) and immature animals alarm called less frequently than adults (Fig. 4.6).

The male who gave the most first alarm vocalisation was the top ranking male RO ( $X^2 = 18.573$ ; 1 df;  $p < 0.001$ ). The post-reproductive female TO and the additional male LE (12%) were next (Fig. 4.6). TO gave more first alarm calls than additional males as a group (TO/additional males:  $X^2 = 7.83$ ; 1 df;  $p < 0.05$ ) and reproductive females ( $X^2 = 27.523$ ; 1 df;  $p < 0.001$ ). Finally, the frequency with which adult females with dependent infants gave 1st alarm vocalisations vary ( $X^2 = 16.750$ ; 6 df;  $p < 0.05$ ) independently of their rank ( $r_s = -0.012$ ; 7 df;  $p = 0.97$ ).

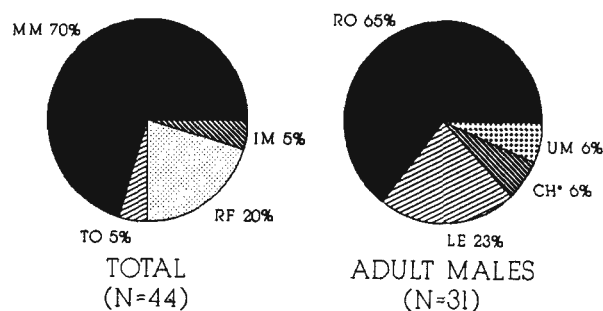
In summary, the main first vocaliser was the alpha male, the post-reproductive female next, closely followed by the additional males as a group. The animals giving less alarm vocalisations were those more prone to predation, that is adult reproductive females and immature animals. No evidence was found indicating that higher ranking females alarm called more often than other reproductive females.

### FIRST ALARM CALLS



\*CH/PE only present in 7/13

### SUBSEQUENT ALARM CALLS



\*CH was only present in 8

Figure 4.6. Proportion of first and subsequent alarm calls given by an adult (MM) or the subadult male (SA), a reproductive female (RF), the post-reproductive female (TO), or by an immature (IM). The dominance rank for the adult males was RO > LE > PE > CH (UM: unidentified male).

#### 4.2.3. Non-first alarm vocalisations

Alarm vocalisations towards possible predators were generally given only once (76.5% of the times) due to the risk of attracting the attention of the predator. Therefore, these subsequent calls may represent more a threat towards predators than a warning of their presence.

The adult monkeys giving subsequent alarm vocalisations were mostly males (70%) (adult males/reproductive females  $X^2=42.976$ ; 1 df;  $p<0.001$ ). This was mainly due to the action of the alpha male ( $X^2=16.050$ ; 1 df;  $p<0.001$ ). The post-reproductive female vocalised as often as expected for an adult female (Fisher's exact test, two-tailed, NS) and did not differ from the additional males ( $X^2=1.125$ ; 1 df; NS). However, the reproductive females alarm called (after the troop had already been warned of the proximity of a predator) less often than additional males ( $X^2=8.036$ ; 1 df;  $p<0.05$ ) (Fig. 4.6).

The monkey who gave the most subsequent alarm calls was the alpha male. The differences between the other classes were not significant except for the reproductive females who gave less calls than the additional males.

#### *What elicits alarm vocalisations?*

The major cause of alarm calls were large raptors ( $X^2=9.652$ ; 1 df;  $p<0.05$ ). The reproductive females and the two adult males, who remained in the troop for the study period, directed over 50% of their alarms at raptors. These results corroborate observations of one successful and a few failed attempts by crowned eagles to capture vervets. The second major cause of alarm vocalisation were big birds (vultures, hadedas, hornbills, storks). Finally, humans and baboons also evoked alarm calls. The fact that the study troop in Windy Ridge had been culled two years earlier, may explain the long period required to habituate the troop to the presence of the observers.

At least 8% of the alarm vocalisations given by the study troop were preceded by alarms given by neighbouring troops and at least 6% followed by them. These vocalisations were mainly eagle alarm calls, which reinforces the statement that raptors, besides man, are the main potential predator of vervets in Windy Ridge.

Immature vervets gave alarms at falling leaves, birds flying or landing nearby or other objects that did not present any danger (Table 4.7). Alarms evoked by baboons, who sometimes kill vervets, were very scarce (4). There is not enough evidence that adult males only vocalise towards predators that can attack them.

Table 4.7.

Species to which alarm vocalisations were given by immatures (IM); reproductive females (FF); the post-reproductive female (TO); adult males (MM), particularly the dominant (RO) and the subordinate (LE). Only those observations when the first alarm caller was identified have been considered (N=117).

\* Alarm calls towards predators by other troops.

	IM	FF	TO	MM	RO	LE	TOTAL
Eagle & hawk	1	16	2	18	11	6	37
Big bird	1	4	1	6	3	3	12
Small bird	1	2	0	2	1	1	5
Humans	0	1	8	1	1	0	10
Baboons	1	2	1	0	0	0	4
OT Vocal*	2	2	0	4	3	1	8
Snake	2	1	0	1	1	0	4
Crocodile	1	0	0	0	0	0	1
Legavaan	1	1	0	0	0	0	2
Unknown	2	8	8	16	10	3	34
Total	12	37	20	48	30	14	117

#### **4.2.4. Occurrences of alarm when no vocalisations were given**

As mentioned above, the sighting of eagles evoked more alarm calls than the sighting of any other species, while eagle vocalisations inhibited alarm calls more often than expected ( $X^2=24.054$ ; 1 df;  $p<0.001$ ). Consequently, after eagles had been heard vocalising, monkeys alarm called less often than when only sightings occurred ( $X^2=30.558$ ; 1 df;  $p<0.001$ ). The fact that the general reaction of the vervets was similar to that provoked by a vervet's eagle alarm call shows the high degree of adaptation of the vervet signalling system. In other words, it is not necessary to expose themselves to predators by vocalising if they have already been warned by the predator.

In agreement with the above argument, when those avian species which were not a threat to the monkeys vocalised, the number of times the monkeys alarm called did not differ from the number of times they remained silent ( $X^2=2.234$ ; 1df; NS). In addition, when ungulates gave alarm calls in the proximity of the monkeys, they showed distress and did not return the call 36.4% of the times (Table 4.8). The monkeys of Windy Ridge responded to human sightings by giving soft alarm vocalisations (58.3% of the encounters), fleeing when approached at close range, or by hiding in the canopy (Table 4.8).



When encountering baboons the typical reaction was that of avoidance, with the exception of a couple of instances of play. However, the vervet's common reaction was to keep quiet and wait until the baboons left the area.

The fact that eagles, humans and baboons were probably the main predators of vervets at Windy Ridge is again emphasised when one looks at the total number of alarms including the high proportion of silent alarms evoked when the above predators were detected by their own vocalisations, or in the case of humans by the sound of the car engine stopping.

There were times when an individual could have given an alarm but did not. This occurred with the second ranking adult male at least three times when he rushed into a tree after sighting an eagle and uttered no call. On these occasions he was more than 50 m from any other monkey. It could be hypothesised that: first, audience effect played an important role, and second, that this particular animal did not want to expose itself. Cheney and Seyfarth (1990, p.190) pointed out that withholding or concealment of information was more common among low ranking vervets. On the other hand, when other troops were heard alarm calling ( $n=8$ ), the study troop always reacted by alarm calling (Table 4.8) possibly because the caller was not at risk by giving the alarm.

Table 4.8. Total number of 1st alarm vocalisations given to predators or suspected predators, events in which alarm was shown by an individual or more members of the troop and no alarm vocalisation was heard and the percentage of silent reactions.

	N	VOCAL	SILENT	%SILENT
Eagle & hawk	53	47	6	11.3
Eagle vocal	13	1	12	92.3
Big bird	15	12	3	25.0
Small bird	7	5	2	28.6
Bird vocal	4	1	3	75.0
Humans	24	14	10	41.7
Baboons	8	2	6	75.0
Baboons vocal	6	2	4	66.7
Snake & crocodile	5	5	0	---
Legavaan	4	2	2	50.0
Ungulate alarm	11	7	4	36.4
Other troop	8	8	0	---
Unknown	35	29	6	16.2
TOTAL	193	135	58	30.1

## GENERAL CONTEXT OF ALARM VOCALIZATIONS

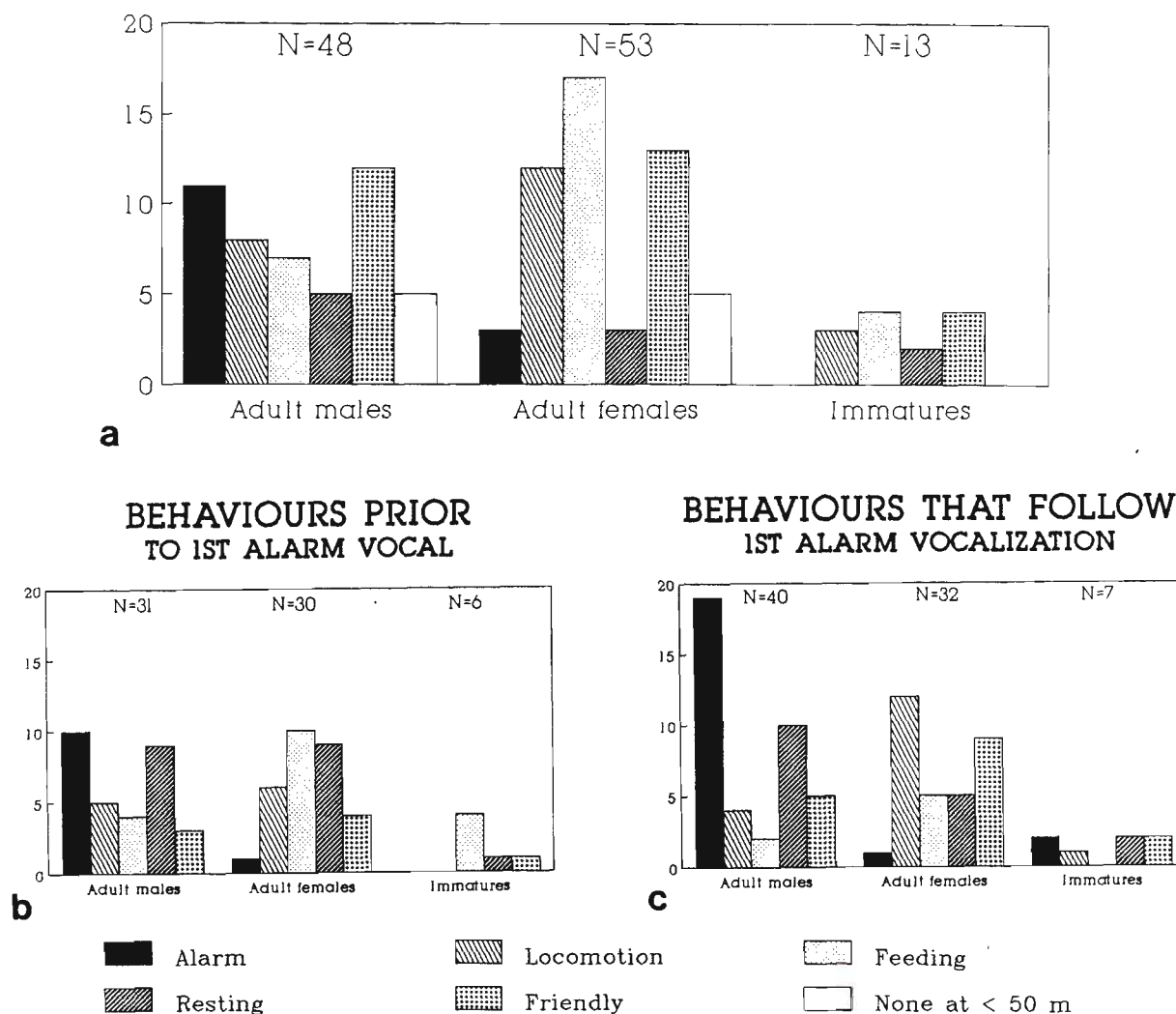


Figure 4.7 a) The general context of the troop (or if away from others) when first alarm vocalisations were given by adult males, adult females or immatures; b) The most common behaviour of males, females and immatures when they gave a first alarm call; c) The behaviour of callers after giving an alarm.

### 4.2.5. Behaviour prior and after giving the 1st alarm call

The general context when adult males gave the first alarm more often than females, was that of alarm ( $X^2=4.920$ ; 1 df;  $p<0.05$ ). Males and females did not differ in the total number of times they alarm called during general feeding ( $X^2=3.343$ ; 1 df;  $p=0.07$ ), resting ( $X^2=0.265$ ; 1 df; NS), locomotion ( $X^2=0.252$ ; 1df; NS), social behaviour ( $X^2=0$ ; 1 df; NS) or when at more than 50 m from any other member of the troop ( $X^2=0$ ; 1df; NS) (Fig. 4.7 a). Immatures displayed higher levels of fright when concentrating on feeding (see Fig. 4.7 b).

The above results explain why males were in a state of alarm prior to giving an alarm call more often than females ( $X^2=6.784$ ; 1 df;  $p<0.05$ ). Females spent more time feeding, in general, than adult males (see chapter 3). Therefore, it was predictable that females would alarm call more often when feeding, than males (Fisher's exact test, one-tailed  $p<0.05$ ). There were no gender differences among adults for locomotion ( $X^2=0.004$ ; 1 df; NS) or resting (see Fig. 4.7 b) prior to alarm calling. In addition, vigilance preceded 26% of the vocalisations given by males and 23% by females (resting/vigilance included:  $X^2=0$ ; 1 df; NS) which corroborates the finding that adult males are not more efficient than females in giving alarm calls during vigilance (Fig. 4.5).

The adult males reacted when detecting predators in the vicinity by either threatening them away or by remaining vigilant (Fisher's exact test; two-tailed,  $p<0.001$ ) (Fig. 4.7 c). Adult females generally reacted by retrieving their infants (social friendly) and running into cover more often than males (Fisher's exact test; two-tailed,  $p<0.05$ ).

#### **4.2.6. Encounters with predators**

The martial eagle *Polemactus bellicosus* is found in Windy Ridge. It is possible that no attacks by this eagle were witnessed because the study troop inhabits a substantially bushy area and the martial eagle is more adapted to hunting in open country. In contrast the crowned eagle *Stephanoaetus coronatus* has better manoeuvrability in forested areas (Brown 1977, cited in Isbell, 1990).

The only predator seen taking a vervet during the study period was a crowned eagle (*Stephanoaetus coronatus*). On the 17th October 1987 at 16:15 a crowned eagle was seen flying away with a young juvenile (SI). The immediate reaction of the troop was to alarm call and threaten the eagle from the top of the canopy. The next morning from about 6 am, the dominant male, RO, was heard vocalising (alarm and threats), and at 6:15 he was found "guarding" the corpse of a youngster on the ground. The eagle returned a number of times to retrieve its prey but was repeatedly chased away by the excited male, who spent most of the time in the middle level of the canopy. There must have been some physical contact between them because the adult male had a fresh wound on his right eyelid (for similar reports see Struhsaker & Leland, 1979 for *C.a.sabaeus*; van Schaik & van Noordwijk, 1989 for capuchins). At 10:55 am, almost 5 hours later, the dominant male left the area and joined the troop which was feeding about 250 m away.

A few unsuccessful attacks by eagles ( $N=4$ ) on the study troop were witnessed. The top ranking male always took the most active part in threatening them, while the rest of the troop took cover. During a typical encounter many 'Threat-alarm-barks' and 'chirps' (Struhsaker, 1967c) were heard and the females and juveniles remained hiding for different lengths of time. On one occasion the top ranking female (HI) pushed her young juvenile (FE) off a branch onto a clump of trifid weed and a crowned eagle just missed it. The eagle settled near the troop and was repeatedly threatened and chased by the dominant male. This observation agrees with the data on predation from Amboseli (Kenya), which showed that top ranking lineages were more prone to attacks by predators because they were at the head of the progressions (Cheney *et al.* 1981). In other situations when eagles approached the study troop the monkeys, mainly infants and juveniles, ran into the bushes and remained silent (see above).

A leopard was the probable predator of a pregnant female (SH). On the day she disappeared a loud crashing noise was heard followed by a chorus of alarm vocalisations and dispersion of the troop. During this time leopard had been sighted in the area and spoor was often seen. However, in Amboseli National Park leopard kills accounted for most of the 70% of the deaths due to predation on vervet monkeys during 1987, which has reduced the population by 65% (Isbell, 1990). This increase was explained as the result of a general deterioration of the habitat and a possible increase in the number of leopards in the area, as well as a 'specialisation' by them on this prey.

The quantitative analysis of the data on vigilance and alarm calls agrees with qualitative data in the following ways: i) the main predators of vervets at Windy Ridge were eagles, ii) the alpha male dedicated more time to vigilance, iii) the main alarmist was the alpha male and iv) the alpha male took the most active part threatening and chasing raptors away. In addition, when subordinate males threatened potential predators they did so from a safe distance.

#### 4.3. ECOLOGICAL SEGREGATION

It is expected that animals spend the minimum time in positions where they are more vulnerable to predation. The reasons for exposing themselves could be to; i) acquire food, ii) sight potential predators, iii) influence the movement of other troops or lone males.

To maintain troop cohesion and reduce the risk of predation, vervets vocalise more often in bushy areas when out of sight of each other (Seyfarth & Cheney, 1984). These vocalisations are 'grunts' (Struhsaker, 1967c; Cheney & Seyfarth, 1982a) which also help to coordinate the movement of the troop during general progressions.

General progressions are those when all or most of the members of the troop move out of an area where they have spent some time. When one of these general movements occurred, a point was chosen, and the first and the last monkey crossing were recorded. To be in the front or at the rear of a progression implies an increased risk of predation. In the first case an knowledge of the area and of the troop's requirements is also needed.

Vigilance was predominantly observed in Windy Ridge when the monkeys were on top of the canopy (high and top level), with vigilant males spending more time on top of the canopy than any other age/sex class (Fig. 4.8).

Solitariness was a rare event and the most common behaviour when away from other monkeys ( $> 100$  m) was vigilance ( $b=0.04$ ;  $t=2.84$ ) ( $F=8.083$ ; 87 df;  $p<0.01$ ).

Table 4.9

Percentage of time adult males and females spent in potentially dangerous positions. SOL: solitary ( $> 100$  m from the closest monkey -infants excluded-); PER: peripheral (none -except own infant- between 50 and 100 m); TL: on top of the canopy (exposed on top or outside the trees) and GL: on the ground. Chi-square tests to detect sex differences were all highly significant (\*\*)  $p<0.001$ . The total number of scan samples is given (N).

	<u>SOL</u>	<u>PER</u>	<u>TL</u>	<u>GL</u>	<u>N</u>
<b>Males</b>	1.1	3.2	7.7	8.7	3500
<b>Females</b>	0.1	1.1	2.2	5.4	6133
	**	**	**	**	

In agreement with the total time males spent in dangerous positions in comparison to females, the monthly proportion of time individual males spent in marginal positions was higher for males than females; that is, males spent more time than females solitary (Kolmogorov-Smirnov two-sample test:  $DN=0.56$ ;  $p<0.001$ ), peripheral ( $DN=0.36$ ;  $p<0.05$ ), on top of the canopy ( $t=8.934$ ;  $p<0.001$ ) and on the ground ( $t=3.606$ ;  $p<0.001$ ).

A question not yet explained is why males spend far more time exposed and apart from other monkeys. If it is for social reasons or is dependent on the extent of their integration within the social network of the troop, then seasonal and rank-related differences are predicted.

#### **4.3.1. Apart from other monkeys**

Time spent at the periphery of the troop was inversely related to time resting ( $b = -0.04$ ;  $t = -2.62$ ) and time socialising ( $b = -0.13$ ;  $t = -3.78$ ). Both variables entered the model when all the adults were considered ( $F = 12.93$ ; 86 df;  $p < 0.001$ ).

When the test was re-run for males alone, month number ( $b = 1.54$ ;  $t = 6.0$ ), followed by vigilance ( $b = -0.41$ ;  $t = -4.88$ ); social friendly ( $b = -0.67$ ;  $t = -3.69$ ) and locomotion ( $b = -0.31$ ;  $t = -2.71$ ) correlated with time peripheral ( $F = 14.704$ ; 20 df;  $p < 0.001$ ).

Conversely, for females, resting ( $b = -0.04$ ;  $t = -2.62$ ), time solitary ( $b = 1.18$ ;  $t = 2.4$ ) and rank ( $b = 0.33$ ;  $t = 4.06$ ) affected time spent away from others. Low ranking females spent more time peripheral than their dominant counterparts ( $\rho = 0.465$ ;  $n = 8$ ;  $p < 0.001$ ).

As expected, the subordinate males were more often apart from other monkeys ( $> 50$  m.) than the dominant male was (Fig. 4.9a). However, RO and LE spent a similar time vigilant ( $X^2 = 1.981$ ; 1 df; NS), in alarm or vigilant ( $X^2 = 1.422$ ; 1 df; NS) and feeding ( $X^2 = 0.004$ ; 1 df; NS) when peripheral. Therefore, the reason for subordinate males remaining peripheral was not to avoid food competition, but rather for social reasons.

#### **4.3.2. Time exposed on top of the canopy**

When on top of the canopy, vigilance increases ( $b = 0.36$ ;  $t = 10.32$ ) and time spent away from other monkeys is minimal ( $b = -0.28$ ;  $t = -2.94$ ) for all adults ( $F = 53.67$ ; 86 df;  $p < 0.001$ ) (Plate 4.3).

For males, dominance rank ( $b = -2.93$ ;  $t = -4.86$ ) is the factor that mostly explains the variation in time spent on top of the canopy ( $F = 23.608$ ; 22 df;  $p < 0.001$ ). It was clear that the high ranking males spent more time on top of the canopy as the mating season approached.

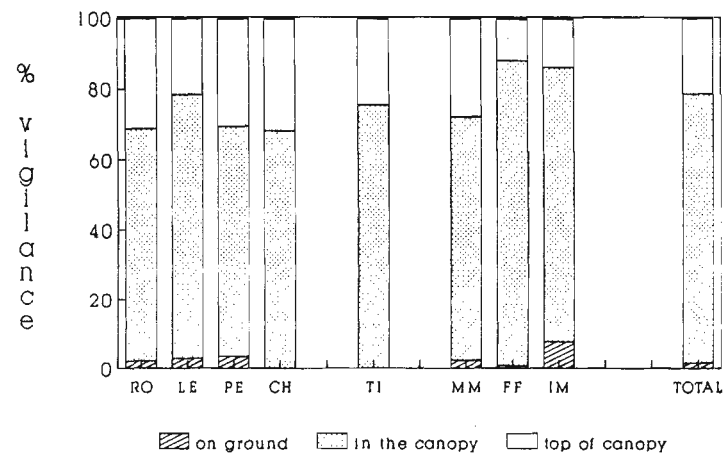


Figure 4.8. Positioning of vigilant males (MM: RO, LE, PE, CH), subadult male (TI), adult females (FF) and immatures (IM).



Plate 4.3. Vigilant vervet protruding from the canopy.

Vigilance frequently occurs when females are in an exposed position ( $b=0.12$ ;  $t=3.67$ ), meanwhile agonistic behaviours are rare ( $b=-0.13$ ;  $t=-2.17$ ). It seems that the major motivation for females to be exposed is either to scan their surroundings or do so unintentionally while feeding in unprotected places ( $F=12.962$ ; 61 df;  $p<0.001$ ).

Males spent significantly more time on top level when vigilant than any other age-sex class ( $X^2$ ;  $p<0.001$ ). The alpha male spent more time exposed on top of the canopy than subordinate males (Fig. 9 b), principally in order to be vigilant (see above).

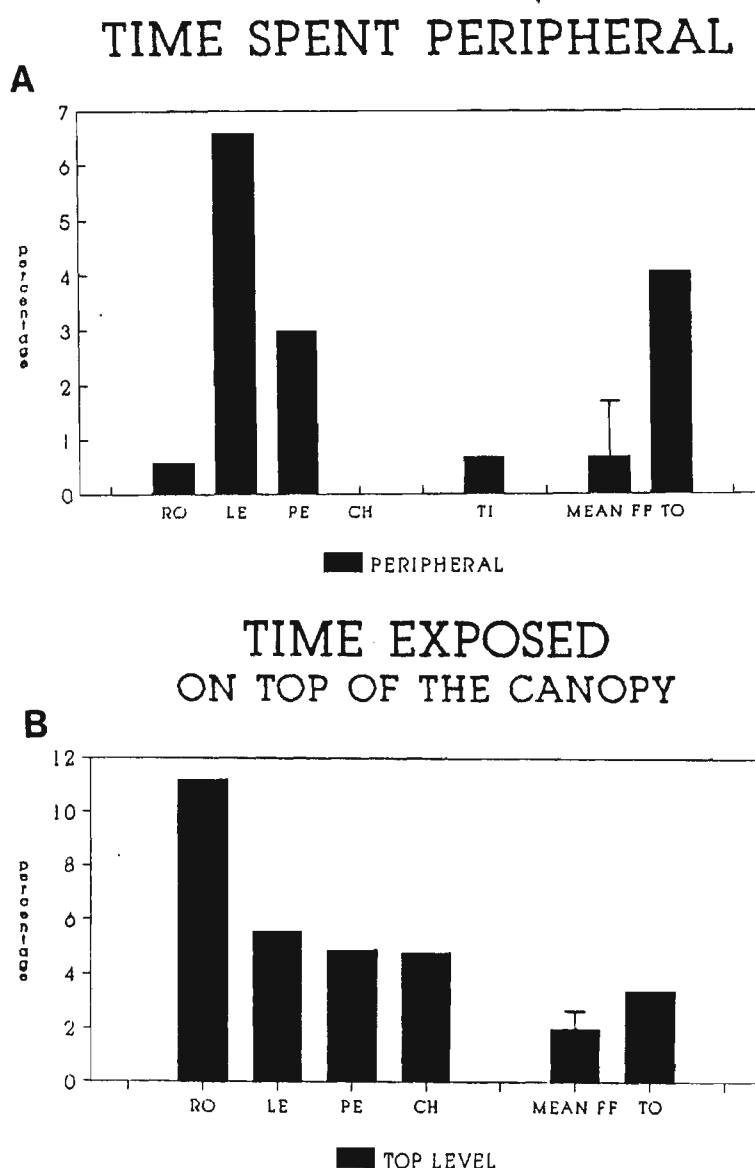


Figure 4.9. Proportion of time each adult male (RO>LE>PE>CH), the subadult male (TI) and the post-reproductive female (TO) spent a) apart from other monkeys (> 50 m) and b) on top of the canopy, in comparison the mean for reproductive females (FF) of the Windy Ridge Troop



### **4.3.3. On the ground**

Time spent on the ground was negatively correlated to resting ( $b = -0.12$ ;  $t = -2.9$ ) and social behaviours ( $b = -0.22$ ;  $t = -3.70$ ) for all adult individuals ( $F = 13.392$ ; 86 df;  $p < 0.001$ ). For males, the only behaviour that accounted for most of the variation was resting ( $b = -0.25$ ;  $t = -2.90$ ) ( $F = 8.387$ ; 23 df;  $p < 0.01$ ). Furthermore, for females apart from resting ( $b = -0.2$ ;  $t = -3.06$ ) and social time ( $b = -0.21$ ;  $t = -3.12$ ), month number ( $b = -0.66$ ;  $t = -2.25$ ) also entered the model ( $F = 5.752$ ; 60 df;  $p < 0.01$ ).

In addition, the proportion of the total time feeding spent on the ground varied with the month ( $X^2 = 44.472$ ; 7 df;  $p < 0.001$ ). This last result can be partly explained by the females' strategy of feeding on grasses during the wet season (Isbell, 1990).

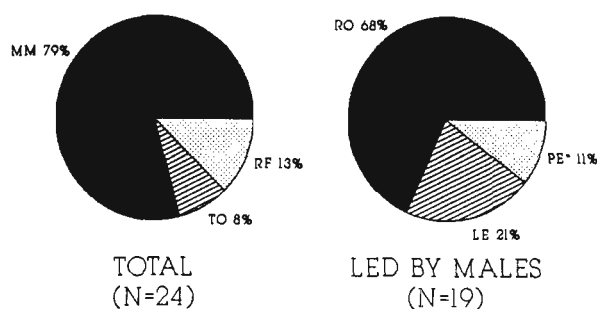
### **4.3.4. Who leads the progressions?**

A typical general progression after a resting period would start as follows: first, high ranking adult females and immatures would congregate slowly around the dominant male, second, females and immatures would partake in grooming and other friendly social interactions; third, the more distant subgroups would approach the main group and finally the dominant male, usually within visual contact of the subordinate males, led the troop to another area in half of the recorded moves (see Fig. 4.9a). They generally followed customary routes through the canopy or on the ground.

Of the 24 progressions recorded, 19 (79%) were led by an adult male, 2 (8%) by the reproductive female and the rest (13%) by the post-reproductive female. When correcting these values for the time the subjects were with the troop, clear differences were found ( $X^2 = 30.171$ ; 2 df;  $p < 0.001$ ). In addition, the alpha male (RO) led most of the male progressions ( $X^2 = 11.936$ ; 1 df;  $p < 0.001$ ). The post-reproductive female (TO) was at the head of the progression as often as the additional males (Fisher's exact test, two-tailed,  $p > 0.05$ ). The only reproductive females that were seen leading were the high ranking ones (HI twice and MO once). These observations are in partial agreement with those of other authors (Cheney *et al.* 1981).

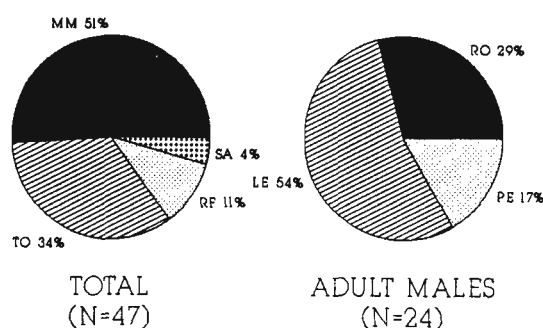
In summary, the alpha male led most of the progressions, the additional males did not differ from the post-reproductive female, and the reproductive females were seen in the leading position less often than expected (Fig. 4.10).

### WHO GOES FIRST?



\* PE was only present in 13

### WHO KEEPS THE REAR?



\*PE was present in 11 progressions

Figure 4.10

During general progressions, who goes first more often and who last? Proportion of progressions with an adult male (MM), reproductive female (RF) or the post-reproductive female (TO): a) at the head or b) at the rear. The adult males ranked as follows: RO > LE > PE.

#### 4.3.5. Who brings up the rear?

The monkey at the end of the progression, who waited for the rest to pass or came from behind was considered as the one keeping the rear. Sometimes, an adult monkey was seen patrolling the area where the troop had been, then joining the troop. This suggests an intention to gather or herd slacking members.

Males tended to occupy the rear position (24 times of the 47 progressions recorded). When correcting for the number of individuals present in the troop, adult males were at the rear of the troop more often than reproductive females ( $X^2=158.3$ ; 1 df;  $p<0.001$ ). No differences between individual males were found (Fisher's exact test: all  $p>0.05$ ). The post-reproductive female was last more often than the reproductive females ( $X^2=63.900$ ; 1 df;  $p<0.001$ ) but slightly less than the additional males ( $X^2=3.409$ ; 1 df;  $p=0.06$ ) (Fig. 4.10).

In contrast to results found for who was at the head of the general progressions, the females at the tail of the group were the lowest ranking breeding females (WE and VE once and the lowest ranking female ET, three times). Were the females there to protect the troop or to avoid direct food competition? The fact that subordinate monkeys trailing behind the main group tended to stop to feed and look toward the main group i.e. to maintain group cohesion while avoiding food competition, suggests that the second point is true.

#### 4.4 DISCUSSION

It has been argued that one of the advantages of animals living in groups is to increase their ability to avoid predation (e.g. van Schaik, 1983; Terborgh, 1983; see also introduction). The reason why some authors have overlooked the problem of predation in non-human primates is that there are differences between 'actual predation' and the 'risk of predation' (Dunbar, 1988 p. 53-54). This issue is reviewed in this chapter in terms of vigilance, alarm calls, time spent in dangerous locations, male defence against predators, and finally other proximate causes for high levels of alertness. A pattern of vigilance mostly by males is to be expected in polygynous species subject to high levels of predator pressure (Kavanagh, 1980). This should be specially true in multi-male groups to outweigh the costs imposed upon females and immatures by direct food competition (see Wrangham, 1980). However, in uni-male groups the male can also defend the troop against predators (Cheney & Wrangham, 1987).

##### 4.4.1. Sentinel males

Adult males in Windy Ridge, particularly the top ranking male, spent a higher percentage of their time scanning for predators and/or observing the movements of neighbouring troops or solitary males than adult females did (for captive *C.a.sabaeus*: Fairbanks & Bird, 1978; for *Cebus albifrons* and *C. apella*: van Schaik & van Noordwijk, 1989).

Vigilance by adult males was correlated with their dominance rank but the same did not apply for females. There was some evidence that older females were more vigilant than younger females, especially the post-reproductive female. This could be understood as a result of her occupying dangerous positions more often and due to her lower nutritional and infant care requirements.

The classification of 'pacing the perimeter' (Tollman & Lucas, 1979) as vigilance could explain why the relationship between male rank and time spent vigilant was not significant in the Cage.

The primary advantage of dominant and subordinate males being more vigilant than females during feeding and locomotion is that they reduce the risk of predation. A secondary advantage of feeding asynchrony is that males as a group fed with other members of the troop less often than was expected (the alpha male in particular) thereby reducing the cost to females of food competition.

Vigilance while the rest of the group was foraging or in progress was higher for the adult males than females, especially the alpha male. The post-reproductive female TO again showed the highest vigilance rate for females in this context, with values comparable to those of subordinate males.

*Does the presence of more males imply a reduction in time vigilant?*

The proportion of time spent vigilant was expected to be inversely proportional to the total number of vigilant individuals (see Underwood, 1982 for different species of antelope). Adult male vervet monkeys were three times more vigilant than adult females, so it is understandable that the individual level of vigilance is inversely related to the total number of adult males in the troop. Vigilance peaks during the mating season (see also Underwood, 1982), probably due to a major influx of extragroup males (Henzi & Lucas, 1980) and a higher excitability due to an increase in the levels of the sexual hormone testosterone (see chapter 7). However, it would be interesting to compare these data with other studies, to see whether male vervet monkeys' vigilance rates are more directly related to the number of adult males in the group (in order to maintain a certain level of vigilance for predators), or are more influenced by the mating season and an increase in the influx of exterior males (to control intertroop interactions).

### *Proximate causes of vigilance*

The costs of vigilance are that, first, it occurs at the expense of time spent in other fitness-enhancing behaviours and, second, successful, vigilant animals must be exposed themselves to predators. In fact, the variables that increased with higher levels of vigilance were: i) time spent on top of the canopy, with the alpha male spending more time in that position, ii) time spent peripheral, which was more common for the subordinate males and post-reproductive female and iii) month number which meant that the animals were more vigilant as the mating season approached.

The primary question that arises is whether the cost of vigilance is borne equally by all individuals. The costs incurred by vigilant animals are that they spent less time foraging (van Schaik & van Noordwijk, 1989; chapter 3) with the dominant male being the most efficient forager.

Second, vigilant animals are more at risk from predators (Hall, 1967 for patas; Poirier, 1972 for St. Kitts vervet; Kavanagh, 1980 for *C.a.tantalus*). Since there are fewer males than females in those groups, even though they migrate, an investment in behaviours that reduce the risk of predation may enhance male inclusive fitness by reducing mortality rates and constraints in time budget of potential mates and probable offspring (Kavanagh, 1980; Hamilton, 1984). In addition, from these lookout posts, males can spot extragroup male competitors, thereby males would protect the females and perhaps indirectly the food resources of the troop.

The above arguments are emphasised when considering the high levels of participation in these 'costly' behaviours by the post-reproductive female in Windy Ridge. On the other hand, additional males apart from benefiting from the high levels of vigilance by the alpha male, are forced to be more vigilant than reproductive females because they generally occupy a more peripheral position in the troop (see also Underwood, 1982 for antelope; van Schaik & van Noordwijk, 1989 for *Cebus albifrons* and *C. apella*, see also Pulliam & Caraco, 1984). However, the alpha male moves to the top of the canopy in order to scan its surroundings. Even if vigilance is not proximately related to predators but to other males, it may lead to predators being seen more frequently. But then, how can the high levels of vigilance shown by the post-reproductive female be explained?

In Windy Ridge adult males showed the highest levels of vigilance during the mating season (April-June). This is in accordance with expectations of a major influx of males during this period (Henzi & Lucas, 1980) and to an increase in intratroup mate competition. On the other hand, adult females increased their vigilance rates gradually from January until May, possibly in accordance with the acquisition of independence from their offspring. This corresponds to a higher risk of predation to the infant or perhaps to an increase in potential infanticide by newly immigrated males.

The steady increase in time dedicated to vigilance by the subadult males suggests that the development of this behaviour proceeds as a continuum (but see Fairbanks *et al.* 1978). It has also been argued that vigilance is less determined by the animals' recent history than by the innate response and possible cultural transmission (Underwood, 1982).

The finding that less observation time was required for an intertroup vocalisation to be recorded during the pre-mating and mating season than during the birth season (unpublished results) supports the argument that higher levels of vigilance are either prompted by or facilitate the detection of potential male competitors (Henzi, 1985).

#### **4.4.2. Warning of the troop**

Assisting relatives (nepotism) is the most likely function of alarm calls (Sherman, 1977). Therefore, communicating danger to other conspecifics is a mechanism that implicates kin selection more than altruistic behaviour (Hamilton, 1964).

It has been concluded that high ranking individuals alarm call more often than lower ranking animals (Cheney *et al.* 1981; Cheney & Seyfarth, 1981;1990 p.190). Surprisingly, Cheney *et al.* (Cheney *et al.* 1981; Cheney & Seyfarth, 1990, p.190) reported that animals giving more first alarm calls were not necessarily more vigilant and they could not detect differences in vigilance for animals positioned in vantage points. However, in Windy Ridge the number of times an individual gave a first alarm vocalisation was directly correlated to time spent vigilant and time spent in vantage locations. The differences found between Amboseli and Windy Ridge vervets could be explained by the fact that leopards, as the main predator in the former location (Isbell, 1990) are more difficult to avoid than raptors these being the most frequent attacker in Windy Ridge. Therefore, in Amboseli where the number of trees that offer protection against leopards has been depleted (Cheney *et al.* 1988), the best strategy upon detection of a leopard would be to run for safety rather than warn the rest of the troop.

Considering that the high ranking adult vervet male appears to copulate more often (Struhsaker, 1967b; but see Whitten, 1983 cited in Cheney & Seyfarth, 1990) than other (sub)adult males, long-term resident high ranking males can have more genes spread in the group than any of the females. This could explain why high ranking adult males alarm called more often than adult females and risk themselves more on encountering predators. However, although low ranking males do not appear to father many offspring (this study), male rank changes and they may have done so in the past or will do so in the future. Consequently, by risking themselves low ranking males may be investing in their offspring or prospective mates.

The fact that time spent vigilant was directly related to the number of alarm calls given, agrees with Dawkins's (1976 p.182-183) hypothesis that the individual could endanger himself by not giving an alarm.

On the other hand, silent alarms while crop raiding have been reported for baboons, tantalus monkeys (Kavanagh, 1980), patas and redtail monkeys (Chism & Rowell, 1988). The finding that vervets seldom alarm call when eagles vocalise, agrees with Seyfarth *et al.* (1980) results of playback experiments, during which vervets seldom responded by alarm calling, although the response evoked did not vary from a real one. It can be concluded then that vervets only alarm call to warn the rest of the troop.

Adult vervets are more selective than juveniles about giving alarm calls (see also Seyfarth & Cheney, 1982). Cheney and Seyfarth (1981) suggest that selective forces affecting predator alarm calls on vervet monkeys have evolved by individual selection although they do not ignore the idea that kin selection has played an important role. This has been mainly explained by vervets giving alarm vocalisations to predators from which they were at greater risk (Seyfarth *et al.* 1980). This was only partly confirmed in Windy Ridge, because males never vocalised towards baboons, but they did towards eagles. Although crowned eagles are suspected to take all age and sex classes (Cheney & Seyfarth, 1990, p.103), they preferably take youngsters or adult females.

#### **4.4.3. Occupying risky positions**

Time spent solitary (no other monkeys at less than 100 m) or peripheral (none at less than 50 m, but one or more at less than 100 m), reduces direct competition and the chances of social interaction. A differential use of vertical space could also represent a strategy to avoid conflict. Males spent significantly more time away from others, exposed on top of the canopy and on the ground than females. The alpha male goes to the top of the canopy in order to be vigilant. In contrast, subordinate males are more peripheral than other members of the troop, without being related to higher levels of vigilance, precisely because they avoid being exposed when away from other monkeys (cf. van Schaik & Noordwijk, 1989).

In Windy Ridge vervets were observed gathering others before starting a general locomotion. Occasionally, one of the adult older members would remain vigilant in a tree or in a position where he was clearly visible to other members, and wait for them to pass. It is speculated that in this way the actor would serve as a signalling post and enhance group cohesion.

That adult vervet males lead a greater proportion of general progressions agrees with observations done on baboons (Rowell, 1969; DeVore, 1964; Altmann, 1979). Although the post-reproductive female was as often at the head of the progression as additional males, the movement was often keyed by the alpha male (Poirier, 1970 p. 324 for Nilgiri langurs). Struhsaker (1967 b) also emphasised that the initiator of a progression was an old or dominant individual who was not always the same as the one determining where the troop went. In a patas group, the adult females lead progressions more often than the adult male, except during the mating season (Chism & Rowell, 1988). This suggests that one of the reasons adult male vervets may be leading the troop is to keep females away from other extra-group male competitors.

The additional males did not differ from the alpha male in the number of times they kept to the rear of a general progression, and once again the post-reproductive female did not differ from additional males. The reproductive females, as found for the other dangerous situations, withdrew from occupying the rear of the troop.

Males in other multi-male species also show a tendency to position themselves near the ends of the progressions (Schnell *et al.* 1985) and during dangerous situations in order to protect the more vulnerable members of the troop (Altmann, 1979).



#### **4.4.4. Concluding remarks**

The results obtained from this study agree with those which emphasise the important role male Old World monkeys hold in detection of and protection against predators (e.g. Eisenberg et al. 1972; Goss-Custard, *et al.* 1972; for *C. aethiops*: Cheney & Seyfarth, 1981; for *Cebus albifrons* and *Cebus apella*: van Schaik & van Noordwijk, 1989).

The fact that the alpha male was more prominent in vigilance than other males, agrees with results found for other multi-male species (e.g. for chacma baboons: Saayman, 1971).

'The alpha male typically positioned himself in a conspicuous place with the white pelage of his ventral surface maximally exposed, while the rest of the troop raided crops' (Horrocks & Hunte, 1986).

Horrocks and Hunte (1986) pointed out that adult male vervets serve as visual markers and that frequent scanning for predators was replaced by periodic glances at the sentinel. This strategy could only be successful in 'centripetal groups' where adult males constitute a permanent focus of attention in case of danger and during troop leading (Chance & Jolly, 1970; personal observation) and with an 'attention structure' (Torres de Assumpção & Deag, 1979) focussed on the highest ranking animal (see also Poirier, 1970 p.325).

Males benefit the females and immatures during feeding by increasing the general level of vigilance and acting as 'sentinel males'; this is specially true for the alpha male of the troop (see also Harrison, 1983a for *C.a.sabaeus*). During locomotion animals are also prone to predation and sentinel males are advantageous to the troop.

The adaptive significance of the emancipation of the vocal signalling system towards a more visual communication, has been emphasised; as exemplified by a very soft alarm call given when the predator has not yet detected the prey or when it is still far enough away (Gartlan & Brain, 1968; Seyfarth *et al.*, 1980; Kavanagh, 1980). This is possible through 'local enhancement', the ability of a social model to direct the attention of an observer to some salient feature of the environment (Strayer, 1976).

Even if the alpha male's main reason for spending more time than others in dangerous positions is to control the arrival of other adult males, the possibility that other members of the troop benefit from the increased vigilance is not excluded.

It can also be concluded that old females (grandmothers or post-reproductive), are more valuable to the troop as protectors against outside threat than reproductive females or younger and/or subordinate males (see also Dawkins, 1976 p.134; Fairbanks, 1988a for vervets). Blaffer Hrdy's (1974) reasoning to explain the presence of old female langurs seems to apply for vervets.

The males' contribution to lower the pressure of predation by being vigilant can be facilitated by males spending less time feeding and occupying strategic positions more often than females (see also van Schaik & van Noordwijk, 1989). The greater participation of the alpha male in defence of the troop could be the result of his metabolic requirements being more easily satisfied and be more successful than others because of the centripetal attention structure of vervet monkeys which focuses on him (unpublished results) thereby facilitating communication with the rest of the troop.

The benefits to the alpha male could be explained in terms of gene-selfishness (Dawkins, 1976) because by defending the troop he is protecting his potential mates and probable offspring (the alpha male performed most of the copulations).

The fact that the alpha male of the Windy Ridge troop was the only male to mob predators cannot be regarded as a general rule for vervets since the encounters with predators witnessed were scarce and the other male that was in the troop for the period of study was not in his prime. Other younger males could have reacted differently (see van Schaik & van Noordwijk, 1989 for capuchins). Apart from the alpha male's disproportionate contribution, additional males and older females contributed to increase the level of safety for reproductive females and immature animals; this agrees with the argument that low ranking animals in spite of suffering more from competition for food and other resources, benefit by living in groups (Cheney *et al.* 1981; van Schaik, 1983).

It remains unclear whether other free-ranging troops of vervets, where additional males father more infants and/or mate more often (Andelman *et al.* 1985 for vervets in Amboseli), show similar levels of vigilance and defence against predators as the alpha male (van Schaik & van Hooft, 1983 for capuchins). Adult vervets in Amboseli did not differ in vigilance according to their dominance rank, although high ranking males and females gave more alarm calls than their lower ranking counterparts (Cheney & Seyfarth, 1990, p.190).

## 5. SOCIAL INTERACTIONS AMONG MALES

Adult males living in multi-male female-bonded (Wrangham, 1980) groups show very low levels of affiliative behaviour towards each other. In contrast, females are more involved in grooming (vervets: Struhsaker, 1967 b; Seyfarth, 1976, 1977, 1980; rhesus: Sade, 1965; chacma baboon: Hall & DeVore: 1965) and mainly direct it to close relatives (vervets: Seyfarth, 1980). As social relations affect spacing, the distance among females is less than among males and between females and males (Schnell *et al.* 1985; Lopez-Lujan *et al.* 1989). Consequently, male-male grooming is less frequent than male-female and female-female grooming (for baboons: Smuts, 1987, p. 38).

On the other hand, intra-gender aggression in female-bonded primates is more common among males than among females (Bramblett & Coelho, 1987) and male-male relationships are mostly agonistic (Henzi, 1982 for vervets). In addition, levels of competition are predictably higher among non-kin, and male dominance hierarchies are not as stable as those of females (see chapter 1).

There are different mechanisms which reduce the costs of open aggression among monkeys: dominance hierarchies (Slobodchikoff & Schulz, 1988 p.18), avoidance reactions (Schaller, 1963 p. 255), submissive acts (e.g. lipsmacking: Chalmers & Rowell, 1971), grooming (Carpenter, 1942b) and presenting in a non-sexual context (Zuckerman, 1932; Carpenter, 1942b; Hall & DeVore, 1965; Saayman, 1971). Apart from the above, other more sophisticated strategies have evolved which permit the coexistence of unrelated adult males (*i.e.* yawning and canine display: Hall & DeVore, 1965; 'notifying': Kummer, 1968; Bachmann & Kummer, 1980; Abegglen, 1984 for male hamadryas baboons).

In addition to displays of dominance by male vervet monkeys (see p. 50), a self initiated display of submission -'Homage' (Henzi, 1982; 1985)- has been described. The above patterns agree with data found from other species of Old World monkeys which show that most male-male interactions are accomplished in a non-violent manner, through visual cues (*i.e.* Poirier, 1970 p. 322).

Male-male agonistic encounters are more frequent or more severe when there are reproductive females present (Hausfater, 1975, p.136-137; Henzi & Lawes, 1987) must be understood in terms of mate competition, which for males accounts for a greater variation of reproductive success than for females (see Emlen, 1973). Some of the counter strategies which reduce male agonism are: i) greater inter male distance (Hausfater, 1975, p.138), ii) increased displays of dominance occurring more often (Struhsaker, 1967b) and frequent submissive behaviour (Hausfater, 1975, p.138; Henzi, 1982 for vervets).

However, certain issues remain poorly documented for vervet monkeys. These are male-male proximity relationships outside the mating season and seasonal changes in male social relationships. These would explain how unrelated males, living together in direct competition for females, manage their interactions.

To determine the nature of male-male social relationships I have: i) analysed male-male proximity relationships and compared them with those for male-female pairs, ii) investigated seasonal and rank effects on the proportion of time pairs of males were found in proximity to one another, iii) attempted to provide some insight into the proximate causes of grooming interactions involving males, iv) compared adult and subadult (supposedly natal) male social relationships, v) analysed in detail any type of interaction that could be classified as being of an agonistic nature and related this to its possible adaptive significance in regulating and facilitating male-male coexistence, vi) explored the seasonal and age/sex class differences in total number of wounds received, their severity and location for the three study troops and vii) compared the social costs to dominant and subordinate males of remaining in the troop outside the mating season (see chapter 3).

My predictions for vervet male interactions, based on studies done on this species or other polygynous species of Old World monkeys are outlined below.

1. Subadult and in general subordinate adult, male vervet monkeys will be peripheral to the central part of the group, where females and juveniles will be most often found (Hall & DeVore, 1965, p.70 for baboons). At the same time, the most dominant male will be closer to adult females than the subordinate males (Hill, 1986 for rhesus). Consequently, the top ranking male will be further apart from other males than from adult females; friendly interactions involving the alpha male and subordinate males will be less common than friendly interactions between the alpha male and females; finally, subordinate males will hardly, if ever, interact with females.

2. The dominant male will be closer to females during the mating season than at other times and additional males will be prevented from approaching females by the dominant adult male. Therefore, an increase in proximity to adult females during the mating season is only expected to occur for the top ranking male.
3. The use of grooming as an appeasement behaviour among males will be supported if the highest ranking males receive more grooming from other males than *vice versa* (Hall & DeVore, 1965 for baboons).
4. Males are expected to direct more submissive behaviour towards other more dominant males than towards females because of their general higher basic rank (Fedigan & Fedigan, 1988, but see Rowell, 1971; Kaplan, 1987). In addition, male-male aggression should be more frequent than male-female aggression (i.e. Poirier, 1970 p. 319) and show a peak during the mating season. These differences will be reflected in the temporal distribution of wounds (Struhsaker, 1967 a; Hausfater, 1975; Henzi & Lucas, 1980).
5. It has been found that displays of dominance are exclusive to high ranking males (Struhsaker, 1967a; Henzi, 1982; 1985) while subordinate males are generally precluded from carrying them out. As displays of dominance serve the purpose of reinforcing dominance relationships, I predict that these would be mainly directed at closely ranking males, as occurs with aggressive acts (cf. Struhsaker, 1967b; Johnson, 1989) and increase at the time when male competition for females is most intense, i.e. during the mating season (Struhsaker, 1967 a).
6. Homage, self-initiated submissive behaviour is directed to the alpha male of the troop (Henzi, 1985) and is expected to reduce open aggression between interacting animals. Therefore, a reduction in the amount of homage should be related to an increase in aggression received by the subordinate. Whether self-initiated displays of submission deter the highest ranking male from keeping the additional males at the periphery of the troop, would be supported if a reduction in time spent peripheral corresponds to more homage.
7. Male-male agonistic coalitions are common among baboons and macaques but have never been reported for vervets (see review: Smuts, 1987, p. 289-390; Cheney & Seyfarth, 1990). If males support other males against higher ranking males, those males would be genetically and spatially closer and more involved in affiliative behaviours than other males (for female vervets: see review in Cheney & Seyfarth, 1990).

8. The absolute amount of interaction between males should be related to their respective rank; with closely ranking males interacting together more often than with other males.

If the results found in this study are similar to those found for other clearly multi-male species (baboons and macaques) the multi-male nature of the vervet monkey's social structure should no longer be questioned (see chapter 1).

### *Analysis of the data*

Two distance categories were distinguished for analysis. First, **close proximity** relates to animals found in contact or within a radius of 2 m for the Windy Ridge troop, and those found in contact or at less than 1 m for the Cage Troop. Second, **social environment**, was defined as all neighbours within 10 m of the focal animal in Windy Ridge and given the restricted space in the captive conditions, at less than 2 m in the Cage.

Proximity rates were calculated by dividing the frequency with which a pair of adults was found in close proximity or in each others social environment by the number of samples for the appropriate season. The Chi-square test was applied. Only data obtained with scan (WT) and instantaneous (CT) sampling were used to study proximity relationships.

Close proximity, except during agonism, which only accounts for about 5 percent of male time budget (see chapter 3), implies that there is an affiliative relationship. Meanwhile, when monkeys are not found within the social environment of each other, a lack of socialisation is implied.

### **5.1. MALE-MALE VERSUS MALE-FEMALE PROXIMITY**

To determine whether the probability of finding an adult member of the troop in close proximity or within the focal male's social environment was related to its sex, the Mann-Whitney U test was used. Data was corrected by the number of scans done each season.

### **5.1.1. Close neighbours**

In Windy Ridge, adult animals were found in close proximity to the adult males RO and LE independently of their sex (Table 5.1). The same results were found over all three seasons. Therefore, seasonality did not affect the gender of RO and LE's companions. In contrast, during the birth season the two lowest ranking males had more male partners than expected when taking low numbers into account (Table 5.1). It must be emphasised that these were young animals and both emigrated during the next season.

For the Cage troop, the dominant male (FT) preferentially associated with females during the non-mating period. However, there were no significant sex differences for the subordinates' close neighbours. Preference for male partners during the birth season could have been overlooked when regrouping the data for the non-mating period (Table 5.2).

Table 5.1

Adult sex differences in close proximity (<2 m) for the adult males (RO>LE>PE>CH) of the Windy Ridge Troop (n=number of other adult males; m=number of adult females and U=values obtained for the Mann-Whitney statistic (a negative value means that the focal male is closer to males than to females) and its level of significance (NS=non significant; \* <0.05 and \*\*<0.001). For the birth (B), pre-mating (N) and the mating (M) seasons. The number of samples for each focal male is given in Table 5.9.

FOCAL MALE	SEASON	n	m	U	P
RO	B	3	8	-0.627	NS
	N	3	8	0.000	NS
	M	2	8	+0.131	NS
LE	B	3	8	-1.538	NS
	N	3	8	-1.330	NS
	M	2	8	-0.527	NS
PE	B	3	8	-2.277	*
	N	3	8	-1.739	NS
CH	B	3	8	-2.369	*
	N	3	8	-0.323	NS

Table 5.2

Adult sex differences in proximity rates ( $<1$  m) for the adult males of the Cage Troop (CT). Legend as for Table 5.1. The data for the non-mating season were regrouped to increase the number of samples. The total number of samples for each adult male are given in Table 5.10.

FOCAL MALE	SEASON	n	m	U	P
FT	BN	4	6	+2.266	*
	M	2	5	+1.743	NS
GO	BN	4	6	+0.107	NS
RN	BN	4	6	+0.320	NS
	M	2	5	+0.977	NS
FY	BN	4	6	+0.536	NS
	M	2	5	+0.391	NS
LU	BN	4	6	-0.541	NS

### **5.1.2. Social environment**

During the birth season, the probability of finding a particular individual within the two higher ranking free-living (RO and LE) males' social environment depended on its gender (Table 5.3). Both RO and LE associated predominantly with other males (compare Fig. 5.1 and 6.3). Moreover, for the time they were in the troop, the two younger and less dominant males were as often at less than 10 m from other males as from females.

The social environment of adult males in the Cage consisted of adult individuals independent of their gender. One exception was FT, who was found in the vicinity of females more often than expected during the non-mating period (Table 5.4 and compare Fig. 5.2 and 6.4). These results agree with those obtained for close proximity relationships (Table 5.2), but differ from the results found for the free-ranging males' social environment (Table 5.3).

The discrepancy in the results obtained for both troops could be explained by kin relationships. Most adult males in the Cage had been born or spent a minimum of 10 years coexisting with the adult females and a very limited number of males were introduced over the years (Henzi, personal communication). Therefore, the males were more related to the females than in natural conditions, resulting in the absence of an intra-gender preference.



Table 5.3

Adult sex differences in proximity (<10 m) for the adult males of Windy Ridge troop (n=number of other adult males for that particular season; m=number of potential female neighbours and U=values obtained for the Mann-Whitney statistic and P=probability). For the birth (B), non-birth and non-mating period (N) and for the mating (M) seasons. When there were significant differences, a negative value of U, indicates that the focal male was closer to individual males than females.

FOCAL MALE	SEASON	n	m	U	P
RO	B	3	8	-2.158	*
	N	3	8	-1.327	NS
	M	2	8	0.000	NS
LE	B	3	8	-2.158	*
	N	3	8	-1.735	NS
	M	2	8	0.000	NS
PE	B	3	8	-2.250	*
	N	3	8	-2.250	*
CH	B	3	8	-2.353	*
	N	3	8	-2.271	*

Table 5.4

Adult sex differences in adult proximity rates (<2 m) for the adult males of the Cage Troop. The rest as for Table 5.3.

FOCAL MALE	SEASON	n	m	U	P
FT	BN	4	6	2.459	*
	M	2	5	1.743	NS
GO	BN	4	6	0.000	NS
RN	BN	4	6	1.502	NS
	M	2	5	0.782	NS
FY	BN	4	6	0.000	NS
	M	2	5	0.000	NS
LU	BN	4	6	0.569	NS

## 5.2. MALE PREFERENCES IN PROXIMITY TO OTHER MALES

Chi-square tests have been run to test for individual differences in male-male proximity. The proportion of time each male spent in close proximity or within the social environment of the other males is compared.

### 5.2.1. Close proximity

The alpha male of the Windy Ridge troop (RO) associated preferentially with certain males each season (Table 5.5). High rates of close proximity with the third ranking male PE for the non-mating period could be explained by the high rate of affiliative interaction between them (see below). The low proximity to CH could be related to the large difference in rank between them. During the mating season the newly immigrated male (GR), spent less time near RO than expected.

The second ranking male (LE) spent a comparable amount of time with each of the other adult males during the birth season. This was not so for other periods. During the pre-mating season (N), he was found near PE (next lower ranking) more often than expected, while CH was more distant. The differences found during the mating season are due to the limited amount of time spent in the immediate vicinity of the new arrival (GR). PE was more distant from the lowest ranking male CH than from other males during the pre-mating season, probably because CH had become very peripheral before migrating, and closer than expected to LE (Table 5.5 and Fig. 5.1).

Table 5.5

Male individual differences in proximity relationships to other males (<2 m) in Windy Ridge troop. Chi-square test values ( $X^2$ ), degrees of freedom ( ) and significance level (\*  $p < 0.05$ ; \*\*  $p < 0.001$ ; NS: non-significant) are shown for each season (B: birth; N: non birth-non mating season and M: mating).

FOCAL	SEASON	$X^2$
RO	B	9.545 (2) *
	N	7.168 (2) *
	M	5.000 (1) *
LE	B	2.250 (2) NS
	N	11.994 (2) *
	M	5.000 (2) *
PE	B	1.083 (2) NS
	N	8.566 (2) *
CH	B	1.889 (2) NS
	N	2.500 (2) NS

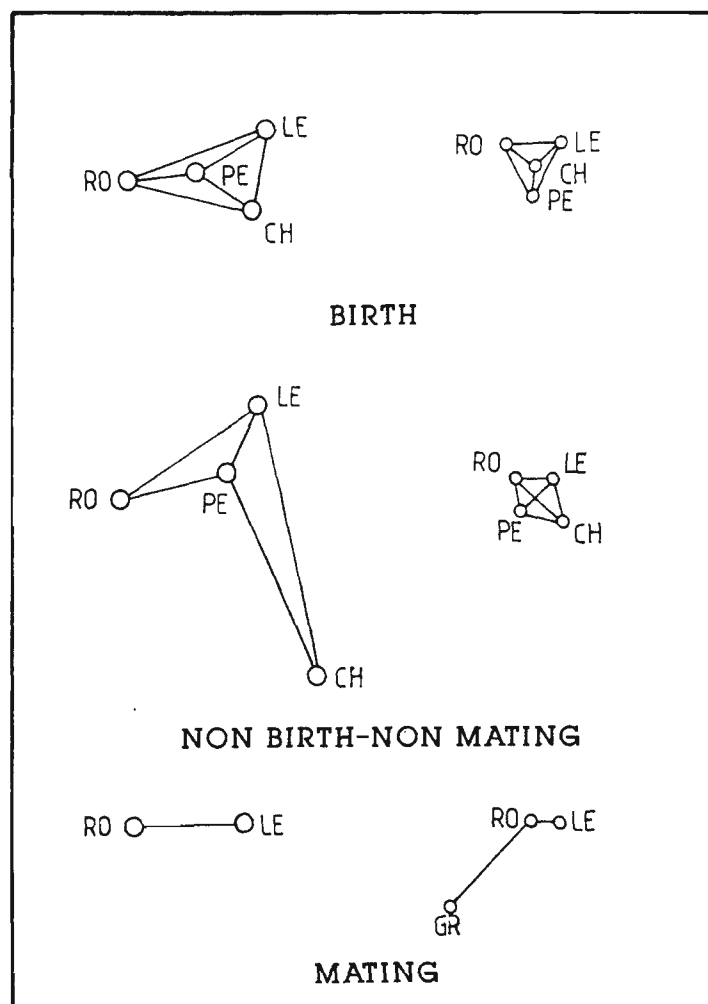


Figure 5.1. Proximity relationships for adult males of the Windy Ridge Troop (left column: less than 2 m and right column: within 10 m). The distance between males represents the inverse of the proportion of time they spent in proximity.

In the Cage, during the mating season the dominant male (FT) spent more time at less than 1 m from the next ranking male, than at the same distance from the lowest ranking male (FY), while no differences were detected for the middle ranking male (RN). It is conclusive that the lowest ranking male (FY) was always further than expected from the highest ranking male (FT) (Table 5.6 and Fig. 5.1).

It can be concluded that proximity relationships were preferentially established between closely ranking males, and males with a dominance rank difference of two or more were often farther apart than expected.

Table 5.6

Male individual differences in proximity relationships (<1 m) to other males in the Cage Troop during the non-mating (BN) and mating (M) season (legend as for table 5.5)

FOCAL	SEASON	$\chi^2$
FT	BN	6.333 (3) NS
	M	5.857 (1) *
GO	BN	2.333 (3) NS
RN	BN	1.825 (3) NS
	M	1.143 (1) NS
FY	BN	8.750 (3) *
	M	10.000 (1) *
LU	BN	3.250 (3) NS

### 5.2.2. Social environment

In agreement with data obtained for close proximity, RO was found less than 10 m from PE more often and from CH less often than expected during the pre-mating season (Table 5.7 and Fig.5.1). During the mating season, the newly immigrated male (GR) was further from RO than the other long term resident male was.

During the non-mating season LE had the other three adult males of the troop within 10 m with the same frequency (Table 5.7), but during the mating season he was closer to RO than to the newly immigrated male. The two lower ranking males (PE and CH) did not show any preferred male neighbours during the time they stayed in the troop (Fig. 5.1).

In the Cage, the highest ranking adult male (FT) spent more time less than 2 m from RN than from other males. The absence of high proximity rates for the closely ranked male dyad FT and GO could have been caused by their high rates of antagonism (see below). The low ranking male (FY), spent more time than expected in the vicinity of the next ranking than near the most dominant male during the entire study (Table 5.8 and Fig. 5.2).

These results are similar to those found for close proximity, which suggest that when males are ranked two or more dominance levels apart, they are spatially more segregated.

Table 5.7

Male individual differences in inclusion in the focal male's social environment (<10 m) in Windy Ridge troop during the birth (B), pre-mating (N) and mating (M) seasons. Chi-square test values, degrees of freedom () and significance levels (as for table 5.1).

FOCAL	SEASON	$\chi^2$
RO	B	3.069 (2) NS
	N	9.447 (2) *
	M	17.064 (1) **
LE	B	2.077 (2) NS
	N	3.203 (2) NS
	M	30.928 (1) **
PE	B	1.844 (2) NS
	N	2.907 (2) NS
CH	B	3.088 (2) NS
	N	1.667 (2) NS

Table 5.8

Male individual differences in inclusion in the focal male's social environment (<2 m) in the Cage troop during the non-mating (BN) and mating (M) season (legend as for table 5.1).

FOCAL	SEASON	$\chi^2$
FT	BN	10.556 (3) *
	M	1.952 (1) NS
GO	BN	7.583 (3) NS
RN	BN	4.866 (3) NS
	M	1.786 (1) NS
FY	BN	15.789 (3) **
	M	10.097 (1) **
LU	BN	3.400 (3) NS

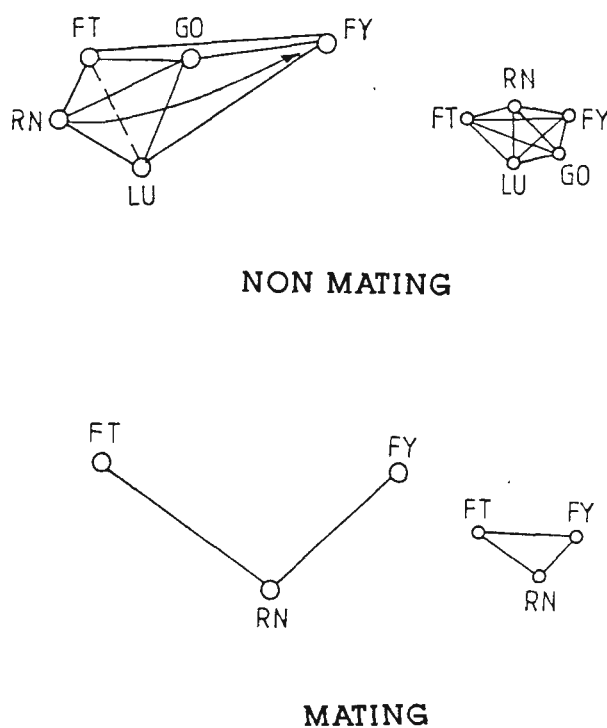


Figure 5.2.

Proximity relationships for the adult males of the Cage Troop (left column: less than 1 m and right column: within 2 m).

### 5.3. SEASONAL EFFECTS ON MALE-MALE DISTANCE

To investigate seasonal variation in male-male proximity, the two distance categories have been analysed separately. Chi-square was again used to detect significant differences. As the data in Windy Ridge was taken concurrently, the analysis had to be carried out independently for each focal animal. While sampling A, individual B could be recorded as being within 2 or 10 m, but a sample of B was only done if all its neighbours could be identified. This explains why some differences are not equally significant (Table 5.9 and 5.11).

However, in the Cage only one male was sampled at a time, which allowed the data to be combined for each pair of animals (Table 5.10 and 5.12).

### 5.3.1. Close proximity

The dominant male (RO) was found in close proximity to the two lowest ranking males (PE and CH) less often during the pre-mating season than during the birth season, though for PE the differences were slight (Table 5.9 and Fig. 5.1). These differences might have had either a seasonal component or they could have been a consequence of PE and CH remaining more peripheral prior to leaving the troop.

Table 5.9

Seasonal differences of proximity relationships (<2 m.) for the adult males of WT. S=season; O=Observed frequency; E=Expected frequency and N=number of samples done on the focal animal during that particular season. Chi-squared values and level of significance of the test (rest as for table 5.1). The degrees of freedom varied from 1 when data from only two seasons were available and 2 from the three seasons.

MALES		S	O	E	N	X <sup>2</sup>
RO	LE	B	6	7	174	2.935 NS
		N	19	24	562	
		M	35	28	662	
	PE	B	19	11	174	7.883 *
		N	23	31	467	
	CH	B	7	4	174	5.250 *
		N	0	3	138	
LE	RO	B	5	6	129	5.568 NS
		N	20	28	575	
		M	35	26	539	
	PE	B	11	10	129	0.126 NS
		N	37	38	496	
	CH	B	8	5	129	3.600 NS
		N	2	5	129	
PE	RO	B	15	10	173	3.542 NS
		N	19	24	419	
	LE	B	12	14	173	0.403 NS
		N	36	34	419	
	CH	B	10	8	173	1.300 NS
		N	3	5	119	
CH	RO	B	7	4	135	5.250 *
		N	0	3	95	
	LE	B	7	5	135	1.800 NS
		N	2	4	95	
	PE	B	12	9	135	2.500 NS
		N	3	6	95	

For the Cage males, it was found that only the middle ranking male (RN) and the low ranking male (FY) were further from FT during the mating season, while no other significant seasonal differences were obtained.

Interestingly, seasonal differences were mainly found among male dyads that differed in two or more ranks. The trend appears to be that subordinate males keep further away from higher ranking males as the mating season approaches.

### **5.3.2. Social environment**

Seasonal differences in total proximity were only found for RO and LE in the Windy Ridge troop and FT and RN in the Cage. For most of the mating season (RO and LE) formed part of each other's social environment more often than expected during that period (Table 5.11; Fig. 5.1). It is probable that RO positioned himself significantly closer to LE during the mating season to prevent him from mating with receptive females.

Contrary to results found for the free-ranging troop, data from the captive troop showed that FT and RN were further apart than expected during the mating season (Table 5.12 and Fig. 5.2).

Table 5.10

Seasonal differences in close proximity (<1 m) for the different male dyads in the Caged troop (CT). BN=Non-mating period and M=Mating season (legend as for Table 5.10).

MALES	S	O	E	N	X <sup>2</sup>
<b>FT-RN</b>	BN	22	12	287	12.180 **
	M	16	26	617	
<b>FT-FY</b>	BN	6	3	280	4.800 *
	M	2	5	617	
<b>RN-FY</b>	BN	12	10	289	0.590 NS
	M	19	21	610	



Table 5.11

Seasonal differences in proximity relationships (< 10 m) for the adult males of the Windy Ridge troop (legend as for table 5.3).

MALES		S	O	E	N	X <sup>2</sup>
RO	LE	B	23	37	174	10.428 *
		N	108	119	562	
		M	164	140	662	
	PE	B	36	37	174	0.037 NS
		N	102	101	467	
	CH	B	27	22	174	2.607 NS
		N	12	17	138	
LE	RO	B	20	31	129	21.509 **
		N	109	137	575	
		M	167	128	539	
	PE	B	29	27	129	0.187 NS
		N	100	102	496	
	CH	B	29	23	129	3.700 NS
		N	16	23	129	
PE	RO	B	31	37	173	1.368 NS
		N	97	91	419	
	LE	B	27	36	173	3.181 NS
		N	96	87	419	
	CH	B	39	34	173	1.822 NS
		N	18	23	119	
CH	RO	B	29	23	135	3.683 NS
		N	11	17	95	
	LE	B	30	26	135	1.457 NS
		N	15	19	95	
	PE	B	42	35	135	3.360 NS
		N	18	25	95	

Table 5.12

Seasonal differences in proximity (<2 m) for the different male dyads of the Cage. BN=Non-mating period and M=Mating season. The rest as for Table 5.12.

MALES		S	O	E	N	X <sup>2</sup>
FT-RN			BN	48	30	287 15.709 **
		M	48	66	617	
FT-FY			BN	13	14	284 0.103 NS
		M	33	32	617	
RN-FY			BN	33	35	289 0.168 NS
		M	76	74	610	

## 5.4. SUBADULT MALE PROXIMITY RELATIONSHIPS

A separate section for those males who did not reach full adult size during the study is necessary to give some outline of ontogenetic changes in male-female and male-male social relationships. Unfortunately only one subadult male was present in the Windy Ridge troop and two in the Cage Troop.

### 5.4.1. Close proximity

In Windy Ridge, the single subadult male (TI) associated preferentially with males and not with females during the pre-mating period (Mann Whitney U-test:  $U = -1.964$ ;  $p < 0.05$ ;  $n = 4$ ;  $m = 8$ ). However, no gender preferences were found for TI during the birth season ( $U = -1.812$ ;  $p = 0.07$ ;  $n = 4$ ;  $m = 8$ ) and the mating season ( $U = 1.534$ ;  $p = 0.12$ ;  $n = 3$ ;  $m = 8$ ).

These data partially agree with the seasonal differences in individual male proximity to TI. The dominant adult male (RO:  $X^2 = 5.821$ ; 2 df;  $p < 0.05$ ) and the subordinate male (LE:  $X^2 = 18.224$ ; 2 df;  $p < 0.001$ ) spent less time near TI during the mating season. No seasonal differences in proximity to TI were found for the two young males PE and CH, who migrated before the mating season started (PE:  $X^2 = 0.997$ ; 1 df; NS and CH:  $X^2 = 0.674$ ; 1 df; NS).

TI's closest male companion during the non-mating period was the lowest ranking and apparently youngest adult male (CH: B:  $X^2 = 22.250$ ; 3 df;  $p < 0.001$  and for N:  $X^2 = 6.533$ ; 2 df;  $p < 0.05$ ). No preference for either of the two adult males who remained in the troop during the mating season was found ( $X^2 = 0.200$ ; 1 df; NS).

### 5.4.2. Social environment

When analysing male inclusion in the free-ranging subadult male's social environment *versus* female inclusion, the rates for the former were higher during the birth (Mann Whitney U-test;  $U = -2.637$ ;  $n = 4$ ;  $m = 8$ ;  $p < 0.05$ ) and non birth-non mating seasons ( $U = -2.463$ ;  $n = 4$ ;  $m = 8$ ;  $p < 0.05$ ). No sex differences in proximity ( $< 10$  m) were found for TI during the mating season ( $U = 0.716$ ;  $n = 2$ ;  $m = 8$ ;  $p = 0.47$ ). These results can be explained as a result of TI being less often within 10 m of LE during the mating season ( $X^2 = 7.277$ ; 2 df;  $p < 0.05$ ).

TI's least frequent male neighbour ( $< 10$  m) was the alpha male RO, and the young low ranking male CH his most common neighbour during the birth season ( $X^2 = 16.111$ ; 3 df;  $p < 0.001$ ). The number of times adult males were found in TI's social environment did not differ significantly during the pre-mating season ( $X^2 = 3.840$ ; 3 df; NS). However, RO spent more time than LE and GR less than 10 m from TI during the mating season ( $X^2 = 15.064$ ; 2 df;  $p < 0.001$ ). This corroborates previous results which show that LE remained farther from TI during the breeding season.

#### **5.4.3. Captive subadult males**

Neither PP nor PA associated preferentially with any of the adult sex classes during the non-mating period (Mann Whitney U-test: all  $P > 0.05$ ). In contrast, during the mating season PA was more frequently found in close proximity to females ( $U = 2.139$ ;  $p = 0.03$ ;  $n = 3$ ;  $m = 5$ ) while PP was found within the females' social environment more often than within the males' ( $U = 2.112$ ;  $p = 0.03$ ;  $n = 3$ ,  $m = 5$ ). PA may have avoided close proximity to adult males during the mating season, but was found within 2 m of all females with a similar frequency during both periods. During the non-mating period PA spent less time than expected near the dominant adult male ( $X^2 = 8.167$ ; 2 df;  $p < 0.05$  and  $X^2 = 11.422$ ; 3 df;  $p < 0.05$ ). Finally, the highest ranking subadult male PP did not show any preference for a male companion at any time ( $X^2$ ; all NS).

### **5.5. MALE-MALE AFFILIATIVE BEHAVIOUR**

A definition of friendly interaction has been given in chapter 2 and its contribution to the time budget commented upon in section 3.3. As the frequency of these interactions was very low, data from continuous focal animal sampling and *ad libitum* observations were added to instantaneous samples in order to compare them. Binomial tests were used to determine differences in the directionality of grooming and antagonistic behaviours between pairs of animals.

#### **5.5.1. Social Play (SP)**

During scan sampling, RO was never recorded playing ( $N = 1398$  scans) while LE was recorded playing 4 times (out of 1243 scans) and only once with another adult male PE. The lower ranking and younger adult males PE and CH were found playing in 10 (out of 592) and 14 (out of 230) scans respectively. Of these, three involved PE and CH and one PE and LE.

### **5.5.2. Friendly (SF)**

Five instances of friendly behaviour (other than play or grooming) were recorded during RO's scans; of these only one was directed at another male. After LE had paid homage to RO, RO wrestled with him without any indication of fighting activity. LE did not reciprocate RO's action and looked away.

For LE, 8 out of 9 records of social friendly behaviour (SF) consisted of intratroup vocalisations (see chapter 2), the remaining record consisted of a contact interaction initiated by PE. PE approached LE, touched him and remained in contact with LE for a while yet showed no intention of grooming him. LE did not solicit grooming. PE did not interact in this way in any of the other 3 scans recorded as social friendly (SF). For the very young adult male CH, all 5 instances of SF were directed towards females and immature animals.

Two conclusions can be drawn from these data. First, males hardly ever interact in a friendly way, other than during grooming; second, when they do, younger males appear to be primarily responsible (chapter 3 for comparative data with adult females).

### **5.5.3. Male-male grooming**

Male-male grooming was uncommon and the dominant RO participated the most (Fisher's Exact test: NS). Clear differences in grooming distribution amongst males were found. The lower ranking of the pair did most of the grooming and the top ranking male received most. There also appeared to be individual differences in male tendency to groom. The second lowest ranking male (PE) was the most active groomer and groomed all the other males. He groomed the lowest ranking male once and the top ranking male 15 times during his scans.

When analysing adult male responsibility for initiating and maintaining grooming interactions with other males (see Fig. 6.7), it was found that the alpha male RO was more sought after as a grooming partner (by PE and CH) and PE the male most interested in maintaining grooming relationships with other males (in particular with RO and CH). Finally, the alpha male received grooming from more individuals (males and females) than any other male (Fig. 5.3) and more often than any other male, while the subadult male TI groomed the subordinate males LE and CH, he never groomed the alpha male.

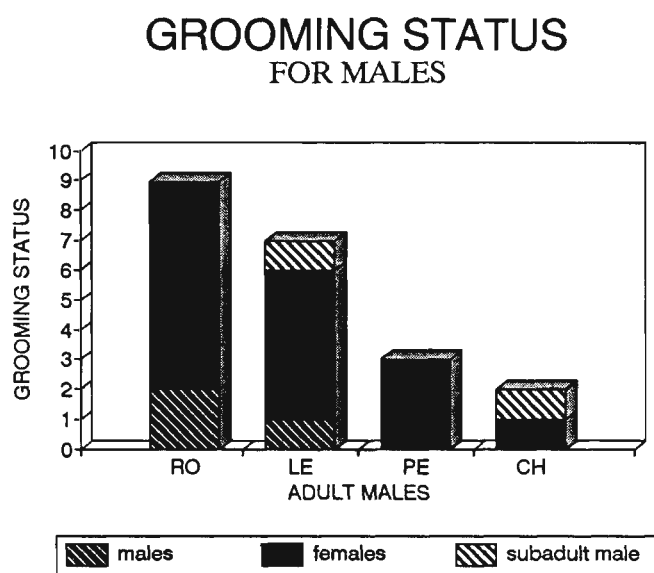


Figure 5.3.

Grooming status for adult males; number of adult males and females and whether the subadult male groomed RO, LE, PE and CH (males ordered in decreasing rank order).

The second ranking male LE took up a higher proportion of the total time he spent within 2 m grooming with females than with males (10.7% and 1.7% of the samples:  $X^2=7.906$ ; 1 df;  $p<0.05$ ). This was not true for the top ranking and the third ranking male, who did not show gender differences (Table 5.13).

In general, male dyads who spent more time than expected within 2 m of one another, did not groom each other more often than other dyads did (Spearman rank correlation coefficient:  $r_s=0.224$ ;  $n=6$ ;  $p=0.62$ ). The exception was RO, who groomed mostly with those males found in proximity more often (compare Fig. 5.1 with the data on grooming above).

Individual differences in the proportion of samples in which Windy Ridge males groomed with males that were within 2 m were not significant ( $X^2=5.738$ ; 3 df; NS). However, when samples for the 2nd (LE) and 3rd (PE) ranking males were compared, there was a difference ( $X^2=4.038$ ; 1 df;  $p<0.05$ ). This reflected LE's lack of motivation to groom other adult males and PE's greater tendency to do so, which may be explained by their age difference.

When the adult males in the Cage were within 1 m from another male, they were involved in grooming independently of their identity ( $X^2=4.748$ ; 4 df; NS). The same results were obtained for the two subadult males ( $X^2=3.282$ ; 1 df; NS). In conclusion, the proportion of time males spent in close proximity to other adult males without grooming did not differ. These results agree with those found for the dominant adult male of the free-ranging troop.

Table 5.13

Sex differences in the proportion of samples where grooming occurred when animals were at less than 2 m. from the focal male. Chi-square values, obtained from the actual counts, significance levels and degrees of freedom are shown (? indicates that there were not enough samples available).

	MALES	FEMALES	$X^2$
RO	6.3	9.5	0.796 (1) NS
LE	1.7	10.7	7.906 (1) *
PE	8.4	8.3	0.000 (1) NS
CH	3.2	2.0	?
Overall			5.738 (3) NS

## 5.6. MALE ANTAGONISM

Agonistic interaction is infrequent among vervet monkeys. A detailed description of the behaviour categories considered here and the proportion of time each age/sex class was involved in any form of agonistic behaviour have already been given (chapter 3).

In this chapter a quantitative analysis will be done first, followed by a qualitative description and a study of the directionality of this behaviour. Finally, an analysis of the distribution of wounds according to age/sex class, their location and their severity will be provided.

As a consequence of the linear hierarchy among males in the free-ranging troop (see appendix A), the top ranking male was the initiator of aggression more often than the recipient, while additional males were the recipients of aggression and displays of dominance more often than they were the initiators and additional males did most submissive behaviour (Binomial test: all  $p < 0.001$ ).

### **5.6.1. Comparing aggressive and submissive acts**

In general, agonistic encounters involving RO and other males were more common than those involving RO and females ( $X^2=827.7$ ; 1 df;  $p<0.001$ ). Similar results were found for LE ( $X^2=480.8$ ; 1 df;  $p<0.001$ ) and for PE ( $X^2=65.385$ ; 1 df;  $p<0.001$ ). Unfortunately not enough data was available for the lowest ranking young adult male to allow a statistical analysis. When combining the data for the two lower ranking and younger males of WT (PE and CH) the trend was not altered ( $X^2=64.207$ ; 1 df;  $p<0.001$ ). Therefore, it can be concluded that adult males interact agonistically more often with other males than with females.

Distribution of male submissive, aggressive and assertive behaviour obtained by continuous focal sampling and scan samples is shown for each adult and subadult male during the non-mating (BN) and mating periods (M) (Figs. 5.4-5.6). For the Cage Troop viewing conditions were excellent and data obtained using *ad libitum* sampling were also included.

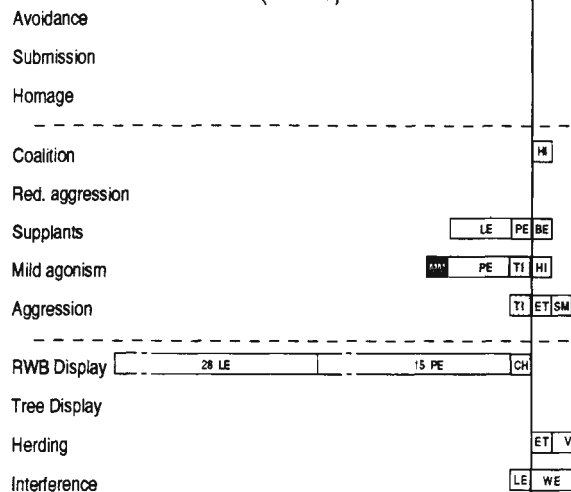
It is apparent that the distribution is biased towards male-male interaction, with male-female antagonistic interaction occurring less often in both troops (Figs. 5.4 and 5.5). However, this was not the case for the subadult males with distributions being less skewed (Fig. 5.6).

Figure 5.4 (see next page).

Distribution of agonistic bouts recorded during scan and focal animal sampling done on adult males (RO>LE>PE>CH) in the Windy Ridge Troop during the non-mating and mating seasons. The types of behaviour that reflect a subordinate role are: avoidance, submission and homage; aggressive behaviours were classified as: agonistic coalition, redirected aggression, supplants, mild agonism or defensive threats and open aggression which can easily lead to attack or physical attack; finally, displays of dominance, such as the Red-White and Blue display, tree display, herding and agonistic interference. On the left when it was directed towards adult (clear) or subadult males (shaded) and on the right towards adult females. Black areas represent extragroup males

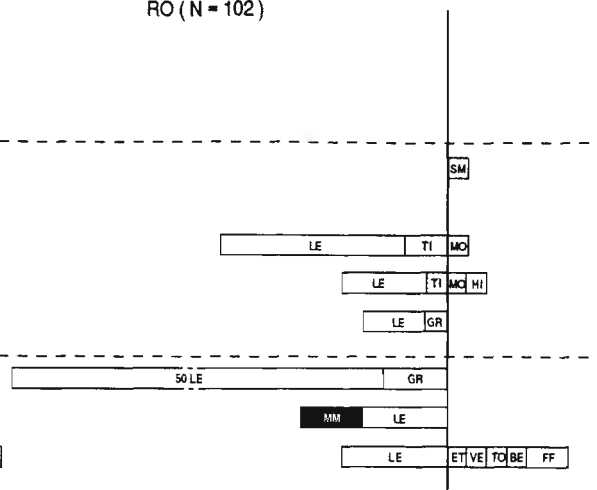
## NON MATING SEASON

RO (N = 74)

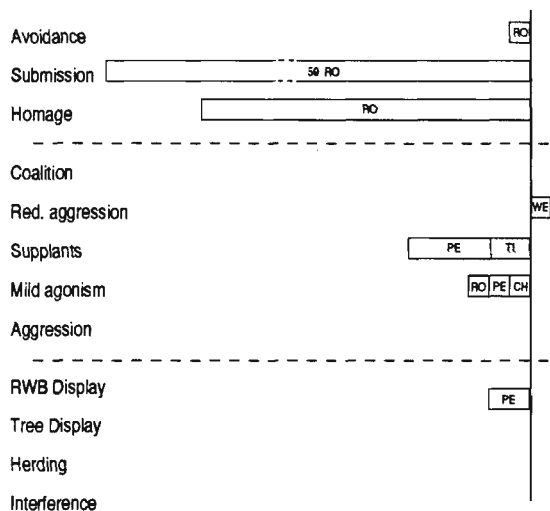


## MATING SEASON

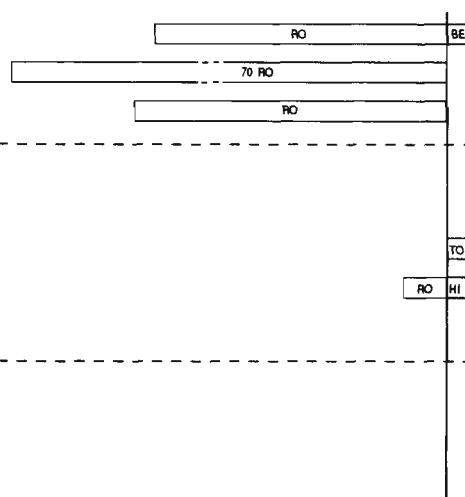
RO (N = 102)



LE (N = 95)

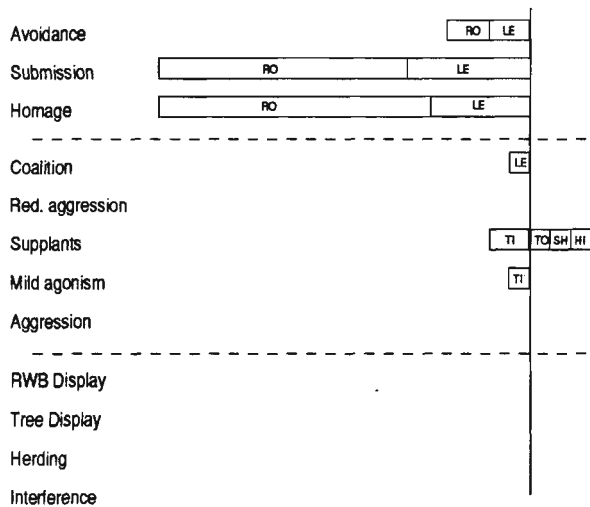


LE (N = 110)

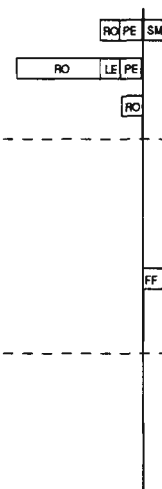


## NON MATING SEASON

PE (N = 52)



CH (N = 11)





## MATING SEASON

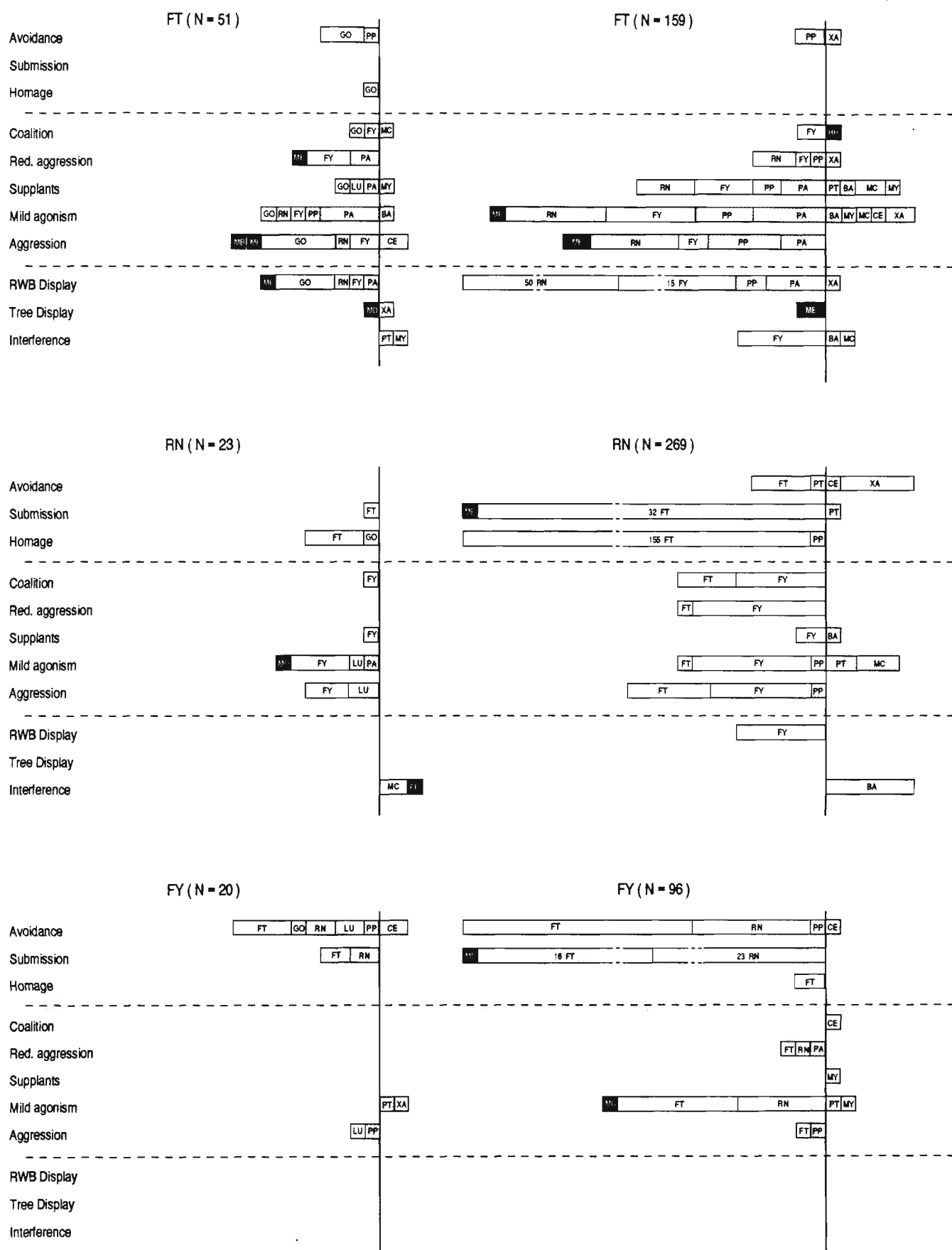


Figure 5.5.

Distribution of agonistic behaviour for the adult males of the Cage troop (FT>RN>FY). Black areas represent subjects of the neighbouring troop (AT) (rest as for Fig. 5.4).

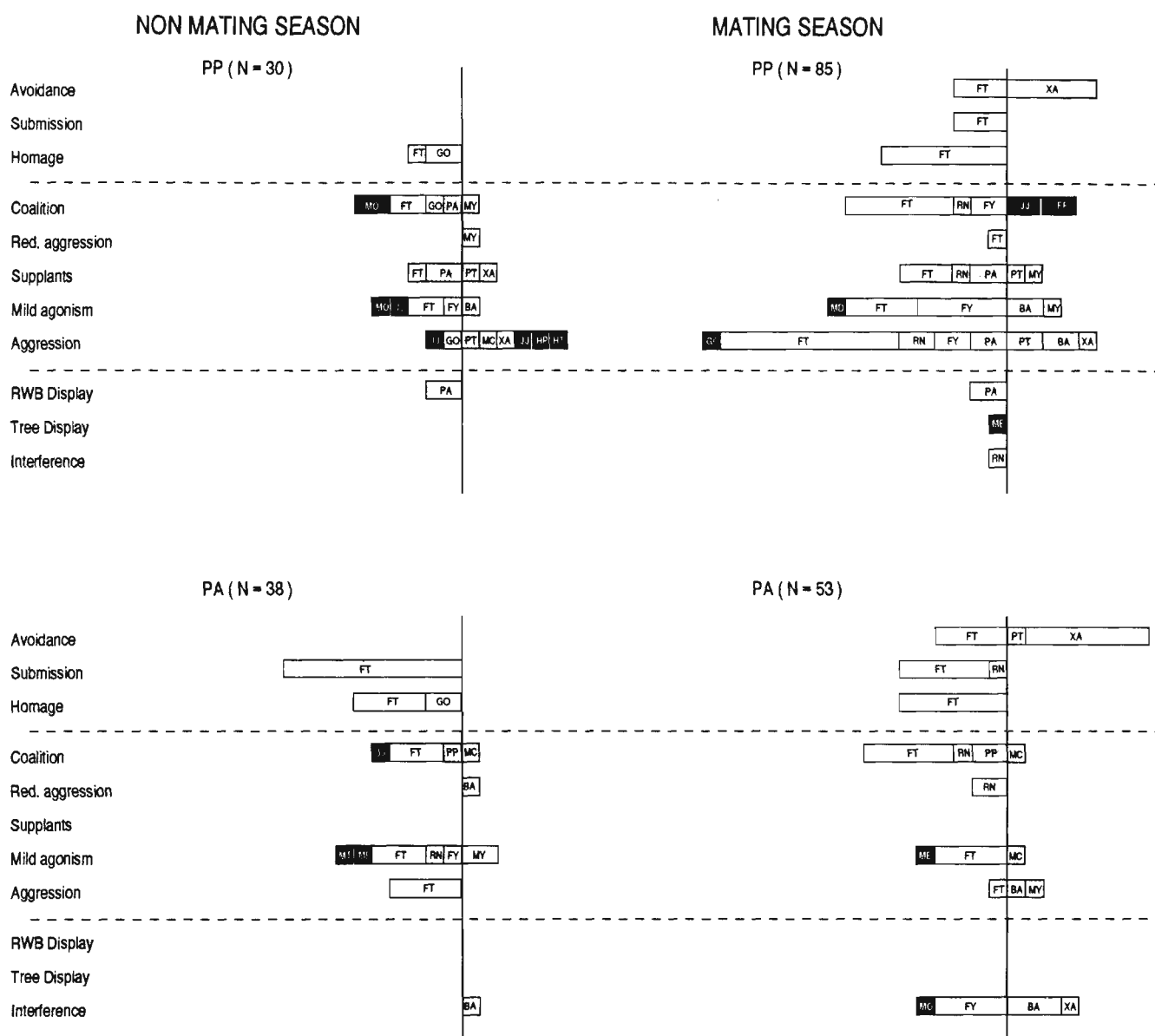


Figure 5.6.

Distribution of agonistic behaviour by the subadult males of the Cage Troop (PP > PA). Black areas represent subjects of the neighbouring troop (AT) (the rest as for Fig. 5.4).

### 5.6.2. Avoidance and submission

In Windy Ridge, the third ranking male PE paid homage to both higher ranking males (13 directed to RO and 5 to LE); and as hypothesised, most were directed at the higher ranking of the two (Binomial test, Probability set at 0.5:  $p < 0.05$ , one-tailed). PE paid homage towards both RO and LE, as many times as they displayed to him (Binomial test: NS).

The proportion of homage in relation to other agonistic behaviours directed to RO varied for LE and PE. LE initiated submissive displays less often than other antagonistic behaviour, while PE directed homage at RO as often as other agonistic behaviour ( $X^2=6.148$ ; 1 df;  $p<0.05$ ). Surprisingly, LE did not increase the proportion of homage towards RO during the mating season ( $X^2=0.695$ ; 1 df; NS).

LE showed subordination (submission or homage) towards RO when there were females in close proximity to him more often during the mating season than during the non-mating season (Fig. 5.7). These results cannot be explained because RO or LE were closer to females during the mating season (see chapter 6). A possible explanation is that females were the main source of competition at that time.

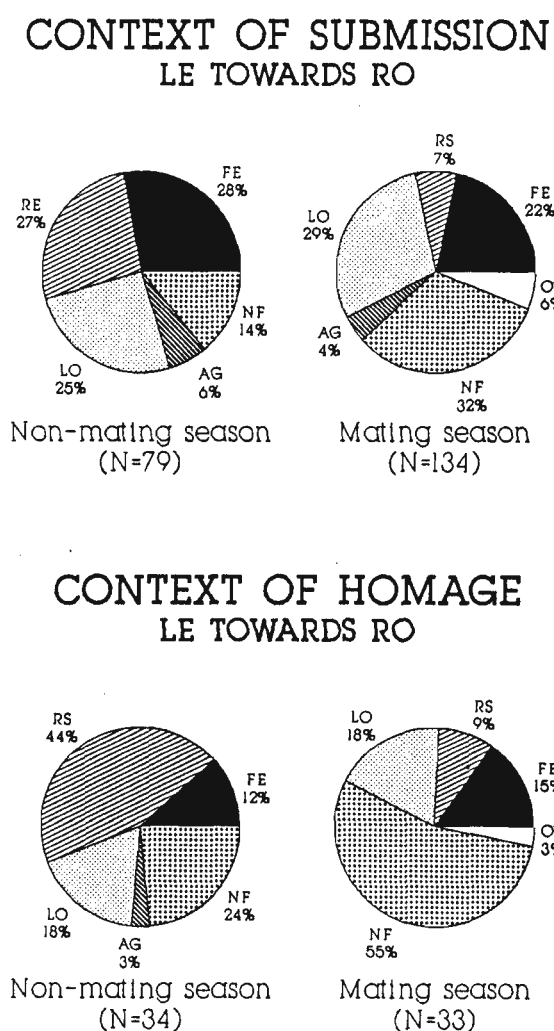


Figure 5.7.

Proportion of submissive bouts and homage by LE towards RO when there were one or more females in their vicinity (NF), or when not present, whether LE and/or RO had been interacting in an agonistic manner (AG), or RO was in locomotion (LO), resting (RS), feeding (FE) or other (OT), during the non-mating and mating seasons.

The above results suggest that a high proportion of homage reduces aggression (see above), and could explain why; i) PE received fewer aggressive bouts from RO than from LE and ii) LE received more aggression from RO during the mating than non-mating season, iii) LE showed his subordination towards the alpha male when near females more often during the mating season.

An interesting observation in the Cage was that: i) the dominant male FT showed submission towards his former subordinate GO and avoided both GO and the subadult male PP (Fig. 5.5), which reflects the instability of the male hierarchy.

During the non-mating period, 5 out of 23 of RN's agonistic bouts were directed at FT and were of a submissive nature (4 were homage). During the mating season 191 out of 269 bouts of an antagonistic nature occurred, these consisted of RN displaying submissive behaviour towards the alpha male (155 were homage).

### **5.6.3. Aggression**

In this section the distribution of male-male aggressive interactions will be analysed; that is coalition (CO), redirected aggression (RA), supplants and mild agonism including defensive threats (MA), and attack or threats which could easily develop into physical contact (AG) (Figs. 5.4-5.6).

The lower ranking animal of a pair, when threatened, could respond with a defensive threat (see chapter 2 for a detailed description of all behaviours), sometimes raising his hair.

Male-male agonistic coalition was observed in the Cage, although it was not as frequent as female-female or female-immature coalition (Fig. 5.8). Male-male coalition was mostly among subordinate animals (the middle ranking male RN, and the two subadult males PP and PA) against the most dominant male, supporting other males (9% of all coalitions recorded), or aiding other age/sex classes (16% of all the coalitions recorded) (see Fig. 5.9). Although statistical analysis did not apply because of the low number of observations and the inclusion of *ad libitum* data, these results are exciting because male-male coalition has not been described in previous studies of vervet monkeys.

## AGONISTIC COALITION

Involving males (MM) and/or others (OT)

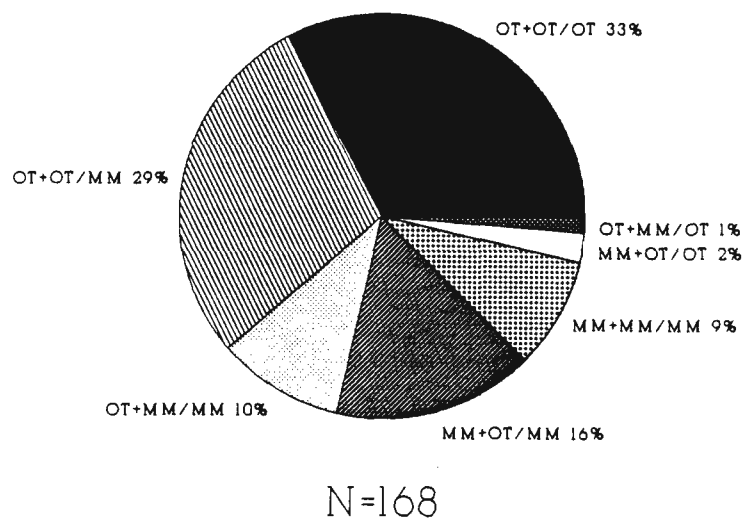


Figure 5.8.

Proportion of agonistic coalitions that involved adult females and/or immatures (OT), and or (sub)adult males (MM) in support of (+) and against whom (/).

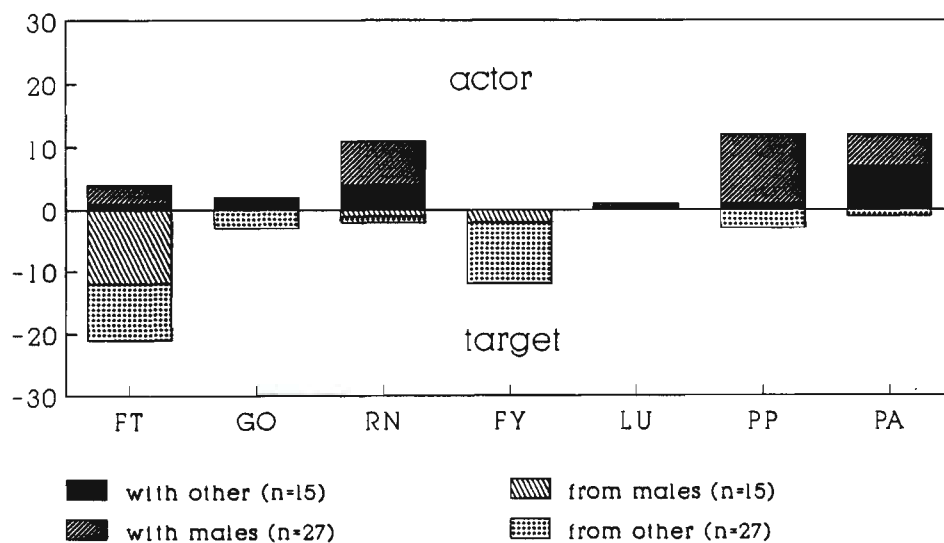


Figure 5.9.

Total frequency of male agonistic coalition towards other males (subadult males included) when each adult male was the actor or the target of the coalition.

Finally, those few instances in which an adult or subadult male in the Cage approached males involved in an agonistic encounter (one of the two lowest ranking males was the recipient in all these cases) and did not threaten any of them, were difficult to classify as either agonistic coalition or agonistic interference with males (plotted in the graphs as the latter).

#### **5.6.4. Displays of dominance**

##### *The Red-White and Blue display*

RO and LE were the only adult males that performed the Red-White and Blue Display in the Windy Ridge troop.

RO's displays were primarily directed at LE (28 times) and PE (15 times) during the non-mating season. Although the differences were not significant when analysing the data from scan sampling (10 in 738 scans and 4 in 645 scans respectively:  $X^2 = 1.194$ ; 1df; NS), in general, the tendency was to direct displays of dominance towards the next lower ranking male more often than to others (Figs. 5.4 and 5.6).

The displays of dominance performed by subordinate males were different from those performed by the alpha male, as the subordinate actors mostly used the hand on shoulder modality (see chapter 2). The higher ranking subadult male in the Cage (PP) was observed twice doing an uncompleted form of display towards his lower ranking counterpart (PA).

In addition, in Windy Ridge the second ranking male LE displayed his scrotum and erect penis at the third and lowest ranking male PE. He did so while sitting on and then off the ground in front of PE while keeping his left hand on PE's shoulder. PE responded with mild submissive gestures and scratched nervously. The dominant male RO saw the interaction and self-stimulated himself until he achieved erection and ejaculated; he then rushed at the interacting pair. After a short submissive act, PE left the area crouching low. LE immediately put his hands over his genitalia, concealing them. RO threatened LE by jerking his body in front of LE and displayed around the subordinate. LE responded with submissive acts. Once the interaction was over, LE repeatedly performed 'homage' towards the dominant male.

RO directed a similar proportion of displays in relation to aggressive behaviour towards LE and PE (Fisher's exact test; NS). Although, the number of displays of dominance by RO towards LE were higher than the acts of homage LE paid to RO (Binomial test:  $p < 0.05$ ) during the non-mating season, the difference was more apparent during the mating season (Binomial test:  $p < 0.001$ ).

These results are emphasised by the fact that the ratio of aggression to displays of dominance was higher for RO towards LE during the mating season than during the non-mating season (Fisher's exact test  $p < 0.05$ ).

In contrast, PE paid as many acts of homage at RO as dominance displays received from RO (Binomial test; NS Probability set at 0.5). This suggests that homage has the function of reducing aggression by the dominant male. It cannot be excluded that grooming can also affect the relationships among males, because in fact PE groomed RO more often than any other male did. PE received more displays from RO (15) than from LE (2) and they constituted a higher proportion of the total agonism from RO than from LE (Fisher's exact test;  $p < 0.05$ ). Therefore, the highest ranking male relied more heavily on displays of dominance than on other agonistic behaviours.

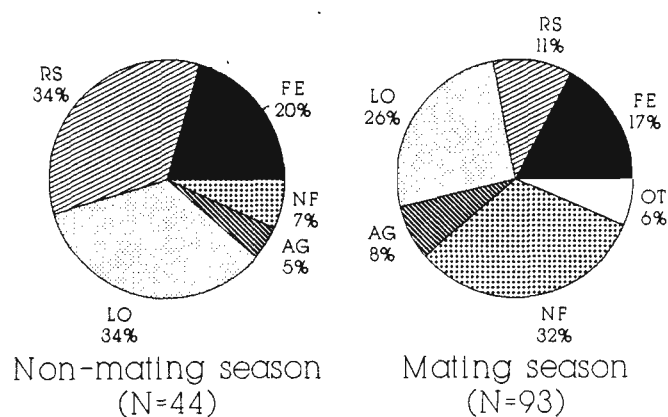
When including data from *ad libitum* and focal animal sampling it emerges that there was a tendency for RO to display towards LE when he was near females more often during the mating than during the non-mating season ( $X^2 = 9.226$ ; 1 df;  $p < 0.05$ ; see Fig. 5.10), as was found for LE's acts of subordination (Fig. 5.7). In addition, RO's displays towards PE occurred 3 times near females and once when feeding apart from females.

Aggression by males toward subordinates consisted mainly of displays of dominance. The Red-White and Blue display (DP) (see chapter 2) was directed mainly at the next lower ranking male.

#### *Other displays of dominance*

Herding of the subordinate male by the dominant male was only observed during the mating season ( $N = 14$ ) (see Fig. 6.4). Four times when LE was at less than two meters from adult females, nine times before starting a general progression (cf. 'notifying' among hamadryas baboons: Abegglen, 1984) and once for no apparent reason. The alpha male herded his subordinate mostly, I suspected, when one or more adult females were sexually attractive.

## CONTEXT OF DISPLAYS (DP) RO towards LE



data from all sampling methods

Figure 5.10. Proportion of times RO performed a Red-White and Blue display towards LE when in close proximity to females (NF), or when both males had been interacting in an agonistic way (submission and homage included) or when not, whether LE was moving (LO), resting (RS), feeding (FE) or other (OT), during the non-mating and mating season.

The 'tree display' was mainly performed by the dominant male of the troop, though on occasions the second ranking male did so as well. This display was mainly prompted by the presence of extra-troop males, except on a few instances when the cause was the highest ranking female of the Cage Troop. In this situation, the tree display was an equivalent of herding but performed away from the female, with no obvious intention to herd her, rather to show his supremacy. It can also be argued that this behaviour could have been categorised as agonistic interference (see chapter 6). Eventually, the top ranking female did a false chase of the dominant male and was joined by most members of the troop.

### **5.6.4. Distribution of wounds**

The Chi-square test was used to determine significant differences in wounds received by each age-sex class and corrected for the number of subjects per age-sex class. Differences in location of wounds and their severity between the three study troops were analysed with the Kruskal-Wallis test.



A total of 136 wounds was recorded: for the Windy Ridge (27), Cage (88) and Altre (21) troops. When considering the observation time, the three troops did not differ in total frequency of wounding, severity or proportion of wounds received on the back quarters, tail and back legs (Kruskal-Wallis test: all  $p > 0.05$ ). However, the Cage Troop showed a higher proportion of wounds inflicted on the front of their bodies (head and forequarters) than the free-ranging troops (Kruskal-Wallis test: 12.527;  $p < 0.01$ ). When considering data for all the troops, fewest wounds were recorded in the birth season (Kruskal-Wallis test: 9.406;  $p < 0.05$ ) and severe wounds were less frequent at this time (Kruskal-Wallis test: 8.242;  $p < 0.05$ ).

Table 5.14

Distribution of wounds for the Windy Ridge troop (WT), Cage troop (CT) and neighbouring free-ranging troop (AT) during the birth (B), non birth-non mating (N) and mating (M) seasons. Observed (O) and expected frequencies when correcting by the number of individuals present in the troop (E) are given. Significant differences between the different age sex classes (AM: adult males; AF: adult females; SA: subadult males and JJ: immatures) obtained with the Chi-square test are shown (\*\*  $p < 0.001$ ; \*  $p < 0.05$ ; NS, non-significant: ? when enough data was not available).

		B		N		M	
TROOP		O	E	O	E	O	E
WT	AM	2	1	9	3	1	0
	AF	0	2	4	7	2	1
	SA	-	-	-	-	0	0
	JJ	1	1	4	7	0	1
		?		14.571(2)**		?	
CT	AM	6	3	13	7	3	2
	AF	1	5	13	9	4	4
	SA	-	-	-	-	2	2
	JJ	8	7	3	13	3	4
		6.343(2)*		14.613(2)**		0.750(3)NS	
AT	AM	0	0	4	1	4	1
	AF	0	0	0	1	2	3
	SA	-	-	-	-	-	-
	JJ	1	1	0	2	2	4
		?		?		?	
All	AM	8	4	26	11	8	3
	AF	1	7	17	17	8	8
	SA	-	-	-	-	2	2
	JJ	10	9	7	22	5	9
		9.254(2)*		30.682(2)**		10.111(3)*	

Adult males received more wounds than adult females, subadult males or immatures (see Table 5.14). These results agree with the fact that males were more involved in agonistic interactions than females during the pre-mating and mating season (see chapter 3). This together with the fact that adult males mostly direct their agonism towards other males shows that competition between females is not as intense as it is between adult males.

Wounds were classified as severe when they were more than simple scratches. Their location could be on the head, forelimbs, hindlegs, back, tail or scrotum. When wounds are inflicted on the front of the animal (head and forelimbs) it implies that the animals were facing each other and when inflicted in the posterior area (hindlegs and tail), the animals were involved in a chase situation. On the other hand, those located in the dorsal area or scrotum were not so clearly classified. In the following analysis, 5 age-sex classes will be distinguished - yearlings considered apart from older immatures.

The proportion of wounds received on the face or head did not differ for the five age-sex classes (Kruskal-Wallis test: 4.954;  $p > 0.05$ ), although immatures tended to receive fewer wounds on their posterior quarters (Kruskal-Wallis test: 11.393;  $p < 0.05$ ). In general, infants were less severely wounded than adults, and adult males more than adult females. However, when comparing the different age-sex classes there was no significant difference in the total number of severe wounds (Kruskal-Wallis test: 8.039;  $p > 0.05$ ).

## 5.7. DISCUSSION

First I will discuss male proximity relationships. Are males closer to females or to other males? Do some male pairs associate more often than others? Does male-male proximity vary as the mating season approaches? Second, grooming and other friendly behaviour will be explained in terms of proximity relationships and male individual differences. Third, quantitative and qualitative differences in agonistic behaviour for the non-mating and mating seasons will be compared with those reported in the literature for closely related species. Finally, a review of the importance of the visual genital signalling system in male vervet monkeys will be presented and its possible physiological regulation commented upon.

### **5.7.1. Male spacing**

Close proximity is a distance category in which animals are either in contact or can easily reach each other. In addition, all animals included in the focal animal's social environment (10 m radius) can easily communicate with facial gestures and soft vocalisations ('social distance': Lopez-Lujan *et al.* 1989 for stumptail macaques).

*Do males associate primarily with other individual males or females?*

In Windy Ridge, adult males never associated preferentially with females. Conversely, during the birth season, the two older and higher ranking males were further than 10 m more often from females than from other males. The lowest ranking adult males and the subadult male were more often in the company of other males rather than females. These results are in partial agreement with previous studies which claim that subordinate males were more peripheral to the main part of the troop than dominant males (Lopez-Lujan *et al.* 1989). The exception was for the second ranking male (LE) who behaved in a way similar to the top ranking male.

On the other hand, the top ranking male of the Cage Troop behaved differently. He remained closer to individual females rather than to individual males during the non-mating season. Although preference for male partners during the birth season could have been obscured when data for both seasons were combined.

That males tend to be closer to females rather than to other males during the mating season, was found to be true for only the subadult males of the Cage Troop. First, the most dominant of the two subadult males was seen within the social environment of females more often than he was with males. Second, the lower ranking subadult male was found less than 1 m from females more often than from males.

*Seasonal differences in male-male proximity*

In Windy Ridge, the two lowest ranking males were predominantly found more than 2 m from the dominant male during the pre-mating season. As this occurred just before they migrated, it was difficult to distinguish between a seasonal and a pre-migratory component. On the other hand, the alpha male and the next ranking male were less than 10 m apart more often during the mating season. This can be explained by RO's persistence in following LE in order to keep him away from females (personal observation).

The subadult male of the free-ranging troop was seen within 2 m and 10 m of RO and LE during the mating season. The caged subadult male (PA) behaved in a comparable way, spending less time near FT during the mating than during the non-mating period. Similar results were found for the adult middle ranking male (RN) but not for the subadult male (PP) in the Cage.

The general trend was for subordinate adult and subadult males to increase their distance from the most dominant male as the mating season approached. Besides the exception of LE in Windy Ridge, the highest ranking of the two subadult males in the Cage did not show any seasonal differences in proximity to the top ranking adult male. It is possible that the contrasting results found for the two troops reflect the capability of the top ranking male to control the movements of other males in a restricted environment, as this is somewhat easier in the Cage than in natural conditions.

In general, adult males associated preferentially with closely ranking males (see Kaufmann, 1967 for rhesus monkeys). An exception was the alpha and third ranking male of the Windy Ridge Troop (RO and PE) who were probably related and spent more time than expected at less than 2 m. This was also the male dyad more involved in grooming.

In summary, individual differences in proximity for each adult male dyad could reflect avoidance by the subordinate males of the alpha male. This is especially true for the lowest ranking males who were further away from the top ranking male during the pre-mating and mating seasons than during the birth season.

### **5.7.2. Affiliative behaviour among males**

Social play involving males was a rare event, and when it did occur it typically involved the younger males (see also Bramblett & Coelho, 1987), and was directed at close ranking males. After puberty intragender competition reduces the frequency of play (Loy, *et al.* 1978 p. 65; Symons, 1978; Bartecki, 1986).

Other friendly behaviour such as body contact and friendly vocalisations are not common among male vervet monkeys. When observed, they were mainly directed toward other age/sex classes.

Grooming between males was directed to the higher ranking individual of the pair (see Kaufmann, 1967 for rhesus monkeys; Sparks, 1967 for a review). The total grooming received by males and the number of adult males and females that groomed a male was related to his rank. The top ranking male, therefore, received more grooming than he gave (see Sade, 1972 for rhesus monkeys) and more adults groomed him than groomed any other male.

The low motivation of the adult males LE and CH to groom other males was in contrast with PE's higher rates, that agrees with the statement that the male tendency to groom other males is related to the age of the actor (Bramblett & Coelho, 1987) and influenced by the relative rank of the male participants (see Seyfarth, 1980 for female vervet monkeys). As agonistic coalitions among male vervet monkeys are uncommon, the use of grooming to improve the chances of achieving an agonistic coalition with a higher ranking adult male seems unlikely, yet not impossible.

The appeasement purpose of grooming among males living in multi-male groups has been suggested, by amongst others, Sade (1965) and De Waal (1991) for rhesus monkeys (see also Hall, 1967 for caged subadult patas monkey). Male-male grooming differs from female-female grooming is that it occurs less frequently and no direct competition exists to groom higher ranking males (grooming supplants never occurred among males to groom other males, although they were found when competing to groom females). In addition, it is inferred that male-male grooming does not have the same long-term implications for the maintenance of social relationships between males that it has between females. This is emphasised when looking at the high rates of grooming shown by PE towards RO, who migrated from the troop not long afterwards.

Other possibilities are that young, less dominant males use friendly behaviours such as grooming to retain proximity with higher ranking males, although when the difference in rank is too great this does not occur, and the obvious consequence is that low ranking males tend not to interact with either males or females (see chapter 6). As a result, low ranking males can be classified as being 'socially inactive'.

Therefore, I suggest that male-male grooming; i) has the same proximate reasons as female-female grooming (cleaning their fur; pacifying the opponent), ii) is mostly directed to the higher ranking animal, iii) occurs between closely ranking males iv) reduces antagonistic behaviours when the animals are in close proximity, allowing higher rates of proximity and v) differs in relative importance from female-female grooming.

### **5.7.3. Male antagonism**

Adult males direct most of their agonistic behaviour towards other males, which corroborates Emlen's (1973) and Wrangham's (1979) theory that the males' most limiting resource is females. On the other hand, subadult males direct more agonism towards females. Does this happen only because they are lower ranking than other males, or is it because they are physically closer and compete more directly with females? I propose that it is due to the adult males holding a higher dominance rank.

Most supplants occurred between closely ranking individuals. They were always directed towards the lower ranking of the pair, the exception being PP, the subadult male who took advantage of FT's bad injury (possibly caused by intertroop fighting) and rose in rank. Supplants, as suggested by Struhsaker (1967 b) for vervets and by Johnson (1989) for olive baboons, as well as benefiting the winner when the resource is scarce, can reinforce the social relationship between closely ranking individuals (Schnell *et al.*, 1985 for white-throated sparrows).

Redirected aggression and supplants were always directed at the lower ranking male of the pair in Windy Ridge. This did not always apply for males of the Cage Troop, where reversals in the direction of open agonism were common. During the non-mating period FT and GO competed openly for the top position. During the mating season, when GO was no longer in the troop, the subadult male PP successfully displaced and directed threats at the dominant male FT. More commonly, defensive behaviour, such as coalitions with other males and/or females, allowed low ranking males to rebel against a more dominant male. Camberfort (1981) only refers to coalitions of juvenile vervets against the adult male, without further specifying the sex, and no mention is made of adult male coalitions. At times, adult females would also join the males and a general 'rebellion' against the alpha male would ensue and it could end with the dominant male heavily threatening other members of the troop and showing scrotal adduction while holding onto the top of the cage.

The above statement could be criticised because it has been reported that adult female vervet monkeys 'false chase' dominant males, the difference with a normal chase being that the persecuted male does not show signs of distress.

The fact that only four adult males were present in the free-ranging troop during the birth and early pre-mating season, the most stable period, and only two adult males during the rest of the study, could explain why male-male coalition was not observed. However, when there were three adult males, the second ranking displayed, supplanted and threatened the lowest ranking male, these actions were met by high levels of aggression from the top ranking male. This observation in some ways could be considered an agonistic coalition with the target male. However, other implications were more obvious, that is the alpha male did not allow the second ranking male to display his genitalia.

The differences which appear between the two main study troops could be explained by: i) the caged males being more related, ii) the smaller distances between animals in the Cage might have favoured rank reversals, iii) the more unstable hierarchy amongst males of the caged troop could also have contributed and iv) redirected aggression was mainly prompted by intertroop agonistic encounters, which were common in the captive troop.

Fighting is energetically 'expensive' as well as dangerous, and natural selection has only favoured fighting behaviour when the benefits exceed the costs. The group selectionist argument is that ritualised signals have evolved to maintain dominance hierarchies (Poirier, 1970 p.322; Symons, 1978).

Submissive presenting by adult males is quite rare among vervets and is not easily distinguished from sexual arousal and play among subadult males (Baldellou, in prep.). That all the males in the Cage were seen acting submissively towards other males proves the point that their dominance relationships were less stable than in Windy Ridge. However, homage or self-initiated display of subordination (Henzi, 1982; 1985) was characteristic of subordinate males ranking one or two below the alpha male.

It appears that homage functions to demonstrate the sender's submissiveness and to appease the higher ranking male. The proportion of homage given to displays received did not vary for any of the male dyads nor did it vary with the season. On the other hand, an increase in agonistic interactions - different from ritualised displays - for RO and LE supports the theory that males are more aggressive during the mating period.

It can be concluded that vervet males occupying adjacent ranks spend more time in proximity and interact more often than expected in both a friendly and agonistic manner (cf. Saayman, 1971 for chacma baboons).

The distribution of wounds and their severity may serve as good indicators of the levels of aggression within a troop of monkeys (Hausfater, 1975, Henzi & Lucas, 1980) and also serve as an indicator of the degree of social stability (Drickamer, 1975). The fact that the proportion of wounds inflicted during the birth season was lower than at other times, shows that the birth season is the most socially stable period (cf. Young, 1981 for howler monkeys).

Struhsaker (1967c) pointed out that the absence of stable dominance relationships among vervet monkeys of different troops could account for a higher proportion of wounds received during intertroop agonistic encounters. As adult males have less stable hierarchies than females, it is not surprising to find that adult males are more wounded and receive more severe wounds than any other age-sex class (see also Struhsaker, 1967a; Henzi, 1982). Infants received less wounds than other age classes.

The finding that wounds, among adults in particular, were most frequently found in the tail and hindlegs (see also Struhsaker, 1967a; Henzi, 1981; Basckin & Krige, 1973) suggests that vervets have a better chance of being attacked when running away, that is when they are not using submissive gestures. In contrast, samango monkey wounds are mostly inflicted on the face and hands (Henzi & Lawes, 1987) and female baboons receive most of their wounds in their backs, because they crouch immobile during attack (Smuts, 1987, p.87-88). The finding that the samangos' pale blue-grey scrotum and pink-grey penis are not used in a similar way as those of vervets (Henzi & Lawes, 1987), could result in differences in the distribution of wounds.

In the Cage, where fleeing behaviour was restricted, there was a comparatively higher proportion of wounds in the face and head than for the two free-ranging troops. On the other hand, no differences in the total number of wounds or proportion of severe wounds among the three troops existed. These results could be explained by the comparable levels of aggression, submission and displays of dominance found for the Cage Troop and Windy Ridge Troops (chapter 3). High levels of relatedness among members of the Cage Troop could have compensated for the lack of escape routes.

#### **5.7.4. Male visual signalling system**

The importance of the genital visual signalling system and other behavioural adaptations in the coexistence of unrelated adult vervet males will be discussed.



Male intratroup displays of dominance depend heavily on the vivid colours of the genitalia, are performed by the higher ranking male of the pair (see also Struhsaker, 1967b; Henzi, 1982; 1985) and are mainly directed towards the next ranking males. These displays were exclusive to the two highest ranking males and the most frequent displayer was the top ranking male of both troops. During the Red-White and Blue display, the actor may put one or both hands on the head or shoulders of the recipient while sitting or standing bipedally in front of the recipient (Struhsaker, 1967a, but see Henzi, 1985). This variation was commonly found among non-dominant males and I suggest that in this way the displayer may show his genitalia only to the recipient and keep the act concealed from the dominant male.

I have included 'confident walk' as a dominance display which is generally not directed at a single adult male but rather at the troop in general (chapter 6). The 'confident walk' is an assertive walk most often performed by the top ranking male. The elevated tail and assertive body posture of the alpha male serves to attract the troop's attention, and often occurs before a general progression is initiated or when the direction of the group has changed radically. It has the function of gathering members of the troop around the dominant male, when it is necessary to maintain the troop's unity. RO usually performed this behaviour along the river bank or in open country, where it served as a visual signal for other members to follow.

All the displays of dominance and 'keep out signals' enhance the male's genitalia and have the advantage of being less costly than an attack (van Rhijn, 1980). Henzi (1985) emphasises the specific signalling functions of the penis and scrotum suggested by their different colouring. Finally, natural selection may have favoured concealment of the genitalia by subordinate male vervets in order to stop an escalating attack. Over the course of the study, a few occurrences of males concealing their genitalia from the higher ranking male's sight were witnessed. When a low ranking male for sexual (chapter 7) or other reasons exposed his penis (generally consisting of an extension; total erection was rare), he avoided being seen by the dominant male. Testicular adduction occurred when the dominant entered the subject's vicinity.

In summary, concealment of the adult male's genitalia, which has the effect of preventing overt aggression among males, can be achieved by: i) testicular adduction (physical response) (Henzi, 1985); ii) tail down (physical and/or behavioural response); iii) crouching low (behavioural response), which can also be associated with testicular adduction and/or iv) hands or body hiding the genitalia (behavioural response) (see De Waal, 1982 for chimpanzees).

These responses protect the male's genitalia from injury when threatened or attacked or when exposed to a Red-White and Blue Display (see also Henzi, 1981; 1985). They therefore are related to a subordinate role. In this study, adult males were seldom seen with scars or even blood on their scrotum. The fact that these wounds were inflicted during periods of high level of aggression and instability when the interacting males did not always adopt submissive postures, stresses the highly adaptive nature of these behavioural responses. Other visual signals associated with subordination are 'lipsmacking' (Redican, 1975) and 'teeth chattering' (both have an auditory component) and occur during encounters where the focal animal behaves submissively.

#### **5.7.5. Defence of females and/or food resources**

Males typically migrate to or visit other troops just before or during the mating season (Henzi & Lucas, 1980; Cheney & Seyfarth, 1983; this study). The most common reaction of the higher ranking resident male is to chase the outsiders away, 'tree display' and/or herd the females away from the extra-group males. Adult males participated in intertroop agonism when the adult males of the neighbouring troop were involved (cf. Fedigan & Fedigan, 1988). The only two exceptions (one by FT and another by GO) could have been classified as male coalition with females and immatures of their own troop against females of the other troop. The fact that these behaviours were also elicited outside the breeding season questions the argument that a male is primarily concerned in stopping other males from inseminating 'his' females.

Non-human primates have the ability to rank all the other members of the troop (Seyfarth, 1976; 1980; Johnson, 1989) and some members of neighbouring groups (Cheney & Seyfarth, 1982b). Therefore, if male participation in intertroop encounters is not exclusively directed towards stopping males from gaining access to his females, the benefits to the male are more long term strategies, such as reinforcing his rank in relation to other extragroup males (see Cheney & Seyfarth, 1982b).

It cannot be disregarded that infanticide is reduced by males keeping extra-group males away from the central part of the troop outside the mating season. This is accomplished by first, regrouping the females, through aggressive herding or even by attacking them, which also serves to chase immatures away from the edges of the troop and seek protection with their mothers and second, by performing a tree-display, the branches shake and much noise is created, directing the attention of the troop to the alpha male.

The end result might be that these behaviours regroup the troop and the females and immatures remain alert and vigilant. Therefore, displays such as confident walk, herding of females and tree-display are more common during the mating season. These behaviours may facilitate the control of females by the dominant male.

During the mating season, RO was seen herding LE in the same way that he herded females. The effect of this was that LE followed the leader of the progression when the troop moved off. One implication could be that the top ranking male benefited from the second ranking's presence in the troop. Alternatively, the highest ranking male could have been directing the subordinate to a position where he could keep him in view and control his interactions with females of the troop.

What hypotheses could be formulated when considering what adult males defend when participating in inter-troop agonism? They could either defend females or food resources. Unfortunately, not enough data was obtained in this study to substantiate either claim. However, what was clear from observations done in the Cage Troop was that adult males only participated in intertroop agonistic encounters when external males were involved. Only on two occasions did adult males (high ranking) form a coalition against external females and both occurred when the caged females were already involved in an agonistic encounter with the free ranging females. This could be viewed as the equivalent of intragroup agonistic interference (see chapter 6). Subadult males were involved in intertroop agonism with females and immatures of the outside troop (AT) more often than adult males.

Male chimpanzees generally remain in their natal areas and defend territories (food and females) against neighbouring groups (review in Wrangham, 1986). Males may form coalitions (related and unrelated males) to protect these resources and they can also aid each other against status competitors. This, together with the fact that male chimpanzees may give food calls and cooperate to catch vertebrate prey, suggests that here coalition and defence of food resources is not a matter of sex but of kinship.

In summary, adult male vervet monkeys' tree display and herding of females are mostly performed by the top ranking male of the troop. Exceptions do occur, especially when the dominance hierarchy is unstable. The function of this behaviour is to defend the females of the troop and possibly to stop potential infanticide by extra-troop males, although the data collected in this study questions the direct defence of food resources by adult males. Males by keeping external males away from females, may also deter other troops from depleting their troop's resources.

The proportion of male coalitions with other members of the troop was much higher in the Cage where individuals were more related than in natural conditions. This difference between the study troops and the fact that subadult males formed coalitions against adult males more often than adult males could indicate that coalitions are mostly related to kinship rather than to other factors.

Variations in male feeding activity were mostly explained by time dedicated to agonistic interactions. For females, an increase in time spent feeding was correlated to a reduction in resting, locomotion and time socialising (chapter 3). The above findings emphasise the relative importance of agonistic behaviour *versus* other maintenance and social activities for males as opposed to females. In contrast, adult females have been found to rely heavily on grooming, which is distributed in accordance to kinship and relative social position (Rowell, 1971; Seyfarth, 1977; Cheney & Seyfarth, 1990).

Five consistent patterns emerge from the results on male-male interactions: i) there are similarities between the different measures of dominance (Richards, 1974); ii) like adult males in other multi-male, multi-female groups (Emlen & Oring, 1977) vervet males adopt behavioural strategies in order to inhibit the sexual behaviours of subordinate males, without implying higher levels of open agonism (see Keverne *et al.* 1984); iii) adult males interact (positively or negatively) more often with closely ranked males, a tendency which is also reflected in their proximity relationships (see Kaufmann, 1967, for wild rhesus monkeys); iv) male-male coalition among vervets has been described in this study, which is also characteristic of other polygynous species (see review: Smuts, 1987); finally, the complex visual signalling system that has evolved in vervet males (Henzi, 1982; 1985), cannot be understood if it is not in terms of male coexistence in multi-male troops. Therefore, there seems to be a quantitative rather than qualitative difference between vervet multi-male society and other typical multi-male species, which is in partial agreement with Henzi's (1985) argument that vervet multi-male structure is not as complex as that of baboons and macaques.

## 6. MALE - FEMALE SOCIAL INTERACTIONS.

The degree of affiliation among non-human primates has been frequently studied by analysing spatial (Carpenter, 1942a; Sade, 1965; Bartecki, 1986) and grooming relationships (e.g. Hinde, 1977; Seyfarth, 1978a,b; Smuts, 1983). These will be the two main aspects of male-female association described in this chapter.

A growing body of evidence indicates that adult males living in multi-male societies may form long-term friendly bonds with females based on high proximity rates, grooming and agonistic support (e.g. for savanna baboons: Seyfarth, 1978 a,b; Altmann, 1980; Rasmussen, 1983; Smuts, 1983; 1985; Strum, 1983 and for macaques: Kaufmann, 1967; Chapais, 1983a, 1986; Hill, 1986; see review by Smuts, 1987). These bonds persist in the absence of any immediate sexual relationship and may benefit females and young offspring (e.g. Deag & Crook, 1971; Smuts, 1983, 1985; Altmann, *et al.* 1988; see also Taub, 1984) as well as males (Hamilton, 1984, p.309).

Males may use infants during agonistic buffering to reduce the risks of injury in inter-male encounters (for macaques: Deag & Crook, 1971; Witt, *et al.* 1981; for baboons: Hausfater, 1975; Strum, 1983; 1984) and those infants are primarily those of females with whom they maintain close associations (Strum, 1984).

'As duration of adult male-female associations increases, the opportunity for extended allocation of paternal care and extended duration of infant dependence upon both parent could also increase'(Hamilton, 1984, p.330).

Male agonistic dominance rank has generally been found to affect mating behaviour in non-human primates (see review, Packer, 1979b; see chapter 7). However, it has been argued that males copulate mainly with those females with whom they have maintained friendly bonds when the female was not cycling (e.g. Smuts, 1985; see Hill, 1986 p.170 for exceptions) and that other males' success in mating with those special female friends is restricted by female choice and male sexual interference (Smuts, 1987).

Together with the finding that subordinate males: i) establish long-term social bonds with females more than with higher ranking males (*e.g.* Saayman, 1971); ii) provide more intensive infant care (Altmann, *et al.* 1988); and iii) that female choice accounts for most of the male's reproductive success even in highly dimorphic species (Altmann, *et al.* 1988; Smuts, 1987) suggest that male-female social bonds are ultimately related to reproductive success (Smuts, 1985).

Vervet monkeys have been described as a species lacking similar adult male-female bonding relationships as described for baboons and macaques (*e.g.* Henzi, 1985; Smuts, 1987), which is surprising due to their otherwise similar societies (Cheney & Seyfarth, 1990, p.46). The only exception is an experimental study which found that some male-female pairs present stronger social bonds than others (Keddy, cited in Cheney & Seyfarth, 1990 p.45 and 230).

Relationships between adult or subadult males and adult vervet females have not been as extensively studied as female-female and female-immature relationships (review in Cheney & Seyfarth, 1990). Studies have been generally carried out either on captive animals (Rowell, 1971), limited to a particular male-female couple (De Moor & Steffens, 1972) or restricted to copulatory behaviour (*e.g.* Andelman *et al.* 1985; Andelman, 1987; Cheney *et al.* 1988).

It is necessary to analyse in more detail male-female relationships in vervet monkeys to ascertain whether special bonds do exist. If should special friendly relationships among vervets exist, they would be more or less stable throughout the year.

Therefore, it is predicted that forming special bonds with females could be one of the most important reasons adult males remain in the troop outside the mating season. In other words males may establish relationships with females throughout the year in order to improve the likelihood of mating.

De Moor and Steffens (1972) radio tracked a male/female vervet dyad, and found that during the birth season they spent equal amounts of time less than and beyond 21 m of each other. During the non-birth/non-mating season which included August to October and corresponded to the dry season, they were apart more often, and during the mating season they were close to one another more often. The question which arises at this point is whether all adult males increase their proximity to females during the mating period.

The benefits females derive from males seem to be directly correlated to the degree of sexual dimorphism. If males are bigger and possess larger canines, females and immatures would benefit from their protection against intratroup agonism, excessive allomothering (Hamilton, 1984) and infanticide (Dunbar, 1985, p.107; Collins, 1986). Though body weight and canine size do not differ between male and female vervet monkeys as much as for baboons (Bramblett & Coelho, 1987 p.76; Fedigan & Fedigan, 1988, p.395), females may still benefit from associating with adult males because males generally have a higher basic rank than females (Jones, 1981; Kaplan, 1987).

If females groom and form special bonds with males in order to obtain protection and access to preferred resources (Kummer, 1968 for hamadryas baboons), they would therefore compete among themselves to groom the highest ranking male. Whether females compete for proximity to and grooming of the alpha male will be evident if: i) female differences in grooming the alpha male are rank related (Kaufmann, 1967 for rhesus; Zucker, 1987 for patas and bonnet monkeys); ii) the alpha male grooms with females more often than additional males (Kaufmann, 1967 for rhesus); iii) the groomer is more often the female; iv) the female initiates and maintains the grooming interaction and iv) females attempt to supplant one another in order to groom the top ranking male.

Therefore, if males particularly support females with whom they maintain high rates of grooming and proximity, this could support the existence of male-female bonds (*sensu* Smuts, 1985) in vervet monkeys.

However, the more peripheral position taken by additional males reduces their chances of involvement in grooming interactions with females, as close proximity to females, especially those that are sexually receptive, is expected to be controlled by the alpha male. As a result, male intraspecific competition, especially during the mating season, can also affect rates at which peripheral males are groomed by females, .

Seasonal differences in affiliative behaviours and proximity relationships are expected between males and females, as they attempt to increase their immediate mating opportunities. This has been found to be true for other female-bonded species (Kaufmann, 1967; Hill, 1986 for rhesus monkeys; Hall & DeVore, 1965, p.105 for baboons) and for species where the females are the migrating sex (Wrangham, 1986 for chimpanzees).

I hypothesise that in vervet monkeys an increase in male-female proximity during the mating season in addition to improving mating opportunities, could also raise the levels of male-female affiliative interaction. Michael and Herbert (1963) pointed out that in rhesus monkeys, males groom females more often than females groom males at midcycle, and this qualitative change preceded a peak in mounting.

In order to detect special bonds between male-female dyads and to determine whether male-female relationships change for the mating and non-mating seasons, I will: i) determine with whom adult males preferentially associate; ii) identify seasonal changes in proximity for each male-female dyad; iii) investigate the extent to which male vervet monkeys associate with adult (possibly unrelated) females of the troop in accordance with their respective ranks; iv) compare male proximity to adult females with other types of affiliative behaviours (e.g. grooming); v) assess whether individual males or females give or receive a higher proportion of grooming, and who is more responsible for its maintenance; vi) analyse the distribution of male-female agonistic behaviour.

A qualitative study of male-female agonistic interaction per season would serve to clarify the nature of inter-gender social relationships in vervet monkeys. Male-female agonistic interaction is expected to be mainly based on resource competition during the non-mating period and on sex (herding behaviour) during the mating season. Quantitative and/or qualitative differences in agonistic behaviour are also expected to be the consequence of hormonal changes in both males and females during the reproductive period (review in chapter 7).

Finally, male agonistic interference (IN) in female agonism is a behaviour which has the effect of terminating ongoing agonism and will be analysed separately (cf. Struhsaker, 1967 c; see p. 50).

A comparison of behaviours occurring between the Cage (adult males and females who were more related) and the Windy Ridge troop, and those between adult and subadult males will be carried out with the intention of explaining how relatedness and/or familiarity affects male-female relationships.



In summary, these are the crucial points: first, do vervet males attempt to use social interactions with females outside the breeding season to improve mating opportunities? If so, do females select for specific traits as suggested by Tsukahara (1990) for Japanese monkeys? Finally, do vervet females compete to be near and groom specific males? To help to clarify the above, I will test whether there is a seasonal difference in the general pattern of male-female association and social interactions (excluding sex), and if it exists whether it differs for the dominant and additional males. In the last section a review of vervet adult male-infant relationships will be presented so as to determine the possible benefits or costs imposed on all the members of the troop by males remaining in the troop. These costs obviously affect the females' reproductive success.

## 6.1. MALE-FEMALE SPATIAL ASSOCIATIONS

To study the proximity relationships between the different male-female dyads, data from scan samples on adult males of the Windy Ridge Troop and from instantaneous samples for males at the Cage Troop were analysed to detect male differences in proximity to each adult female during the birth, non birth-non mating and mating season. When statistical differences (Chi-square test, significance level of at least 0.05) were found, a Spearman rank correlation test was undertaken to determine whether those were rank related (by convention the higher ranking female was assigned rank = 1).

When reference is made to a male's preferred female partner, I do not imply that the male was mostly responsible for the maintenance of affiliative behaviour. Nevertheless, the responsibility for maintenance of grooming relationships will be analysed (section 6.3.5).

The distance categories were the same as those for male-male pair proximity relationships, i.e. **close proximity** which includes animals in contact and at less than 2 m from one another for the Windy Ridge Troop, and within a 1 m radius for members of the Cage Troop. **Social environment**, refers to all the animals at less than 10 m for the Windy Ridge Troop or at less than 2 m for those of the Cage Troop.

### 6.1.1. Close proximity

In the previous chapter it was found that in general, adult males associated with each other as often as they did with females (corrected by the number of individuals in each class). However, there were two exceptions. First, the two lowest ranking and younger males in Windy Ridge (PE and CH) spent less time near females than males during the birth season (see Table 5.1). Second, the top ranking male in the Cage remained closer to females than to males during the non-mating season (Table 5.2).

#### *Windy Ridge Troop*

In Windy Ridge, females differed in their spatial proximity to the alpha male (RO) during the pre-mating and the mating seasons (Table 6.1 and Fig. 6.1). The most dominant females were found within 2 m of the top ranking male more often than the less dominant females (N:  $r_s = -0.771$ ,  $n=8$ ,  $p=0.04$  and for M:  $r_s = -0.814$ ,  $n=8$ ,  $p=0.03$ ). The subordinate male LE associated with certain females more often than he did with others for all three seasons (see Table 6.1 and Fig. 6.1). Individual differences were not related to female rank (all Spearman rank correlation:  $p > 0.05$ )

Table 6.1

Individual differences in female proximity (<2 m and <10 m) for the adult males (RO>LE>PE>CH) and subadult male (TI) of the Windy Ridge troop. Chi-square tests were run to determine if there were significant differences (\*  $p < 0.05$ ; \*\*  $p < 0.001$  and NS: not significant) during the B (birth), N (non birth-non mating) and M (mating) seasons (S). If the differences were statistically significant, then a Spearman rank correlation test ( $n=8$ ) was carried out to see if these differences were related to the rank of the female (highest ranking female was given a value of 1 and lowest ranking a value of 8). A negative value means that higher ranking females spent more time near the focal male than lower ranking ones.

MALE	S	< 2 m.		< 10 m.	
		$\chi^2$	$r_s$	$\chi^2$	$r_s$
RO	B	5.000 NS		11.688 NS	
	N	75.235 **	-0.771 *	107.24 **	-0.810 *
	M	21.727 *	-0.814 *	66.156 **	-0.857 **
LE	B	17.750 *	+0.627 NS	28.727 **	+0.482 NS
	N	28.539 **	+0.359 NS	40.954 **	+0.643 NS
	M	14.222 *	+0.386 NS	24.576 **	+0.143 NS
PE	B	6.833 NS		22.412 *	+0.071 NS
	N	21.222 *	+0.455 NS	30.370 **	-0.262 NS
CH	B	9.333 NS		20.308 *	+0.299 NS
	N	17.000 *	+0.774 *	11.600 NS	
TI	B	4.750 NS		14.765 *	0 NS
	N	12.500 NS		7.578 NS	
	M	18.100 *	-0.405 NS	29.184 **	-0.886 *

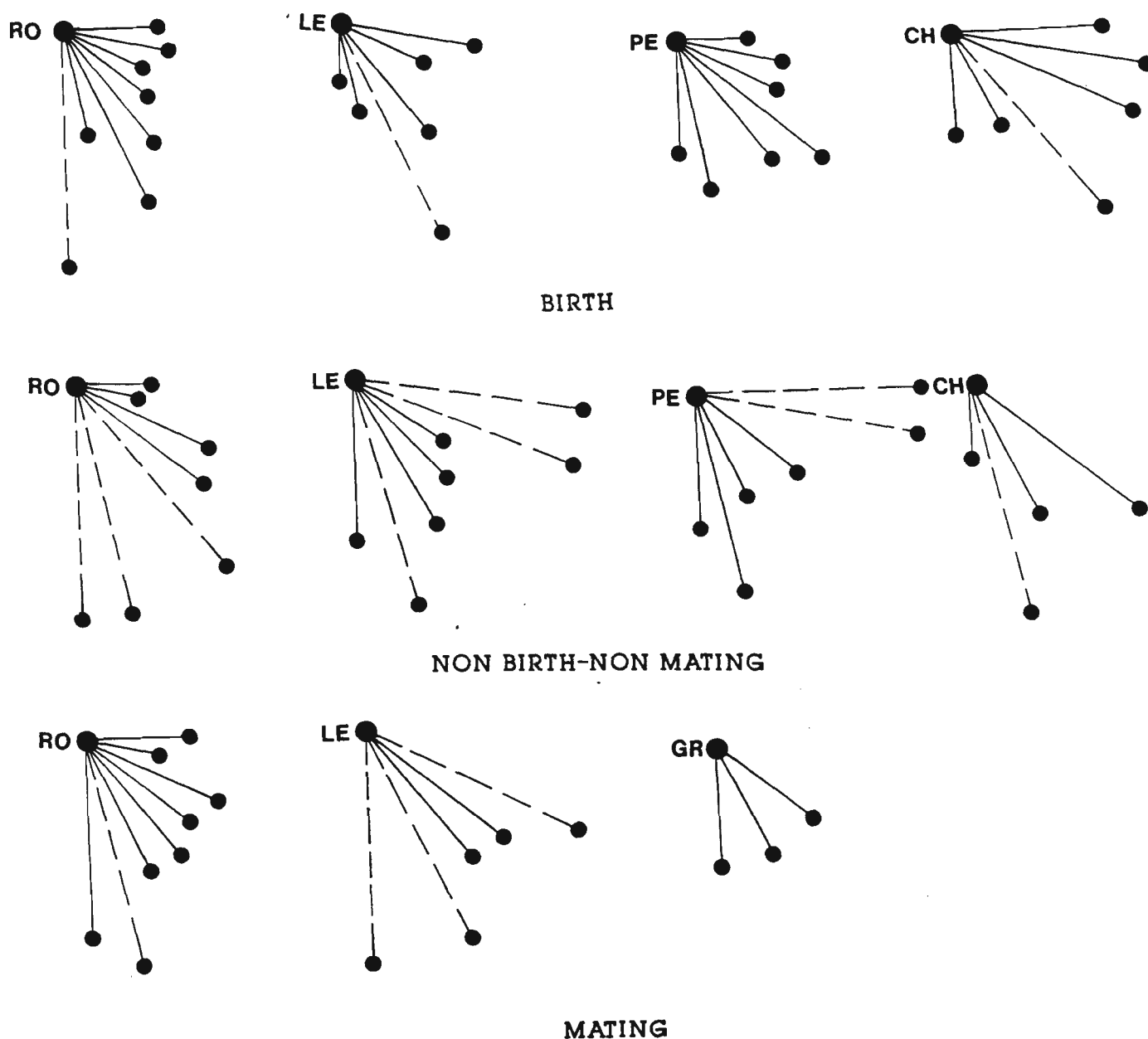


Figure 6.1.

Adult male (RO > LE > PE > CH) proximity relationships with the females of the Windy Ridge Troop. Females are ordered in decreasing rank order (clockwise). The distance indicates the inverse of the proportion of times each male was found within 2 m from the various females during the birth (B), pre-mating (N) and mating (M) season. Broken lines when the value obtained was between 0.5 and 1.0, no line when value exceeded the unit.

The two lowest ranking males showed variations in their proximity to individual females for the pre-mating season. PE did not show any preference for females that could be correlated to female rank ( $r_s = 0.455$ ,  $n = 8$ ,  $p = 0.2$ ) (Table 6.1; Fig. 6.1), although the three top ranking females were found further than 2 m more often than expected. However, CH was found in the company of females according to their rank ( $r_s = 0.774$ ,  $n = 8$ ,  $p = 0.05$ ), more frequently with the lower ranking females (Table 6.1).

The single subadult male of the Windy Ridge troop (TI) spent more time than expected nearer some females than others during the mating season. Even though these preferences were not directly related to the rank of the female, the 3 lowest ranking females were found near TI less often than expected (Table 6.1).

### *Cage Troop*

In the Cage the dominant adult male (FT) was less than 1 m from some of the females more often than expected (Table 6.2). Female rank did not account for the relative closeness of females to the top ranking male ( $r_s = -0.657$ ;  $n = 6$ ; NS). However, there was a tendency for higher ranking females to be near the alpha male more often than expected (Fig. 6.2).

When the lowest ranking female (HH) - who was in the troop during only 60 of FT's samples - was removed from the analysis the correlation between female proximity to the alpha male and to her rank was significant ( $r_s = -1.000$ ;  $n = 5$ ;  $p < 0.001$ ). The female HH was subject to high levels of aggression from the other adult females. She may, therefore, have sought the proximity of the leader for protection.

The sexual consortship between the dominant male FT and the female MY (post-reproductive -4th ranking-) (see chapter 7) could have caused the results found for the mating season (see Table 6.2).

Proximity of the middle ranking male (RN) to females was related to the female rank during both the non-mating ( $r_s = +0.928$ ;  $n = 6$ ;  $p < 0.05$ ) and mating season ( $r_s = +0.975$ ;  $n = 5$ ;  $p < 0.05$ ). RN was found mainly in the company of low ranking females (Table 6.2 and Fig. 6.2). Differences in female proximity to the other adult males (GO, FY and LU) and subadult male (PA) were not found (Table 6.2 and Fig. 6.2).

The dominant subadult male PP associated mainly with certain females of the captive troop during the non-mating season (Table 6.2). PP was mainly found in the vicinity of the middle ranking female MC.

Table 6.2

Individual differences in female proximity (< 1 m.) for the adult (FT>GO>RN>FY>LU) and subadult (PP>PA) males of the cage troop (CT). All the Chi-square tests with 5 degrees of freedom for the non-mating (BN) and 4 for the mating season (M). Spearman rank correlation values (n=6 for BN; n=5 for M) and its significance level (see table 6.1).

MALE	S	X <sup>2</sup>	< 1 m r <sub>s</sub>	X <sup>2</sup>	< 2 m r <sub>s</sub>
FT	BN	29.330 **	-0.657 NS	21.842 **	-0.928 *
	M	34.593 **	-0.900 NS	25.650 **	-0.900
GO	BN	8.714 NS		6.417 NS	
RN	BN	10.528 *	+0.928 *	4.095 NS	
	M	17.571 **	+0.975 *	4.095 NS	
FY	BN	3.411 NS		1.967 NS	
	M	4.875 NS		4.909 NS	
LU	BN	5.333 NS		0.567 NS	
PP	BN	19.188 **	-0.462 NS	10.683 *	-0.700
	M	6.519 NS		1.017 NS	
PA	BN	0.818 NS		3.563 NS	
	M	3.500 NS		2.978 NS	

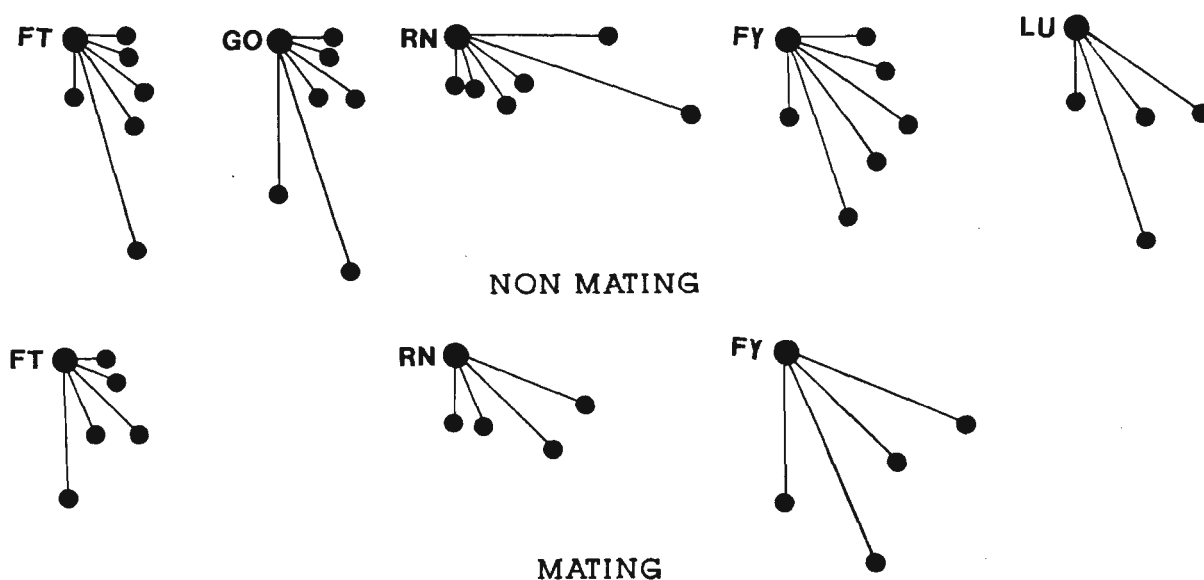


Figure 6.2. Adult male (FT>GO>RN>FY>LU) proximity relationships with females of the Cage Troop. The distance indicated the inverse of the proportion of times each male was found within 1 m from the various females during the non-mating (BN) and mating (M) periods (the rest as for Fig. 6.1).

### **6.1.2. Social environment**

#### *Windy Ridge Troop*

For the Windy Ridge Troop, the dominant adult male (RO) spent an equivalent proportion of time less than 10 m from all the females during the birth season only (Table 6.1 and Fig. 6.3). However, during the pre-mating and mating seasons he associated preferentially with high ranking females ( $r_s = -0.810$ ,  $n=8$ ,  $p < 0.05$  and  $r_s = -0.857$ ,  $n=8$ ,  $p < 0.05$  respectively). These results agree with those found for close proximity.

The two next ranking adult males (LE and PE) followed a similar pattern for all the seasons. Certain females spent significantly more time within their social environment, although their presence was independent of the female's rank (Table 6.1; Fig. 6.3). The lowest ranking female ET and the post-reproductive TO were always among those females closer to LE, but PE was slightly closer to high ranking females than LE was.

The lowest ranking and apparently youngest adult male (CH) was within the social environment of some females more often than others during the birth season. However, these differences were not related to the females' rank (Table 6.1; Fig. 6.3). During the next season, he did not spend more time than expected within 10 m of any of the females. The subadult male (TI) was within 10 m of high ranking females more often than lower ranking females, during the mating season. On the other hand, the differences in female proximity found for the birth season were not related to the rank of the females (Table 6.1).

In summary, only the highest ranking adult male of the Windy Ridge Troop was found within a 10 m radius of the high ranking females more often than he was from other females during the pre-mating and mating season (Fig. 6.3). In addition, the subadult male was closer to higher ranking females than lower ranking females during the mating season. This introduces the question of whether male or female choice plays a more important role in determining male-female associations.

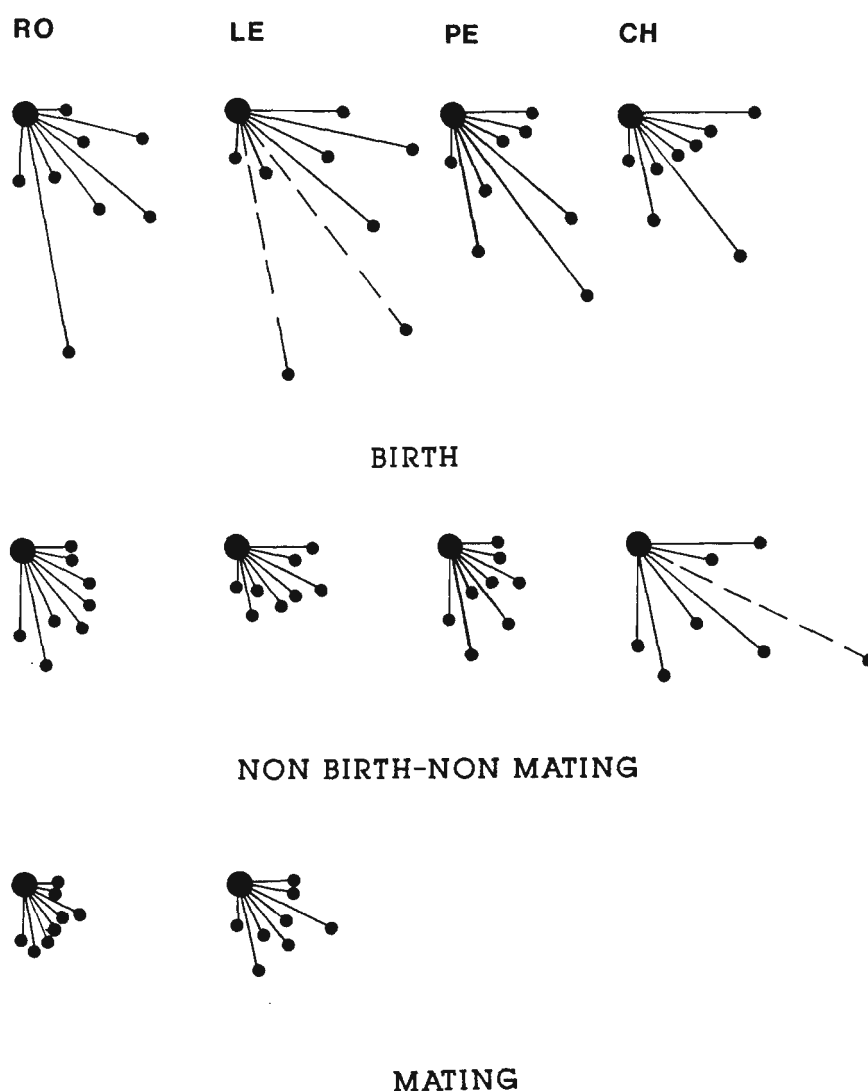


Figure 6.3.

Male-female proximity relationships in the Windy Ridge Troop. The distance indicated the inverse of the proportion of times each male was found within 10 m from the various females during the birth (B), pre-mating (N) and mating (M) seasons. Females are ordered in decreasing rank order (clockwise). The rest as for Fig. 6.1.

### *Cage Troop*

During the non-mating season, high ranking females were found significantly more often within the alpha male's (FT) social environment than low ranking females ( $r_s = -0.928$ ,  $n = 6$ ,  $p < 0.05$ ). During the mating season the trend remained, but the result was non-significant ( $r_s = -0.900$ ,  $n = 5$ ,  $p > 0.05$ ).

Differences in female proximity were also found for the second ranking male (RN) during the mating season (Table 6.2). Although female rank did not correlate significantly with time spent at less than 2 m. from RN ( $r_s = +0.900$ ,  $n=5$ ,  $p > 0.05$ ), RN showed a slight tendency towards staying within the social environment of low ranking females (Fig. 6.4).

The highest ranking subadult male (PP) was within 2 m of some of the females more often from others during the non-mating period. PP spent more time than expected near the 3 highest ranking females (especially the middle ranking MC) than the lower ranking females (Table 6.2). No individual differences were found during the mating season. Similar results were found for close proximity, MC being the closest female.

The other subadult male of the caged troop (PA) and the adult males (GO, FY and LU) spent a comparable time within close proximity of individual females and within their social environments (Table 6.2).

In summary, although the results of the analyses were not always significant, a general trend existed for the dominant males of both study troops to be within the high ranking females' social environment more often, and for the next ranking male to be within the lower ranking females' social environment (Figs. 6.3-6.4). Finally, some of the very low ranking males did not spend more time than expected near any specific female.

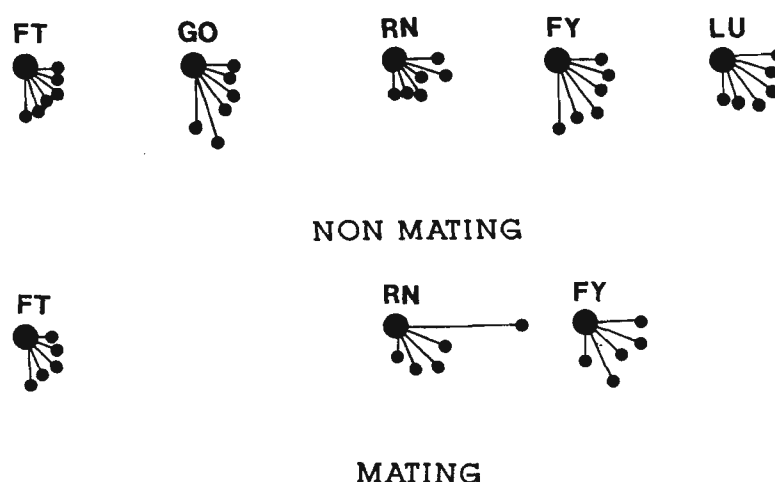


Figure 6.4.

Male-female proximity relationships in the Cage Troop. The distance indicated the inverse of the proportion of times each male was found within 2 m of the various females during the non-mating (BN) and mating (M) periods (see Fig. 6.1).



## 6.2. SEASONAL CHANGES IN MALE-FEMALE PROXIMITY

It was hypothesised that male-female pairs would be found closer during the mating season than during the birth and non birth-non mating season. The null hypothesis was that the probability of finding a particular male and female in close proximity did not vary with the season. The expected values were calculated from the total number of scans done on each male when a particular female was in close proximity and related to the number of scan samples done on that male for that season.

### 6.2.1. Close proximity

#### *Windy Ridge Troop*

The dominant male only showed significant seasonal differences in the number of times he was found in close proximity to the low ranking females TO and VE. He was most commonly found within 2 m of TO (post-reproductive female) during the mating season and closer than expected to VE during the birth season (Table 6.3 and Fig. 6.1 a). The young female VE was possibly avoiding being near RO at the time of maximum female mate competition.

The second ranking male (LE) was found closer to the third ranking (MO) and two lowest ranking females (VE and ET) during the birth season than at other times (Table 6.4 and Fig. 6.1).

The third ranking male (PE) was closer than expected to the top ranking (HI) and third (MO) ranking females during the birth season as compared to the pre-mating season. By contrast, PE spent more time closer to the post-reproductive female (TO) during the non birth-non mating season (Table 6.5). Before PE emigrated, he was not seen with the troop for hours at a time. During the periods when he either travelled or fed with the troop he was mainly at the periphery with TO as his most common neighbour (Fig. 6.1).

The low number of scans for which females were located within 2 m of the lowest ranking male (CH), did not permit a statistical analysis. However, there appears to be a tendency for CH to be more distant from females during the N season than during the B season ( $X^2=4.031$ ; 1 df;  $p<0.05$ ).

In summary, free-ranging high ranking females were, in general, more distant from additional males than from the alpha male. This was specially true when the mating season approached (Fig. 6.1).

Table 6.3.

Seasonal differences in the proximity relationships (<2 m and <10 m) of the dominant adult male (RO) to individual females of the Windy Ridge troop. Females are ordered in decreasing rank. The number of scan samples done on this alpha male was 174, 562 and 662 for the birth (B), pre-mating (N) and mating (M) seasons respectively. All tests with 2 degrees of freedom (see Table 6.1).

MALE-FEMALE		S	< 2 m			< 10 m		
			O	E	X <sub>2</sub>	O	E	X <sup>2</sup>
RO	HI	B	9	9	2.377 NS	22	34	7.077 *
		N	34	28		103	109	
		M	27	33		147	129	
	SM	B	7	11	3.245 NS	15	33	11.382 *
		N	42	35		118	108	
		M	37	41		136	127	
	MO	B	8	5	2.070 NS	25	21	1.341 NS
		N	16	18		62	68	
		M	20	21		83	81	
	BE	B	7	6	0.434 NS	13	21	9.766 *
		N	16	18		55	67	
		M	23	22		98	79	
	WE	B	5	4	4.917 NS	13	18	15.475**
		N	6	12		39	57	
		M	20	15		90	67	
	TO	B	4	4	7.583 *	11	16	5.634 NS
		N	5	12		43	51	
		M	21	14		73	60	
	VE	B	7	3	6.083 *	11	14	4.020 NS
		N	10	10		36	44	
		M	9	12		62	52	
	ET	B	3	3	0.399 NS	15	17	5.776 NS
		N	10	11		44	56	
		M	15	13		80	66	

Table 6.4.

Seasonal differences in proximity relationships of the second ranking male (LE) with individual females of the Windy Ridge Troop (see Table 6.1). The number of scan samples was 129, 575 and 539 for the B, N and M seasons respectively. All tests with 2 degrees of freedom, except for HI's with 1 df.

MALE-FEMALE		S	O	E	< 2 m X <sub>2</sub>	O	E	< 10 m X <sup>2</sup>
LE	HI	B	1	1	0 NS	8	12	5.340 NS
		N	4	4		46	54	
		M	4	4		63	51	
	SM	B	4	2	3.429 NS	8	13	2.395 NS
		N	8	7		57	57	
		M	4	7		58	53	
	MO	B	6	2	9.000 *	13	10	1.018 NS
		N	7	10		41	43	
		M	9	10		39	40	
	BE	B	1	4	4.674 NS	5	16	8.678 *
		N	25	19		72	69	
		M	14	17		73	65	
	WE	B	4	4	0.118 NS	6	13	4.891 NS
		N	19	18		66	58	
		M	15	16		54	55	
	TO	B	2	3	2.485 NS	13	17	4.352 NS
		N	16	12		88	75	
		M	8	11		61	70	
	VE	B	7	2	14.069**	9	11	1.469 NS
		N	7	9		54	48	
		M	5	8		41	45	
	ET	B	10	4	11.463 *	26	21	1.790 NS
		N	15	16		96	94	
		M	9	15		81	88	

Table 6.5.

Seasonal differences proximity relationships of the third ranking adult male (PE) with individual adult females of the Windy Ridge troop (legend as for table 6.1). The number of scan samples was 173 and 419 for the B and N seasons respectively. All tests with 1 degree of freedom.

MALE-FEMALE		S	O	E	< 2 m. X <sub>2</sub>	O	E	< 10 m. X <sup>2</sup>
PE	HI	B	10	5	7.273 *	22	23	0.340 NS
		N	6	11		50	54	
	SM	B	7	4	3.375 NS	20	23	0.549 NS
		N	5	8		60	57	
	MO	B	7	3	7.333 *	24	17	4.077 *
		N	4	8		34	41	
	BE	B	4	6	0.974 NS	10	19	5.987 NS
		N	15	13		56	47	
	WE	B	5	3	2.000 NS	9	11	0.524 NS
		N	4	6		27	25	
	TO	B	2	6	3.897 *	13	23	6.200 *
		N	17	13		64	54	
	VE	B	5	4	0.350 NS	12	12	0 NS
		N	9	10		30	30	
	ET	B	7	6	0.238 NS	29	22	3.152 NS
		N	13	14		46	53	

Table 6.6

Seasonal differences in proximity (<10 m) to females for the lowest ranking adult male (CH) of the Windy Ridge troop. The number of scan samples was 135 for the birth season (B) and 95 for the non mating-non mating season. All Chi-square tests with 1 degree of freedom.

MALE-FEMALE		S	O	E	X <sub>2</sub>
CH	HI	B	10	8	1.167 NS
		N	4	6	
	SM	B	12	11	0.234 NS
		N	6	7	
	MO	B	13	8	7.292 *
		N	1	6	
	BE	B	13	11	0.935 NS
		N	5	7	
	WE	B	6	6	0.000 NS
		N	5	5	
	TO	B	19	13	6.769 *
		N	3	9	
	VE	B	8	8	0.000 NS
		N	5	5	
	ET	B	25	21	1.829 NS
		N	11	15	

### *Cage Troop*

In the enclosure, the different male-female dyads did not show any seasonal differences in time spent in close proximity (<1 m). One exception was FY (the lowest ranking male who remained in the troop during the mating season), he spent less time near XA (the top ranking female) during the mating season than in any other season (Table 6.7).

### **6.2.2. Social environment**

The frequencies with which individual adult females were found within 10 m of males of the Windy Ridge troop or less than 2 m from males at the Cage Troop, were used to determine seasonal differences for each male-female dyad.

The dominant adult male (RO) was part of the 1st (HI), 2nd (SM), 4th (BE) and 5th (WE) ranking females' social environment during the mating season more often than expected (Table 6.3 and Fig. 6.3). HI, SM and BE each gave birth to an infant in the next breeding season. Another female that conceived successfully during that mating season was the 7th ranking (VE) who did so without showing an increase in time spent in proximity to the alpha male during that period. This result can be explained by her low rank and competition with the higher ranking females (see agonism below).

Table 6.7.

Seasonal differences in male-female proximity in the Cage Troop. The rest as for table 6.1. The number of instantaneous samples for the non-mating and mating seasons were for the top ranking adult male (FT) 300/312; for the middle ranking adult male (RN) 146/305 and for the low ranking male (FY) 143/305. All the females specified in this table were in the cage throughout the study and are ordered in decreasing dominance rank.

					< 1 m.				< 2 m.
DYAD	S		O	E	X <sub>2</sub>	O		E	X <sup>2</sup>
FT	XA	BN	39	44	1.124 NS	74	80	0.879 NS	
		M	50	45		90	84		
	CE	BN	33	33	0.000 NS	72	68	0.461 NS	
		M	35	35		67	71		
	MC	BN	20	18	0.433 NS	43	46	0.383 NS	
		M	17	19		51	48		
	MY	BN	16	19	0.924 NS	47	50	0.353 NS	
		M	23	20		55	52		
	BA	BN	7	9	0.844 NS	40	38	0.205 NS	
		M	12	10		38	40		
RN	XA	BN	5	3	2.133 NS	19	10	11.782 *	
		M	3	5		13	22		
	CE	BN	3	5	1.200 NS	15	17	0.350 NS	
		M	12	10		15	17		
	MC	BN	9	7	0.857 NS	25	19	2.818 NS	
		M	12	14		33	39		
	MY	BN	9	9	0.000 NS	18	18	0 NS	
		M	20	20		39	39		
	BA	BN	15	12	1.096 NS	24	27	0.497 NS	
		M	23	26		58	55		
FY	XA	BN	10	4	13.000 **	19	16	0.827 NS	
		M	3	9		31	34		
	CE	BN	8	5	2.618 NS	14	14	0 NS	
		M	8	11		30	30		
	MC	BN	5	5	0 NS	16	18	0.330 NS	
		M	10	10		39	37		
	MY	BN	5	4	0.375 NS	12	11	0.128 NS	
		M	7	8		26	27		
	BA	BN	4	5	0.300 NS	15	18	0.737 NS	
		M	11	10		41	38		

During the mating season, the second ranking free-ranging adult male (LE) only showed a significant increase in time spent at less than 10 m from the 4th ranking female (BE) (Table 6.4 and Fig 6.3). BE, as mentioned above, conceived an infant that season.

The third ranking adult male (PE)'s social environment included the 3rd ranking female (MO) more often than expected during the birth season (Table 6.5 and Fig. 6.3). The fourth ranking BE and the second lowest ranking TO (the post-reproductive) females were PE's neighbours more often during the pre-mating season than during the birth season. During this period PE became peripheral and these three travelled and fed at the tail of the troop.

The lowest ranking male (CH), as was found for PE, was closer to MO during the birth season. The post-reproductive female (TO) was CH's social neighbour more often than expected during the birth season (Table 6.6 and Fig. 6.3). No other significant seasonal differences with the other adult females were found for CH.

In the Cage Troop, only the middle ranking adult male (RN) showed seasonal differences in female proximity relationships (Table 6.7). This male spent less time within 2 m of the top ranking female (XA) during the mating season (see also Fig. 6.4).

### **6.2.3. Subadult male proximity to adult females**

Seasonal differences in close proximity to TI (< 2 m) - the juvenile male who became a subadult male during the study period at Windy Ridge - were found for the lowest ranking females VE and ET. TI was closer to VE and more distant from ET during the mating period ( $X^2=6.578$ ; 2 df;  $p<0.05$  and  $X^2=5.867$ ; 1 df;  $p<0.05$  respectively) (Table 6.8).

Conversely, when analysing the seasonal differences in female composition of TI's social environment (<10 m.) it was found that HI (top ranking), BE and WE (middle ranking) were closer to TI during the mating season. However, VE (low ranking) was closer to the subadult male during the pre-mating season (see Table 6.8). It can be concluded that TI was farther than expected from all the above females, during the birth season (Table 6.8).

Table 6.8.

Seasonal differences in the subadult male TI's proximity relationships (2 m and <10 m) with individual adult females. The number of scan samples was 134, 274 and 304 for the birth (B), pre-mating (N) and mating (M) seasons respectively. All tests with 2 degrees of freedom. Legends as for Table 6.3.

		< 2 m				< 10 m		
MALE-FEMALE		S	O	E	X <sub>2</sub>	O	E	X <sup>2</sup>
TI	HI	B	3	4	1.594 NS	13	24	6.389 *
		N	7	9		52	49	
		M	13	10		63	55	
	SM	B	7	5	3.005 NS	16	25	3.986 NS
		N	7	11		56	52	
		M	15	12		62	57	
	MO	B	2	5	2.791 NS	17	23	1.894 NS
		N	13	10		48	47	
		M	10	11		56	52	
	BE	B	4	5	4.033 NS	11	23	8.655 *
		N	15	10		47	46	
		M	8	12		62	51	
	WE	B	3	4	1.194 NS	11	23	8.655 *
		N	6	8		36	37	
		M	11	9		52	41	
	TO	B	2	3	1.667 NS	16	16	0.000 NS
		N	8	6		39	33	
		M	5	6		31	37	
	VE	B	4	5	6.578 *	7	15	6.826 *
		N	4	9		41	32	
		M	16	10		34	35	
	ET	B	4	2	5.867(1) *	21	18	2.544 NS
		N	6	4		40	36	
		M	1	5		32	40	

In the Cage, seasonal differences for subadult male-adult female proximity were only found for the pair PP and BA (lowest ranking female), who spent more time than expected within 1 m ( $X^2=5.494$ ; 1 df;  $p<0.05$ ) and < 2 m ( $X^2=6.824$ ; 1 df;  $p<0.05$ ) during the mating season (Table 6.9). Meanwhile, PA did not show any significant increase in time spent at less than 1 or 2 m of females during the reproductive period (Table 6.9).

Table 6-9.

Seasonal differences in the proximity relationships of the subadult males PP and PA to individual females of the Cage Troop. The number of scan samples for the non-mating (BN) and mating (M) seasons were 222 and 312 respectively for PP; 228 and 310 respectively for PA.

		< 2 m				< 10 m		
MALE-FEMALE		S	O	E	X <sub>2</sub>	O	E	X <sup>2</sup>
PP	XA	BN	13	13	0 NS	47	43	0.634 NS
		M	18	18		57	61	
	CE	BN	16	17	0.102 NS	45	45	0 NS
		M	24	23		63	63	
	MC	BN	31	28	0.552 NS	50	44	1.390 NS
		M	36	39		57	63	
	MY	BN	13	16	0.954 NS	37	42	1.012 NS
		M	26	23		65	60	
	BA	BN	8	15	5.494 *	24	36	6.824 *
		M	29	22		63	51	
PA	XA	BN	9	11	0.614 NS	28	30	0.233 NS
		M	18	16		42	40	
	CE	BN	11	12	0.142 NS	41	37	0.746 NS
		M	18	17		47	51	
	MC	BN	13	13	0 NS	32	31	0.056 NS
		M	18	18		42	43	
	MY	BN	11	16	2.700 NS	28	36	3.111 NS
		M	27	22		56	48	
	BA	BN	12	12	0 NS	33	33	0 NS
		M	17	17		44	44	

### **6.3. MALE-FEMALE AFFILIATIVE RELATIONSHIPS**

The following aspects of grooming behaviour will be considered. First, the total distribution of male grooming towards different females. Second, whether males groom more often with those females often found in close proximity. Third, seasonal differences in grooming activity for each male-female dyad. Fourth, whether adult males receive more grooming than they give to adult females. Fifth, the degree of responsibility for starting and maintaining grooming for each adult male with the different females. Finally, grooming relationships involving subadult males will be analysed.

Only scan sampling done on WT males and instantaneous sampling performed on captive males will be considered in the first three sections. Data collected in Windy Ridge using all the sampling methods were used in the analyses included in the last three sections, because those refer to the directionality of the behaviour.



### 6.3.1. Distribution of male-female grooming

In Windy Ridge RO was involved in grooming interaction with females independently of their identity ( $X^2=9.600$ ; 7 df; NS) (Table 6.10). The same results were obtained from interactions when RO was the recipient of the grooming ( $X^2=11.333$ ; 7 df; NS).

LE engaged in grooming activity with certain females more often than expected ( $X^2=12.160$ ; 3 df;  $p<0.05$ ). Although female rank was not correlated with these preferences ( $r_s = +0.195$ ;  $n=8$ ;  $p=0.6$ ), the 3 middle ranking females were involved in grooming LE more often than expected (Table 6.10).

Table 6.10

The total distribution of grooming (N) among different male-female dyads. Females are arranged in order of decreasing rank. (-) indicates that observed frequencies are lower (+) higher or (O) equal to the expected ones. Chi-square values (\*  $P<0.05$ ; \*\*  $P<0.001$  and NS: non-significant) are given. Adult males of WT (RO>LE) and CT (FT>RN) were the only ones with enough samples to apply the test. Data obtained with scan sampling only.

MALE	FEMALE	N	$X^2$	$r_s$
RO	HI	9 (+)	9.600 (7) NS	
	SM	6 (+)		
	MO	5 (O)		
	BE	2 (-)		
	WE	4 (-)		
	TO	1 (-)		
	VE	3 (-)		
	ET	6 (+)		
LE	HI	0 (-)	12.16 (3) *	+0.195 NS
	SM	1 (-)		
	MO	3 (O)		
	BE	7 (+)		
	WE	6 (+)		
	TO	4 (+)		
	VE	1 (-)		
	ET	1 (-)		
FT	XA	6 (O)	3.500 (4) NS	
	CE	10 (+)		
	MC	6 (O)		
	MY	5 (-)		
	BA	4 (-)		
RN	XA	1 (-)	5.800 (4) NS	
	CE	3 (-)		
	MC	7 (+)		
	MY	7 (+)		
	BA	6 (+)		

Twelve grooming sessions involving the additional male PE and 1 involving the lowest ranking male CH were observed during scan sampling. This made it impossible to analyse preferences in grooming partners for the two lower ranking and youngest adult males of Windy Ridge troop.

In the Cage, the top ranking male (FT) and the middle ranking (RN) were the only adult males which provided enough data on grooming interactions with females. They did not appear to have any significant preference for specific females as grooming partners. However, there was a trend for the high ranking male to participate mainly in grooming sessions with high ranking females and for lower ranking males to groom or be groomed by middle and low ranking females (see Table 6.10).

### **6.3.2. Grooming and time spent in close proximity**

The possibility exists that males engage in grooming activity with specific females because of the time they spend near each other. In order to investigate this factor, the proportion of time when the animals were found in close proximity and were grooming was analysed.

In the Windy Ridge troop the adult males RO (11.9%), LE (11.3%), PE (9.2%) and CH (2.0%) differed in proportion of time spent grooming when females were in close proximity ( $X^2=9.218$ ; 3 df;  $p<0.05$ ). No significant difference was obtained when comparing the values for the dominant RO against the two next ranking males LE and PE (RO/LE+PE:  $X^2=1.032$ ; 1 df; NS). Therefore, CH was the male that of the time he spent within 2 m of females, he groomed them less.

In addition, RO and LE groomed with individual females within their immediate vicinity at the same rates. The exception was the lowest ranking female (ET), who of the time she spent 2 m from them, groomed with RO more often than with LE (Table 6.11).

Over the entire study period in Windy Ridge, neither RO ( $X^2=9.158$ ; 7 df; NS) nor LE ( $X^2=6.855$ ; 5 df; NS) showed higher rates of grooming some females more than others once they were within 2 m (Table 6.11). Moreover, a correlation between female rates of grooming and proximity to the dominant adult male (RO) failed to be significant ( $r_s=0.431$ ;  $p=0.25$ ;  $n=8$ ). On the other hand, LE groomed mostly with females he spent more time with, than with other females ( $r_s=0.854$ ;  $p=0.02$ ;  $n=8$ ). This suggests that LE might have some special bonds with some of the females (see discussion).

In the Cage, some males when they had females in close proximity groomed with them more than others ( $X^2=14.217$ ; 4 df;  $p<0.05$ ). The lowest ranking males FY (2.7%) and LU (7.1%) groomed those females less often than FT (12.0%), GO (16.2%) and RN (21.6%). The results show that the middle ranking male (RN) could have used the opportunity to groom females more than the higher ranking males (RN/FT+GO:  $X^2=4.521$ ; 1 df;  $p<0.05$ ; FT/RN:  $X^2=4.914$ ; 1 df;  $p<0.05$ ; FT/GO:  $X^2=0.208$ ; 1 df; NS and FT+GO/RN:  $X^2=4.521$ ; 1 df;  $p<0.05$ ).

Neither FT nor RN differed in the amount of grooming they participated in with different female close neighbours. Moreover, FT and RN groomed with individual females at comparable rates (Table 6.11).

Table 6-11

Differences in proportion of time RO and LE of the Windy Ridge troop and FT and RN of the Cage troop were grooming when found in close proximity to females. Significance levels of Chi-square tests for female differences and fisher's exact test (two-tailed) for inter-male differences are given .

WT)

FEMALE	RO	LE	$X^2$
HI	12.9	0	NS!
SM	7.0	6.3	NS!
MO	11.4	13.6	NS!
BE	4.3	17.5	NS
WE	12.9	15.8	NS
TO	3.3	15.4	NS!
VE	11.5	5.3	NS!
ET	21.4	2.9	3.557 *
$X^2$	NS	NS	

CT)

	FT	RN	$X^2$
XA	6.7	12.5	NS
CE	14.7	20.0	NS
MC	16.2	33.3	NS
MY	10.4	24.1	NS
BA	21.1	15.8	NS
$X^2$	NS	NS	

### **6.3.3. Seasonality in male-female grooming**

In Windy Ridge during the non-mating season all four adult males groomed female neighbours at the same rates ( $X^2=3.774$ ; 3 df; NS) and during the mating season similar results were found for RO and LE ( $X^2=0$ ; 1 df; NS).

No significant differences in the males' total participation in grooming with females at 2 m during the mating and non-mating season were found (Table 6.12). However, the trend for the free-living alpha male (RO) and the middle ranking captive male (RN) was towards grooming females in close proximity more often during the mating season (Table 6.12).

Table 6.12

Seasonal differences in proportion of time male-female pairs were grooming when found in close proximity in the Windy Ridge and Cage troop (CT). The dominant male (RO) was the only one for whom enough data were available to test for individual differences. When possible, Fisher's exact test or Chi-square test were used (NS: no significant differences).

	MALE	FEMALE	SEASON		$X^2$
			NON-MATING	MATING	
WT	RO	HI	9.3	18.5	NS
		SM	4.1	10.8	NS
		MO	12.5	10.0	NS
		BE	4.3	4.3	
		WE	0	20.0	
		TO	0	4.8	
		VE	11.8	11.1	
		ET	23.1	20.0	NS
	LE		7.5	12.1	NS
			10.3	11.6	NS
CT	FT		13.2	10.9	NS
	RN		12.8	25.7	NS
	FY		0	5.1	NS

#### **6.3.4. Grooming reciprocity**

Another way of approaching grooming relationships is to determine how many times each individual of a male-female dyad is the recipient of grooming compared to the total number of times this particular pair is involved in a grooming interaction. In this section, the data on grooming obtained along with all the sampling methods will be analysed. To test for significant differences in the proportion of time each male was the recipient of grooming compared to the number of times he was the groomer, the binomial test (two-tailed, probability set at  $p=0.5$ ) was used.

Females, as a class, were groomed by the top ranking male RO as often as they groomed him (Binomial test: NS;  $P$  set at 0.5). The second ranking male groomed females 44 times compared to the 32 times he was groomed by them (Binomial test;  $p=0.07$ ). The same results were found for the third ranking male PE (Binomial test: NS). The lowest ranking male CH was not found grooming with females enough times to carry out the analysis.

The degree of reciprocity in grooming for each adult and subadult males with individual adult females was calculated using Seyfarth's formula (1980).

$$\text{Degree of grooming reciprocity} = \frac{EE-ER}{EE+ER} \quad (6.1)$$

This formula gives an index of the proportion of total grooming received from (EE) and directed to (ER) the focal male. A value of 0 would indicate that the male grooms as often as he is groomed. A negative value would mean that the male does most of the grooming while a positive value would indicate that he receives more grooming than he gives (Fig. 6.5).

Individual females groomed as often as they were groomed by RO and LE (not enough data for RO-TO; LE-XA). Sufficient data were only available for the third ranking (PE) male's interaction with the post-reproductive female (TO). PE and TO were the active participants in grooming each other for a comparable number of bouts (Fisher's exact test: NS).

The period that covered the non-mating months (BN) was analysed separately from the mating season (M) and seasonal differences were determined using Fisher's exact probability test.

During the non-mating season, free-living adult males differed in the degree of grooming reciprocity with females ( $X^2=9.833$ ; 2 df;  $p<0.05$ ). The top ranking male (RO) groomed females on 18.8% of the occasions, therefore he received significantly more grooming from females than he gave. However, the subordinate males LE and PE groomed females more often than females groomed them (68.8% and 66.7% respectively; Fisher's exact test: both  $p<0.05$ ). Only on one occasion did a female groom the lowest ranking adult male (CH) and he only groomed a female once. During the mating season, RO (52.4%) and LE (62.5%) showed comparable levels of active participation in grooming females ( $X^2=0.05$ ; 1 df; NS).

It can be concluded that the alpha male groomed females more often during the mating season than during the non-mating season, in relation to the grooming he received from them.

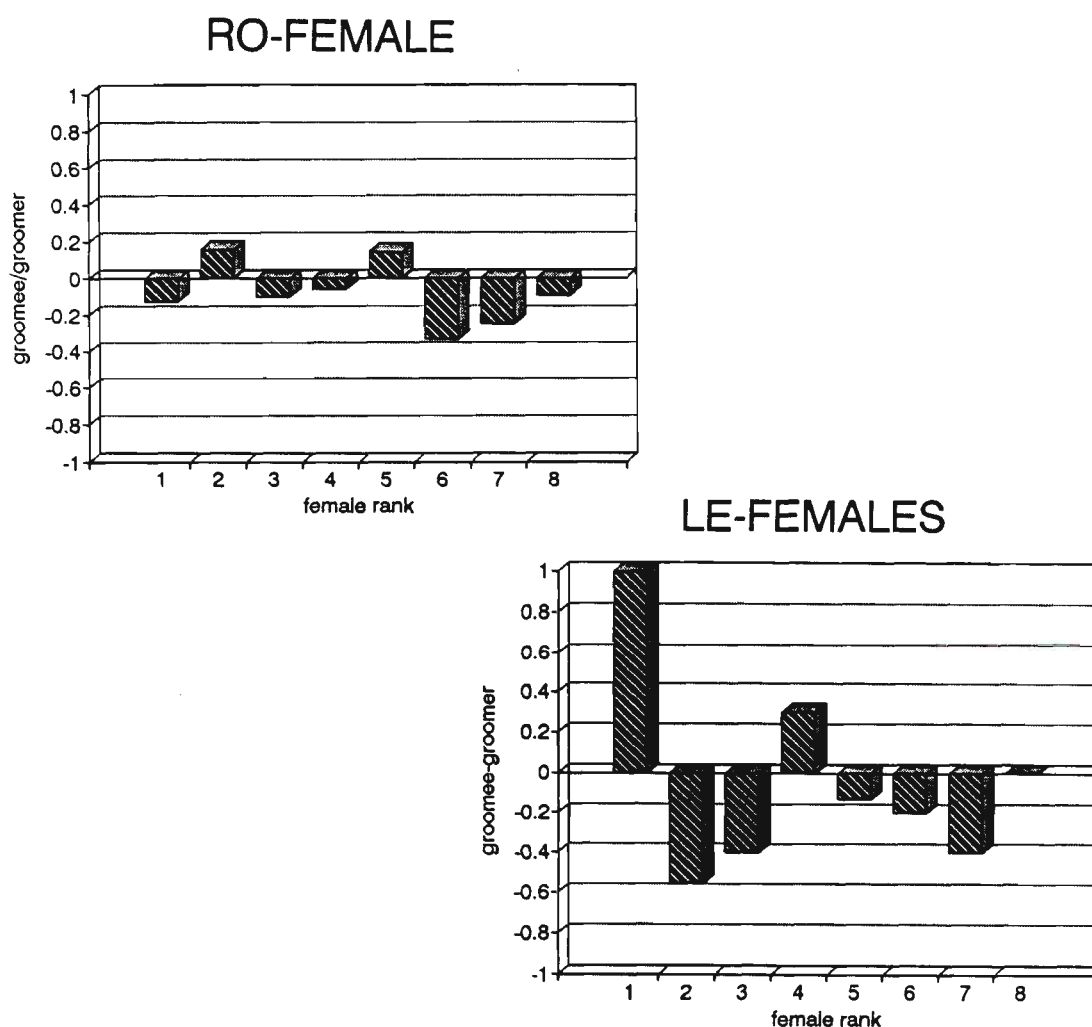


Figure 6.5. Degree of grooming reciprocity between adult males (RO>LE) and adult females (ordered in decreasing dominance rank). The Fisher's exact test gave non-significant differences in all cases except for RO-TO and LE-HI for whom enough records were not available.

### **6.3.5. Grooming responsibility**

The previous section dealt with who was responsible for doing most of the grooming. This section will deal with who is more likely to initiate grooming and maintain a grooming session.

Individual *A* could start a grooming bout with *B* by spontaneously grooming *B*, or by soliciting grooming from *B*. *B*, in turn, either accepts the invitation and grooms *A* or ignores it. A grooming bout may be ended by individual *B* when he moves away from *A* or when he ignores either *A*'s solicitation to be groomed or *A*'s invitation to groom *B*.

First, the ratio of male initiated behaviour to total behaviour between male and female might be more useful than behavioural frequencies (see Fairbanks & McGuire, 1985).

RO's preference for initiating grooming with certain females ( $X^2=15.756$ ; 7 df;  $p<0.05$ ) was not related to female rank ( $r_s=-0.286$ ;  $n=8$ ;  $p=0.45$ ). As post-reproductive females may differ in attractiveness to males, it seemed appropriate to repeat the analysis for reproductive females only (TO excluded) ( $X^2=13.277$ ; 6 df;  $p<0.05$ ) ( $r_s=-0.571$ ;  $n=7$ ;  $p=0.16$ ) and similar results were found.

The order of preference shown by RO in starting a grooming interaction with females was as follows  $VE>BE>WE>MO>ET>HI>SM>TO$ . He had least preference for the post-reproductive female (TO) and the two higher ranking females (HI and SM) followed. The reason why RO initiated more grooming bouts with some of the low (VE) and middle ranking females (BE and WE) more often than with the two high ranking females might be explained as a consequence of female partner competition or perhaps because RO was less confident of their support. These differences may well be explained as a consequence of low ranking females avoiding interaction with the dominant male of the troop, and/or by high ranking females being able to express their preferences.

Second, to have a better idea of who is more interested in maintaining grooming relationships in a male-female dyad, an analysis of the individual responsible for starting and for ending a grooming bout was carried out (6.2).

A coefficient of grooming responsibility was obtained by comparing the number of times each member of a dyad was observed initiating a grooming bout with the number of times they were observed finishing a bout. Data obtained with *ad libitum* and continuous focal sampling for the Windy Ridge troop were used.

The index of grooming responsibility was calculated using the same formula used to calculate responsibility for maintenance of proximity relationships (see Harcourt, 1978; Martin & Bateson, 1986).

$$\text{A's index} = A_S / (A_S + B_S) - A_F / (A_F + B_F) \quad (6.2)$$

Where  $A_S$ : is the number of times A started the grooming interaction;  $B_S$ : number of times B started;  $A_F$ : times A finished the interaction and  $B_F$ : true number of times B ended the grooming. When the index equals +1.0, A is solely responsible for the grooming interactions, and when it is -1.0, then B is the responsible for initiating and maintaining grooming.

Data obtained using *ad libitum* and focal animal sampling were used. To include grooming solicitations by A ( $B_I$ ) or invitations by B ( $A_I$ ) that were ignored, the formula was corrected as follows:

$$\text{A's index} = (A_S + B_I) / (A_S + B_I + B_S + A_I) - (A_F + A_I) / (A_F + A_I + B_F + B_I) \quad (6.3.)$$

A study of the index of responsibility for each male-female pair was only possible for RO, the dominant male of the Windy Ridge troop (Table 6.13 and Fig. 6.6). Only the second ranking female (SM) was clearly more responsible than the dominant male for maintaining grooming.

When all data for grooming maintenance was plotted together, it was seen that RO was as responsible as the females for regulating grooming. The low ranking adult male PE also initiated grooming and terminated it at rates comparable to those of females. However, the second ranking male LE was more responsible than the females in maintaining grooming ((Table 6.14 and Fig. 6.7). Unfortunately, not enough records of CH grooming with females were obtained.



Table 6.13

Total frequency of who started and who finished a grooming interaction between RO and adult females (ordered in decreasing rank). S: starts grooming; F: finishes interaction and I: ignores or refuses grooming solicitation. Data from focal animal and *ad libitum* sampling are included. Chi-square test values and level of significance (\*  $p < 0.05$ ; \*\*  $p < 0.001$  and NS: not significant) and all with 1 degree of freedom (see Fig. 6.6).

PAIR	S	F	I	$\chi^2$
RO	4	7	0	0.890 NS
HI	10	6	0	
RO	5	13	0	5.045 *
SM	20	8	1	
RO	10	7	1	0.859 NS
MO	8	11	2	
RO	7	7	0	0.275 NS
BE	6	5	3	
RO	8	6	0	0.304 NS
WE	6	7	1	
RO	0	2	1	
TO	2	0	0	
RO	5	4	0	0.225 NS
VE	3	4	1	
RO	8	11	0	0.229 NS
ET	13	11	0	

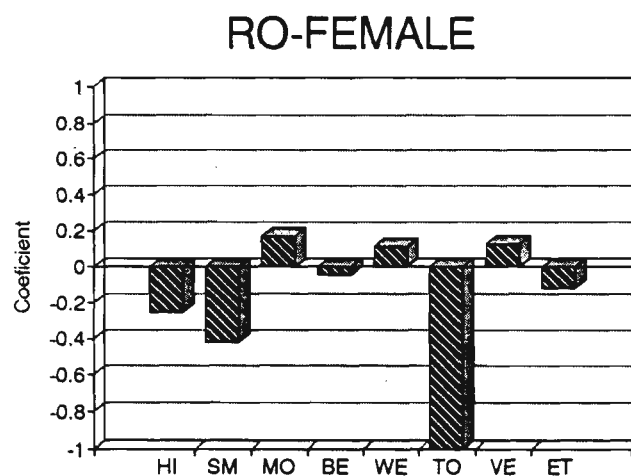


Figure 6.6. The alpha male's (RO) responsibility for maintaining grooming interactions with adult females. Females are ordered in decreasing rank order (a negative value means that the female is more responsible than RO) (see Table 6.13).

Partner supplants were observed among females to groom (3 out of 4) or stay near (2 out of 3) the alpha male during the non-mating season. In addition, high ranking females supplanted other lower ranking females to stay near him (3 out of 4) but never to groom with him during the mating season (none out of 2). There were also some occurrences of males supplanting other males, although only the subadult male supplanted the alpha male in proximity to the top ranking female during the non-mating season.

Table 6.14

Number of times each adult male of the Windy Ridge troop started, finished or ignored a grooming bout (males ordered in decreasing rank order) with adult females (FF). The rest as for Table 6.13 (see Fig. 6.7).

PAIR	S	F	I	$\chi^2$
RO	47	57	2	0.550 NS
FF	68	52	8	
LE	38	20	2	8.706 *
FF	38	41	10	
PE	3	7	3	0.020 NS
FF	3	6	2	
CH	1	1	2	??
FF	0	1	3	

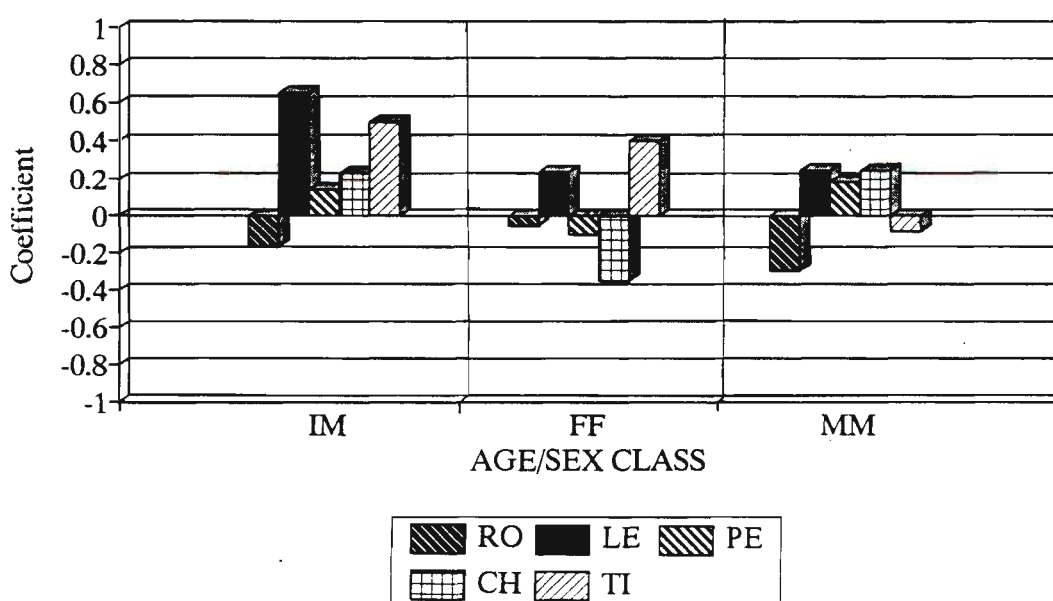


Figure 6.7.

Male responsibility for maintaining grooming interactions with the different age/sex classes (negative value when males are less responsible than the others).

### **6.3.6. Subadult male-adult female grooming**

The subadult male of Windy Ridge troop (TI) engaged in grooming bouts with adults in his immediate vicinity independently of their sex ( $X^2=0.011$ ; 1 df; NS). TI started more grooming episodes and females ended more grooming bouts than expected (Fisher's Exact test:  $p<0.05$ ).

In the Cage Troop, the higher ranking subadult male (PP) was found grooming with MC, the middle ranking female more often than expected ( $X^2=16.667$ ; 4 df;  $p<0.05$ ). For the lowest ranking subadult (PA), five of his nine bouts of grooming females were with BA, the lowest ranking female. During the whole study, PP groomed females (7.0%) in his immediate proximity as often as PA (5.8%) did ( $X^2=0.054$ ; 1 df; NS). Moreover, none of the subadult males in the Cage troop showed any seasonal differences in the proportion of time they groomed females within 1 m of themselves (PP: 3.7% and 9.0% and PA: 5.4% and 6.1% for the non-mating and mating seasons respectively).

### **6.3.7. Other social activities**

The aim of this section is to investigate the seasonal occurrence of affiliative activities (other than grooming) toward females by adult and subadult males. Those can be classified as social play (SP) and other friendly interaction (SF) (see chapter 2). Only the males of the Cage Troop are commented on in this subchapter as friendly interactions at the Windy Ridge troop were very rare. The exception was the lowest ranking female who gave vocalisations towards the injured subordinate male (LE) in order to direct him to where she had been feeding on the ground (LE's locomotion had been impaired by a deep wound on his ankle).

Adult males were never seen playing with adult females. It can be concluded, as it was for male-male and female-female play (chapter 5), that adult males and females hardly ever play with other adult members of the troop.

Among adult males, the proportion of friendly behaviour directed to adult females seemed directly related to male rank. FT directed 63% of his social friendly bouts at adult females, GO 67%, RN 43%, FY 13% and the lowest ranking male LU 20%. The proportion of friendly bouts directed towards females *versus* other age/sex classes, was higher for the most dominant males than for the subordinates ( $X^2=12.871$ ; 4df;  $p<0.05$ ).

No differences were detected in the proportion of time individual males were involved in friendly behaviour with those females found within 1 m ( $X^2=2.350$ ; 4 df; NS). It appears therefore that the higher level of friendly activity found for high ranking males was the direct consequence of these males spending more time in the proximity of females.

The subadult males PA (Binomial test;  $n=1$ ;  $m=18$ ;  $z=3.48$ ,  $p$  set at 0.45) and PP (Binomial test;  $n=2$ ;  $m=16$ ;  $z=2.9$ ;  $p$  set at 0.45) played with females less often than with immature members of the troop. Subadult males (PP and PA) participated in other social behaviour (play and grooming not included) with females as often as with other members of the troop (females/others:  $X^2=0.188$ ; 1 df; NS) and they did not differ from one another in time interacting with adult females (4.1% for PP and 5.8% for PA).

In addition, subadult males in the Cage Troop were seen interacting in a friendly way with a female of the free-ranging troop (AT) during instantaneous sampling (PP twice and PA once).

#### 6.4. INTER-GENDER ANTAGONISM

A comparative analysis based on continuous focal animal sampling, scan (WT) and instantaneous (CT) sampling in male-male and male-female agonism was described in chapter 5. Therefore, only individual and seasonal differences in male-female agonism will be considered here.

RO, the top ranking male, was involved in agonistic interactions with females irrespective of the female's identity during the whole study (B+N:  $X^2=4.231$ ; 7 df; NS and M:  $X^2=5.162$ ; 7 df; NS). When data from scan samples were analysed to determine seasonal differences in the total number of antagonistic encounters between RO and females, and LE and females, no significant seasonal differences were found (RO:  $X^2=0.255$ ; 1 df; NS and for LE:  $X^2=0.570$ ; 1 df; NS). However, when the expected values for RO's antagonism with each female were compared, these showed significant seasonal differences for BE ( $X^2=7.292$ ; 1 df;  $p<0.05$ ) and TO ( $X^2=3.750$ ; 1 df;  $p=0.05$ ). More aggressive encounters involving RO-BE and RO-TO were recorded during the non-mating season.

#### **6.4.1. Aggression and overt competition**

In general, in Windy Ridge the alpha male (RO) was more aggressive towards females than additional males were (Fisher's exact test:  $p < 0.05$ ). During the non-mating period, the top ranking male (RO) was the aggressor in all his antagonistic interactions with females (Binomial test:  $p < 0.001$ ,  $n = 13$ ;  $m = 0$ ). However, additional males were not significantly more aggressive towards females than females were towards them (Binomial test:  $p = 0.12$ ,  $n = 5$ ;  $m = 2$ ). Similarly, during the mating season, RO directed more aggression towards than he received from females (Binomial test;  $p = 0.02$ ;  $n = 10$ ;  $m = 2$ ). Meanwhile, no differences were found when LE was the actor or the recipient of aggression from females (Binomial test:  $p = 0.34$ ;  $n = 2$ ;  $m = 4$ ).

On one occasion the dominant adult male of the Windy Ridge troop (RO) was seen partaking in an agonistic coalition with the second ranking female (SM) against the subordinate male (LE). LE and SM were involved in food competition, then the top ranking female (HI) approached the pair and threatened LE away. Next, RO rushed to the area and attacked LE. LE then ran away and redirected his aggression towards me, while vocalising.

To my knowledge, agonistic coalition of females against males and in support of other adult males has never been reported in vervet monkeys, but it was observed in this study (Fig. 6.8). An instance was witnessed in Windy Ridge, when LE, the resident subordinate male was badly injured and was harassed by the higher ranking male RO. RO had redirected his aggression towards the wounded animal after spotting an external male in their territory. It could also be argued that RO was attempting to force LE away from the females of his group before he started a long pursuit of the outsider. After RO's aggression towards LE all the females grouped together and heavily threatened RO away from LE.

The most common form of male-female agonism is the 'herding of females'. However, a more subtle way to direct the movements of the females and other members of the troop was the 'confident walk' (see Plate 6.1). The dominant adult male was mostly involved in this assertive walk (23 out of 24 observations). Confident walk occurred only once during an intertroop encounter and on 18 occasions it was related to general locomotion, the remainder (4 times) occurred within other contexts. The third ranking male was once seen walking in that way when circling the area where the troop had just been feeding.

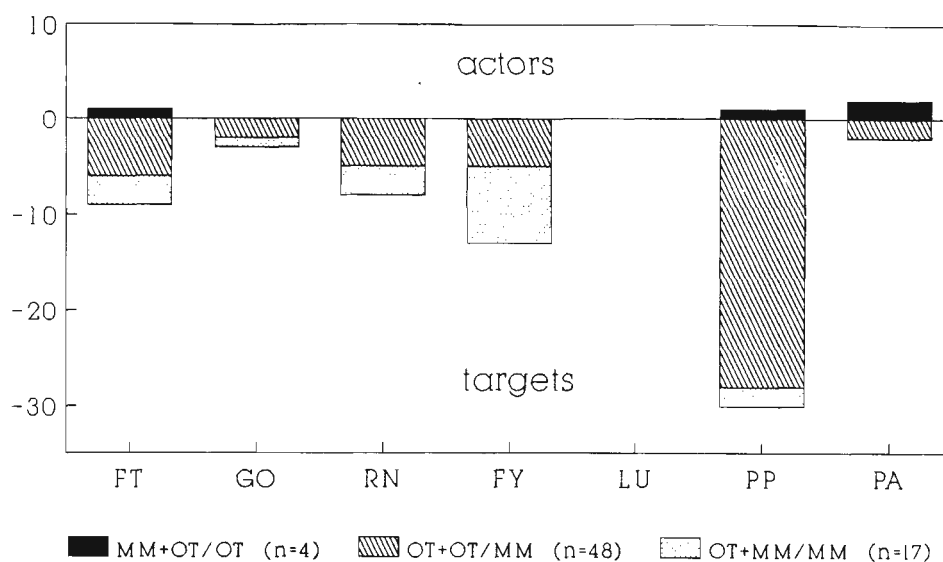


Figure 6.8. Agonistic coalition involving adult (FT>GO>RN>FY>LU) males or subadult males (PP>PA) and other age/sex classes (compare with Fig. 5.8 p.153) when males were the actors or the targets of the coalition by females or immature animals.



Plate 6.1.  
The confident walk (alpha male of the Windy Ridge Troop).

#### **6.4.2. Avoidance and submission**

During the non-mating season, males in Windy Ridge were the recipients of more submissive and avoidance behaviour involving males and females than females were (Binomial test: for RO  $p < 0.001$  and for LE and PE  $p < 0.05$ ). The youngest and lowest ranking adult male (CH) avoided an adult female once and never avoided or received submission from a female.

During the mating season, the alpha male (RO) was never seen exhibiting either avoidance or submissive behaviour toward any female. However, LE avoided the middle ranking female (BE) once when RO was less than 10 m away monitoring their movements. LE appeared to be avoiding RO's reaction rather than the female *per se*.

It can be concluded that the proportion of submissive and avoidance behaviour received by a male from females was dependent on the total number of agonistic bouts he directed towards them, and not on his rank (lowest ranking excluded). This was true for both the non-mating and the mating seasons (BN:  $X^2 = 3.246$ ; 2 df; NS and M: Fisher's exact test: NS).

#### **6.4.3. Male interference during female agonism**

By definition (see chapter 5) male agonistic interference does not imply that the male is involved in a coalition with a specific individual, although the benefits to the lower ranking females and immatures are obvious.

In Windy Ridge, only the most dominant male was involved in agonistic interference (Figs. 5.4 and 5.5). An example of male interference in female agonism is given here. On the 11th of June 1988, at 7:50 am, RO ran to the area where HI (top ranking female) threatened SM (possibly her daughter) then SM redirected her aggression at MO (3rd ranking female). When RO arrived he gave a hard look at them while standing on his back legs in front of them. In this way RO's chest was clearly visible to HI (the closest) and the other two interacting females. The agonistic interaction among the females stopped immediately.

Sometimes, primarily when females competed for food resources, redirected aggression could regress all the way down the female dominance hierarchy to the lowest ranking female, who could in turn threaten an immature. It was obvious in the above case that RO's interference stopped the escalation of a fight.

In the Cage Troop, another modality of agonistic interference was observed. The males did not issue threats, but it seems that their presence alone was sufficient to deter higher ranking females from harassing and attacking lower ranking ones. The immediate benefit to the male was that, either the female who had been the target, or one of the actors of the aggression ended up by grooming him. The difference with the first, more active modality of agonistic interference is that it is slower and threats and chases can continue for a while. It involved the subordinate adult male (RN) and the subadult male (PA) of the caged troop (Figs. 5.6-5.7).

## 6.5. ADULT MALES AND IMMATURE ANIMALS

Adult vervet males hardly ever interact in a direct way with infants or other immatures. The exception was the second ranking adult male of the Cage (GO) who displayed high rates of playful behaviour with a 3 year old male, PA.

In the free-ranging troop, the lowest ranking female (ET) was seen leaving her infant near the dominant male (RO) while the general activity of the troop was resting and she went off to feed. RO did not show much interest in the infant, but his presence alone could have stopped other members of the troop harassing the infant (see also Stein and Stacey, 1981 for yellow baboons). On a few occasions, the dominant females and their offspring had been seen supplanting and threatening the lowest ranking female's infants.

One interesting occurrence which took place in Windy Ridge developed as follows: the newly immigrated male (GR) was feeding in the same tree with the adult female BE and the dominant adult male RO. BE threatened GR (food competition) and RO joined her (coalition). The female left the area and two infants (about 6 months old) formed an agonistic coalition with the troop leader; the infants were in close contact with RO and together they chased GR out of the feeding tree.

The alpha male of the wild troop was seen directing serious attacks towards females with infants. At that time the infants were about 3 months old. It could not be determined if the male was trying to get to the infant or to the female. The occurrence of this behaviour was unexpected; both times the dominant animal rushed to the area where the female and infant were resting and jumped onto them, the female immediately retrieved the infant and ran towards a group of females in her vicinity.



The most spectacular successful attack by an adult male directed at an immature was made by the dominant male against a one year old male. They were both feeding in proximity to the higher ranking females. The male pierced the youngster's ear and the females that were close by merely gave alarm vocalisations and continued feeding.

That vervet females might benefit from having male friends can be inferred from the fact that their infants may be the recipients of female agonism. Observations made in the Cage gave some evidence of the dangerous position young offspring of lower ranking females may find themselves in. The top ranking female (XA) was seen 'dropping' the infant of the lowest ranking female (BA) from a height of about 8 m onto the cement floor. The second ranking female (CE) supposedly XA's daughter, also attempted to do so repeatedly, but the same infant managed to hold onto the poles and escaped undamaged. In none of those instances did adult males take any notice, nor did females for any length of time. The subadult male that maintained a close relationship with this particular female was very sick at this time and could hardly walk. It is not known whether he might have assisted the infant. It is suggested that one of the benefits females may gain by having male friends is to reduce the chances of other conspecifics injuring their infants.

## 6.6. DISCUSSION

Most studies of vervet monkeys do not present data that allows direct comparison of male-female and male-male affiliative relationships (see Cheney & Seyfarth, 1990). My contribution to this matter can be summarised as follows.

### **6.6.1. Male-female spacing**

It can be concluded that the alpha male of both troops was closer to higher ranking females more often than he was to lower ranking females. There were two exceptions for the top ranking male in the Cage troop. First, he was closer than expected to the lowest ranking female at a time when she was constantly the target of heavy aggression from other females. This may have been the result of her seeking FT's protection or female attacks could have been prompted by her proximity to the dominant male. Second, the special sexual interest of FT for the post-reproductive female (see chapter 7), could explain his high rates of proximity to her during the mating season.

In contrast, the middle ranking males spent more time in proximity to middle and low ranking females than they did to high ranking females. These results agree with those found for macaques (*Macaca sylvana*: Witt *et al.* 1981). However, Chalmers and Rowell (1971) predicted that certain social behaviour which existed between adult male and female mangabeys (e.g. being approached, sat next to and groomed) was more related to the age of the female than to her rank. This could partly explain some of the differences in male-female interactions found during the present study that were not rank-related e.g. the youngest adult female being more responsible than any other female in maintaining grooming relations with the alpha male.

In general, adult males did not show any preferences in proximity for adult females during the birth season. This might have been because the males were more peripheral and mainly associated with other males. In addition, individual differences in female proximity to males could have been masked by females forming compact groups with their new born infants and other immatures ('aunting groups' Krige & Lucas, 1974). However, the second ranking male (LE) spent more time than expected near the lowest ranking female (ET) for all the seasons. LE and ET were classed as having a special friendly relationship (*sensu* Smuts, 1985).

The subadult male in Windy Ridge (TI) had a more central position in the troop in comparison to the adult males, at least during the non-mating season. During the mating season he was closer to the middle and higher ranking females than to the lowest ranking females. In the Cage the most dominant subadult male (PP) was more often in close proximity to the middle ranking female (MC) than to any other female. He was also within the social environment of the two highest ranking females (XA and CE) more often than expected during the non-mating season. During the mating season PP's social preferences were not so obvious, although there remained a tendency to associate with the three highest ranking females.

#### *Seasonal differences in male-female proximity*

The post-reproductive females of both study troops were close to the alpha male of their troop more often during the mating season than at any other time. These results could have been due to females without infants presenting longer sexual 'attractive' periods (see chapter 7). A tendency for the lowest ranking reproductive female of both troops to be closer to the dominant male during the birth season could mean that she was looking for protection from him and/or that the high ranking animals accepted them because of their infant (see Goodall, 1977 for chimpanzees).

The subadult male (TI) was closer to the second lowest ranking female (VE) and more distant from the lowest ranking female (ET) during the mating season. Likewise, the subadult male (PP) at the cage increased his closeness to the lowest ranking female (BA) during the mating season. These results agree with those found for stumptailed macaques (*M. arctoides*: López-Lujan *et al.* 1989) as male-female spacing did not vary much over the year.

In general, an increase in proximity between the different male-female dyads during the mating season was not a general occurrence. A trend existed for additional males to be more distant from females as the reproductive season approached.

When looking at which females were mostly within the male's social environment during the mating season, it was found that: i) RO increased his time near the high ranking (XA and CE) and middle ranking (BE and WE) females, ii) the subordinate male (LE) was closer to BE and iii) the subadult male (TI) was nearer HI, BE and WE. In contrast, during the mating season the two subordinate adult males (RN and FY) spent less time near the top ranking female (XA).

#### **6.6.2. Male-female affiliative behaviours**

*Do males groom with females more than they do with other classes?*

Studies done on baboons by Saayman (1971) and by Byrne *et al.* (1989) show that grooming is more common among females than it is between males and females. Moreover, in multi-male multi-female species, grooming involving members of both sexes occurs more often than among males (see Sparks, 1967). Grooming relationships among vervet monkeys agree with the above statements. The results of this study also concur with the argument that the social function of grooming is to establish and maintain affiliative relationships and that grooming mostly occurs because the males approach the females, although the alpha male was approached more by females than other males (see Tsukahara, 1990 for Japanese macaques).

The top ranking male was the only male that received more grooming from females than he gave during the non-mating season. Therefore, it can be concluded that during the mating season, the attraction of higher ranking individuals also applies to intergender relationships. However, during the mating season the alpha male groomed females as often as they groomed him.

### *Distribution of male-female grooming*

The tendency of high ranking males was to groom with high ranking females (see Hill, 1986 for rhesus), while for middle ranking males it was to groom with middle or low ranking females. The alpha male of the Windy Ridge troop did not groom certain females significantly more than others, nor did particular females groom him significantly more often than others (see also Dunbar, 1984, chapter 10 for geladas). However, higher ranking females tended to groom with the alpha male. That female competition inhibited lower ranking females from initiating grooming with the leader of the troop was reflected by the finding that the two higher ranking females initiated grooming with the alpha male more often than did other females. Tsukahara (1990) hypothesises that the presence of partner choice suggests that there is social significance in grooming relationships in Japanese macaques.

When considering who starts, who finishes or who ignores a grooming bout, it was found that the most dominant adult male (RO) was as responsible for grooming interactions as was each one of the females, except the second ranking primiparous female (SM) who was more responsible than the male. It can be concluded that although RO started more grooming bouts with low and middle ranking females, they were more responsible for finishing them, possibly to avoid an agonistic encounter with higher ranking females. The second ranking male and the subadult male at Windy Ridge were in general more responsible than females for the maintenance of grooming. The third ranking male, as occurred for the alpha male of the same troop, was as responsible as females for grooming.

The lowest ranking males of both study troops (ranking 3 or more) groomed females in their immediate vicinity less than other males. This together with the fact that these males were farther away from both males and females (see chapter 5) support the suggestion that very low ranking males are socially inactive.

The top and middle ranking males groomed females in their vicinity, independently of rank (either male's or female's) except LE who spent more time near ET without grooming, than RO did. This could have been due to the low motivation LE showed towards grooming (see chapter 5) and the fact that ET being the lowest ranking female, might have sought LE's proximity to avoid being harassed by other females. This plus the high proximity rates for the pair LE and ET, suggest that they were engaged in some sort of 'friendly relationship' which was not strictly based on grooming (see Smuts, 1985 for baboons). The female ET had previously shown friendly behaviour towards the male LE, when he was badly wounded and could

hardly walk. She would give soft vocalisations in a food patch and LE would approach and feed by her. Late in the afternoon they were often seen occupying the same tree with ET's infant and no other monkeys, suggesting that they spent nights huddled together.

In the Cage Troop females groomed with RN more often than with the higher ranking males (FT and GO) when they were at less than 1 m. In this way RN could have used the opportunity to reinforce social ties with adult females.

The subordinate male LE groomed more often with those females found in close proximity. For the top ranking male this same tendency existed, although a statistical significance was not reached. Similarly, the alpha male of the Cage Troop groomed with high ranking females more because they were found more often in his vicinity. The subadult males behaved in the same way: the most dominant (PP) groomed with the middle ranking female (MC) more often than any other female, and the most subordinate (PA) groomed mostly with the lowest ranking female (BA).

#### *Seasonal differences in male-female grooming*

During the non-mating season the dominant male (RO) was groomed by females more often than he groomed them (<19% of the bouts). In contrast, the subordinate males (LE and PE) groomed as much as they were groomed by females during the non-mating season. It is not known whether the lowest ranking male (CH), groomed very little due to his low rank or to being more peripheral prior to migrating.

The above results can be explained by the fact that the alpha male has the potential to provide more benefits to the females during the non-mating season than do other males (cf. Stambach & Kummer, 1982 for female *Papio hamadryas*).

The most dominant adult male of the Windy Ridge troop (RO) and the middle ranking male of the caged troop (RN) were the only adult males that groomed females in close proximity more often during the mating season than during the non-mating season. The same trend was shown by the subadult male (PP).

I suggest that male-female interactions in vervets, rather than varying for the mating and non-mating seasons show shorter term changes (Carpenter, 1942a for rhesus). That is, an increase in total grooming and more grooming done by the male of the pair could be limited to a period of sexual consortship (Saayman, 1971 for chacma baboons; see chapter 7).

### *Other affiliative behaviour*

Social play was restricted to young males, especially those who had not reached full adult size. Other friendly behaviours were mostly performed by dominant adult males and directed primarily at adult females, especially higher ranking individuals. Subadult males, on the other hand, directed other friendly behaviours towards immatures and adult females.

### **6.6.3. Male-female antagonism**

Male-female avoidance and submissive behaviour followed the opposite pattern to aggression. Adult males received more submissive and avoidance from females than they directed at females. The lowest ranking male (CH) proved to be the only exception. In addition, the number of female acts of submissive or avoidance directed towards an individual male was related to the number of aggressive bouts and displacements initiated by the same male; the alpha male was the most active male in that respect.

### *Aggression*

The dominant male threatened and attacked females and they seldom retaliated. On occasions, attacks or threats would occur without any apparent reason, which agrees with Smuts' (1985, p.96) argument that 'delayed punishment' is occasionally meted out. In contrast, additional males directed aggression at females as often as females did. Therefore, additional males might be lower ranking than, at least, some of the adult females.

Female aggression towards males usually took the form of coalitions, with or without immature animals, and occurred less often with other (sub)adult males. A 'tree display' by an adult male could be followed by a female giving a 'false chase' and other females and immature animals joining her. These theoretically submissive displays would sometimes progress into a 'rebellion' when other males joined in and real threats would occur. It differed from a 'pacific demonstration' in that the target male would retract his scrotum and give fear and/or threat vocalisations. Otherwise, females were hardly ever aggressive towards adult males.

The fact that the youngest adult male and the subadult males were the focus of more female aggression can be understood when considering their similar body weight. Camberfort (1981) reported agonistic coalition of juvenile vervet monkeys against adult males without the support of adult females, this was never observed during this study, although subadult males were observed in this behaviour.

### *Male agonistic support of females*

Interference during agonism has generally been interpreted as the partner's support of one of the interacting animals. In the present study a clear difference was noticed between; i) 'agonistic coalition', when a member of the troop takes sides and supports either the aggressor or the victim of aggression, ii) 'agonistic interference', when the actor actively threatens the interacting animals and stops the fighting, with the peculiarity that threats do not seem to be directed at a specific individual and iii) 'peaceful interference', when the subject approaches an ongoing agonism and his presence alone seems to influence the outcome.

The first type of intervention was commonly carried out by adult females and immature animals. However, cases of adult males forming coalitions with females against other males or females were also witnessed sporadically (see Seyfarth, 1978b for baboons). Typically, the subordinate adult and subadult males allied with females and immatures against the top ranking male. These observations show that one of the main differences that vervet males are said to have from other typically multi-male species (see p.11) does not apply to the two troops studied here.

'Agonistic interference', has been reported for chacma baboons by Saayman (1971) as 'intervention'. Unfortunately, this behavioural category was not defined from the beginning of the study, therefore it was not feasible to compare differences between the breeding and non-breeding season. The top ranking male of the wild troop generally interfered in female agonistic bouts by 'agonistic interference' and was the only one observed performing this presumably altruistic behaviour.

The ultimate causes for the top ranking male's interference in aggressive encounters involving females and immatures vervets could be: i) to protect immatures (who might be his own) and potential mates from injury, ii) to keep the level of aggression in the troop at a minimum and to prevent low ranking females leaving the troop or becoming too peripheral (see Dunbar, 1984, ch.10 for baboons), iii) to reinforce his status and remain a focus of the troop.

A case of altruistic interference (coalition was also included in the definition) by the top ranking female in a caged troop of rhesus monkeys was described by Reinhardt and collaborators (1986). The female in question was not related to any of the other animals, she was the oldest, and even dominated the single adult male of the troop. Reinhardt and collaborators concluded that interference can occur when the probability of being the recipient of aggression is at a minimum.

The third type was commonly used by the middle ranking and the lowest subadult male of the Cage troop. The interferer approached the interacting animals (females with or without immatures) and followed or sat alongside them, without threatening them. Their presence alone might have deterred other females from forming coalitions with the aggressors, or it might have actually stopped the interaction. This form of interference was commonly followed by the interferer being groomed by one of the interacting females (either the actor or recipient of the aggressive act). Datta (1983 p.95) described a similar method of stopping ongoing agonism without the use of threats among rhesus monkeys.

These differences in agonistic interference may be the result of the fact that subordinate males of the Cage troop were more related to the females than in the free-ranging troop yet lacked the competitive power to risk a general female coalition against them. However, an immediate benefit was granted them, as by being groomed by the females improved their opportunities for socialising.

Similar results were found by Saayman (1971) for chacma baboons. A subordinate male initiated most of the troop progressions, participated in more grooming bouts and consorted with females more than other males. He also interfered in female agonism more often, which suggests that he was a long term resident who may have fathered quite a few infants. Therefore, it can be speculated that by interfering on behalf of females and immatures this male possibly increased his lifetime reproductive fitness.

Chalmers and Rowell (1971) proposed that in mangabeys, the presence of the alpha male reassures the other members of the troop, even though he was never seen defending females in their cage troop. In this study some evidence indicates that the vervet alpha male defends females when stopping agonism and that subadult and subordinate males may do so in a more subtle way.



### *Seasonal differences in male-female agonism*

In general, the dominant adult male of the Windy Ridge troop was not more aggressive towards females during the mating season. In contrast, the middle ranking females (BE and TO) were the targets of RO's aggression more often during the non-mating season.

A typical form of male agonistic behaviour towards females is 'herding behaviour'. Resident males chase their own females away from invading males (Wrangham, 1981). In this study, the free-ranging dominant male herded females in different situations: i) away from extragroup males; ii) when they were in proximity to the other resident male; and iii) without the presence of a male competitor, but simply when the females were very spread apart. The above points serve to explain why herding of females was not only restricted to the mating season (cf. Enomoto, 1981 for Japanese monkeys).

#### **6.6.4. Adult male-immature interactions**

The interest newborn infants and their mothers provoke in other adult and immature females is well documented (Seyfarth, 1978 b; Chapais, 1983b; Hooley & Simpson, 1983). However, adult males are excluded from aunting circles (Basckin & Krige, 1973; Krige & Lucas, 1974) and are usually excluded from feeding near females and immature animals (Krige & Lucas, 1975).

Among Catarrhine monkeys, male paternal care has been reported for macaques and baboons (review in Taub & Redican, 1984). However, there is no evidence that adult vervet males dedicate any direct paternal care towards infants. The exception is Hauser's (1986) study which showed that male responsiveness to infant distress calls was mostly related to the probability of a male being the distressed infant's father. Furthermore, vervet infants may benefit by keeping proximity with the most dominant male of the troop.

The results obtained in this study indicate that vervet females may benefit from male agonistic coalition and interference, in particular those females with whom males associate more often. It can be concluded that the benefits they may obtain from close association with members of the other sex are reduced when compared to those baboons and macaques may obtain because vervet monkeys: i) possess a well defined network of female-female relationships (see chapter 1) that may make them more independent of male protection; ii) are less dimorphic than baboons or macaques

(Napier & Napier, 1985); and iii) females concealing the time of ovulation (Andelman, 1987). In this regard, this study must be taken as preliminary and it remains necessary to observe more groups and to assess how often male-female preferences change and whether they are age or rank related.

There is indirect evidence of the danger vervet infants can face when approached by a strange male (see Struhsaker, 1967 c) or risk that they undergo of being injured by members of higher ranking matriline (personal observation). Therefore, if infants are near long-term resident males when their mother is away, they benefit from the presence of the male. This may explain why juvenile vervets remain closer to adults than baboons do (Camberfort, 1981).

In addition, the fact that vervets do not use infants during agonistic buffering (as occurs in other multi-male species) may explain why vervet males do not show much interest in grooming and interacting with infants (cf. Stein & Stacey, 1981, for yellow baboons). Instead, vervets possess well developed displays of dominance and submission which function to reduce male-male aggression (chapter 5).

## 7. SEXUAL RELATIONSHIPS

It has been argued that in mammals the most limiting resource for males is females (Emlen & Oring, 1977). Therefore, males can primarily increase their lifetime reproductive success by maximising the number of females they mate with (see Dunbar, 1988 p.23).

A positive, although not a complete correlation between sexual activity and dominance rank has been found for rhesus monkeys (*e.g.* Carpenter, 1942 b), stumptail macaques (Gouzoules, 1974) baboons (*e.g.* DeVore, 1965; Hausfater, 1975; Packer, 1979b, Hamilton, 1984) and vervet monkeys (*e.g.* Struhsaker, 1967b; Andelman, 1986) which is more apparent when the subadult males are excluded (Cowlshaw & Dunbar, 1991; but see Bercovitch, 1987 for savanna baboons).

Apart from the total number of copulations a male achieves, it is important to analyse when he mates and with whom. The distribution of male copulations in relation to the sexual cycle of the female seems a more adequate tool for understanding vervet male reproductive strategies than simply the number of copulations. The most valuable tests are those that employ genetic markers (Smith, 1980; 1981; Curie-Cohen *et al.* 1981) or DNA fingerprinting to determine male mating success (Dixon *et al.* 1988; Burke, 1989).

The key factor affecting reproductive success in males is probably gaining access to females when ovulation is more likely to occur (Bercovitch & Goy, 1990). In species where females present a swelling or redening of the vulva and/or face (listed in Blaffer Hrdy & Whitten, 1987), adult males limit copulations to the period of maximal turgescence (Altmann, 1962; Hall & DeVore, 1965; Saayman, 1970; Chalmers & Rowell, 1971; Hausfater, 1975; Bercovitch, 1987). Interestingly, there is an association between the presence of female sexual skin and a multi-male breeding system (Clutton-Brock & Harvey, 1976), although some species that live in multi-male groups do not show sexual skin (Blaffer Hrdy & Whitten, 1987).

Visual cues alone cannot explain the peak in copulations which occur three days before deturgescence in baboons. Olfactory cues have been found to be important in arousing male sexual behaviour, although psychological factors may affect sexual performance in both males and females (see discussion).

Apart from males attempting to maintain exclusive access to females when they are more likely to conceive (see Wrangham, 1980; Bercovitch & Goy, 1990), it seems reasonable to hypothesise that males would compete to mate with high ranking females in order to improve their fitness (Berenstain & Wade, 1983). That is, high ranking females, at least in captivity or under provisioned conditions, reproduce more successfully than lower ranking females (Cheney *et al.*, 1986). As Emlen and Oring (1977) pointed out, the ability of a male to control access to fertile females would be constrained by the number of females cycling at the same time.

Male choice may be one of the underlying factors regulating sexual selection in baboons (Saayman, 1970; Hausafter, 1975; Seyfarth, 1978a; Packer, 1979b). Moreover, Trivers (1972) emphasizes that mate competition is greater for the sex that invests more in their offspring, that is females in non-monogamous primates. In fact, it has been argued that female mate competition can play an important role in determining who mates with whom and how often (Lindburg, 1980; Silk & Boyd, 1983; Smuts, 1987).

An age-related factor in sexual attraction has also been discussed; young males tend to interact in a sexual way with immatures or young adult females (Hall & DeVore, 1965; Silk & Boyd, 1983).

Limited data on vervet male reproductive success has been published that does reference to mate choice and timing of the copulations in relation to the menstrual cycle of the females (for exceptions see Andelman, 1986, 1987; Keddy cited in Cheney & Seyfarth, 1990). It is not yet known whether male vervet monkeys assess the reproductive state of females. If so, how do they do this? Do they find out through olfactory or visual inspection of the females' genitalia or do they rely on female soliciting behaviour *i.e.* sexual presenting.

First, it is important to distinguish between behavioural, physiological and vaginal estrus. The term 'estrus' comes from the Latin *oestrus*, which means possessed by the gadfly, in a frenzy (Feder, 1981 p.280). In other words, estrus has often been considered as being synonymous with receptivity (*e.g.* Gartlan, 1969) and corresponds to the time when females with 'true sexual skin' present sexual swelling (Taub, 1980,

p. 291). This would apply to the 'behavioral estrus' that is the period females sexually present, emit solicit calls (Mori, 1979, p.187 for geladas) and readily accept male sexual advances.

The use of the term 'physiological estrus' should be restricted to the period when females show the highest levels of estrogen and lowest levels of progesterone (Jensen, *et al.* 1981). A surge of luteinizing hormone, which is required for the ova to be released from the ovaries, occurs at this time (Feder, 1981 p.352; see also Rowell, 1971).

Despite the fact that a physiological study was not carried out, backdated dates of conception for a few females will be used as a reference for this purpose. Finally, 'vaginal estrus' (*sensu* Feder, 1981 p.281) will be restricted to comments on studies in which vaginal smears were taken to determine the female's reproductive phase. Feder (p.281) also pointed out that behavioural estrus peaks earlier and continues when vaginal estrus begins.

#### *Defining sociosexual behaviour*

For sociosexual behaviour (*sensu* Hanby, 1976 p.3-4) I consider any heterosexual interaction involving a (sub)adult male (>3.5 years old) and adult female (>2.5 years old) that consists of:

**F** - One member of the dyad constantly following the other. Saayman (1971) points out that persistent following could be a good indicator of sexual consortships.

**P** - Female sexual presenting to the male (Gartlan, 1969; Chalmers & Rowell, 1971).

**S** - Males may inspect the female's genitalia in the following ways. Male visual inspection, (**v**) characterised by males holding the female's tail up and closely looking at their genitalia or, by positioning their faces near the area. Second, by tactile inspection (**t**) which occurs during grooming, by inserting finger in vagina or by simply touching the female's perineum. Third, olfactory inspection (**s**) is an obvious movement by the male, in which he directs his face towards the female's genitalia, with or without facilitating his action by holding the female's tail up. Finally, when direct contact between the male's muzzle and the female's genitalia occurs, it is categorized as muzzling (**m**) and 3 year old males do it more often than females (Struhsaker, 1967a). The female may also inspect the male's genitalia (**p**) by either visual, tactile, or olfactory means.

**H** - Male putting his hand on the female shoulder or touching her body while sitting in front of her.

**G** - Male touching, patting or grabbing the female's hips, without adopting the mounting position. Struhsaker (1967a) considers this pattern as a prelude to genital inspection, muzzle or mount (see also Bramblett *et al.* 1975).

**M** - The male adopts the mounting position characteristic of the species, without pelvic thrusts (Gartlan, 1969).

**T** - Male performs irregular pelvic thrusts. Gartlan (1969) found that in Uganda the male vervet monkey's 'nuzzling' ('muzzling': Struhsaker, 1967a) the back of the female's neck always preceded pelvic thrusting. This was never observed in Natal.

**I** - Penile intromission, which normally occurs when the pelvic thrusts become more regular.

**E** - Ejaculation, which is characterised by a long pause and rigid posture (Hall & DeVore, 1965; Andelman, 1987) followed by the male dismounting or the female walking away. Afterwards, females typically 'finger their vaginal area and sniff and/or lick their fingers (Struhsaker, 1967a; Gartlan, 1969).

The first four categories could be classed as preliminary sexual behaviour (P,F,S,H). The next three (G,M,T), which leave no doubt about the nature of the interaction are classed as incomplete mounting. Finally, the last two (I,E) are categorised as complete mounting. Some authors consider mounting complete only when ejaculation could be confirmed, (Andelman, 1987); while others only mention sexual intercourse without implying that ejaculation occurred (Hanby, 1976, p.5; Gouzoules, 1974).

The reasons for placing I and E within the same category are: i) in the field, it was very difficult to distinguish between them, ii) if penile intromission is achieved, the female is accepting the male's sexual approach or the male is reacting to her sexual present (female is receptive and attractive).

All the observations taken at both study sites consisting of any of the above mentioned behaviour will be plotted against the date they occurred, in order to determine seasonal differences and detect rhythms. However, no attempt will be made to determine whether the preliminary behaviour and incomplete mounting

occurred at the time of probable conception. Each female will be represented separately and the identity of the male partner will be stated. In addition, parallel graphs indicating who was responsible for the sociosexual bout will be shown (Fig. 7.1-7.2). Sometimes, it was not possible to determine who initiated the interaction (0), males could initiate a sociosexual bout and females accept it (1) or not (3); or females could sexually present or approach adult males to groom them (2) and be successful or unsuccessful (4); finally, males could smell or mouth a spot where a female had been sitting (5).

### *Sexual consortships*

One of the strategies reported for baboons and macaques which increases male reproductive success is the formation of temporary pair bonds or sexual consortships (*sensu* Hanby, 1976, p.6). These consort relations are characterised by a male having priority of sexual access to a female, a male and female exhibiting continual attention to each other, following each other and maintaining close proximity, normally accompanied by frequent male to female grooming among baboons (Hall & DeVore, 1965; Seyfarth, 1978a; Smuts, 1985; 1987; Strum, 1987) and macaques (Carpenter, 1942b, Kaufmann, 1965; Glick, 1980; Lindburg, 1980; Taub, 1980; Chapais, 1983a; review in Bercovitch & Goy, 1990). Sporadic interactions by male consorts with other mates have also been reported (Seyfarth, 1978a) as well as other males mating with the female when the consort male is away (Bercovitch, 1987). Similarly, in this study vervet males were observed to maintain exclusive sexual access to a particular female, constantly following, remaining in proximity or otherwise visually monitoring her movements, grooming, inspecting her genitalia and mounting her. Occasionally, the female was more responsible than the male in maintaining the pair bond.

In order to introduce a more objective measure, I analysed whether a particular male-female pair was closer than expected during the days that they were involved in a consort relation than at other times during the mating season. This was carried out with a Chi-square test once the other patterns described above had been observed for at least an hour. Unfortunately, the samples on grooming available from the scan and instantaneous sampling were too few to test for differences occurring when the pair was in consort.

### *Other analyses of sociosexual behaviour*

An extensive analysis of male-female sociosexual behaviour will be performed in this chapter with emphasis on the following aspects: first, the daily distribution of

occurrences of sociosexual behaviour for the Cage and Windy Ridge study troops; second, male and female responsibility for initiating sociosexual interaction; third, female individual differences in attractivity, receptivity and proceptivity in relation to each male sexual partner; fourth, how often males inspect the female genitalia and who does or receives most of the visual inspecting; fifth, the alternative strategies vervet males might use to improve their mating success; finally, a determination of whether sexual interference is a mechanism of mate choice reinforcement.

These analyses will facilitate the understanding of male-female relationships in a species that does not have (at least for human observers) any obvious visual signals of female cycling activity. Furthermore, the fact that a restricted birth season corresponds to a limited (although longer) mating period, implies that different females may be cycling at the same time and the exact timing of the female's midcycle is a key strategy for improving male reproductive success.

To my knowledge, this is the first study in which a detailed analysis of the frequency with which vervet males inspect female genitalia (visual, tactile, olfactory and muzzling) has been carried out. Previous studies were limited to mentioning the occasional occurrence of genital olfactory inspection prior to copulatory behaviour (Gartlan, 1969; Girolami, 1985; Andelman, 1987).

The responsibility for sociosexual behaviour can be easily described by determining whether an interaction was initiated by the male or the female. As the data on sexual behaviour was mostly collected by *ad libitum* sampling, only analysis of directionality will be done to assess the responsibility for sociosexual activity.

The number of complete mountings that were observed for each male-female pair were used to determine the female's degree of attractivity and receptivity towards her mating partners while proceptive behaviour were only analysed according to female sexual presents (Wallis, 1981; Blaffer Hrdy & Whitten, 1987)). To determine the proximate mechanisms that regulate sexual behaviour, it is necessary to investigate the behaviour that precedes a sociosexual interaction, that is, the context in which it most commonly occurs. High rates of social grooming prior to or after a sociosexual interaction are characteristic of consort pairs but not exclusive to them.

When alarmed, or during intra or inter-troop agonism, dominant males are expected to be more sexually aroused than subordinate males. Sex occurring at that time or after other members of the troop were involved in a heterosexual interaction, can be



attributed to a peak in plasma testosterone levels or to sexual interference that might not reflect individual preferences for a specific female partner.

On the other hand, an analysis of the frequency of either aggression or social friendly behaviour following a heterosexual bout can contribute towards the understanding of the nature of male-female sociosexual relationships.

Mate choice by males and females may somehow be limited by the interference in sexual interactions of other members of the troop (see Hanby, 1976 for another view). Sexual interference is expected to occur in the direction of high towards low ranking individuals (see 'harassing' Struhsaker, 1967a). Immatures may also attempt to prevent their own mothers from successfully mating which would result in extended maternal care.

In summary, a restricted mating period together with the lack of a clear visual genital signalling of the female reproductive state may impose some constraints on the sexual monopoly of the top ranking male vervet monkey. Subordinate vervet males may have, theoretically, more access to female vervet monkeys than other species with a true sexual skin (see Dixon, 1983).

## **7.1 SEX INVOLVING MALE AND FEMALE FREE-RANGING VERVETS**

The alpha male of the Windy Ridge Troop was observed mating on 21 occasions, and in at least in 17 of them he ejaculated. His subordinate counterpart was observed mating only twice, and no ejaculatory pause was observed. The top and middle ranking females (HI and WE) were RO's mate partners on 7 occasions, the middle and low ranking females (BE and ET) were next with 3 times each.

There is strong indirect evidence that LE mated with the lowest ranking female apart from the rest of the troop: a few times on returning the female was seen autogrooming her genitalia and the dominant male would approach and smell her anogenital area (see also Hall & DeVore, 1965; for baboons maintaining secret consortships).

The subadult male (TI) was unsuccessful in his attempts to investigate and mount females. Finally, the male that immigrated towards the end of the study was observed mounting the second lowest ranking female (VE).

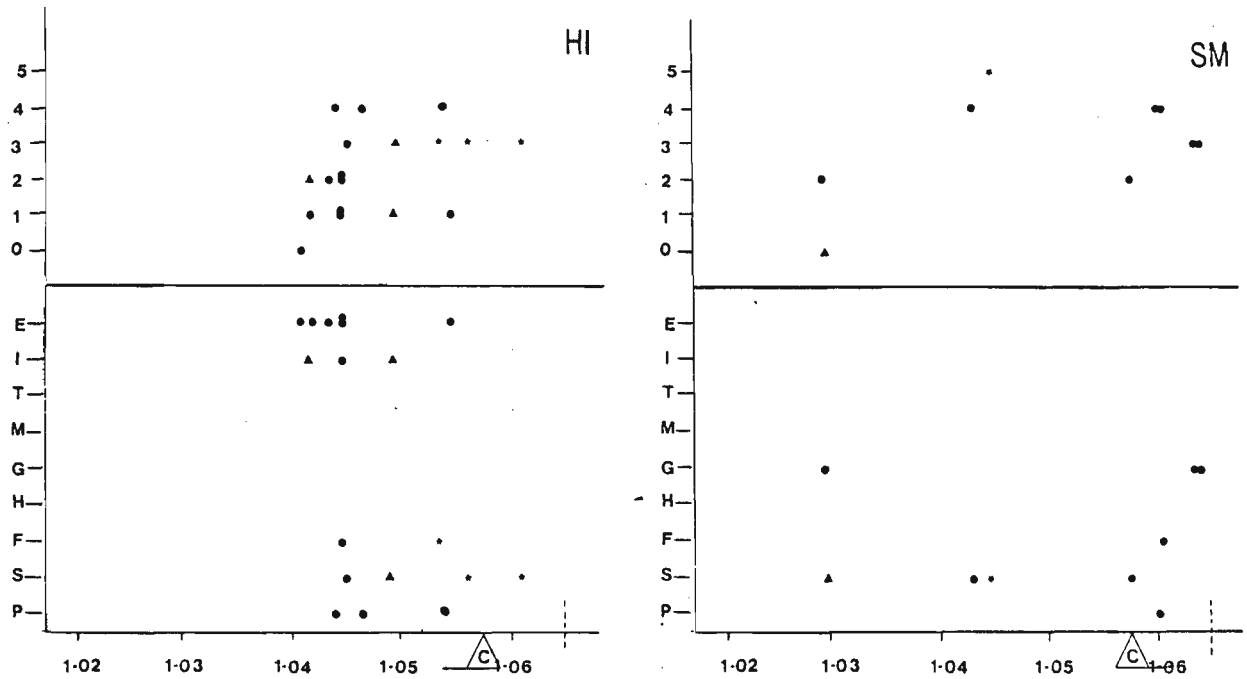
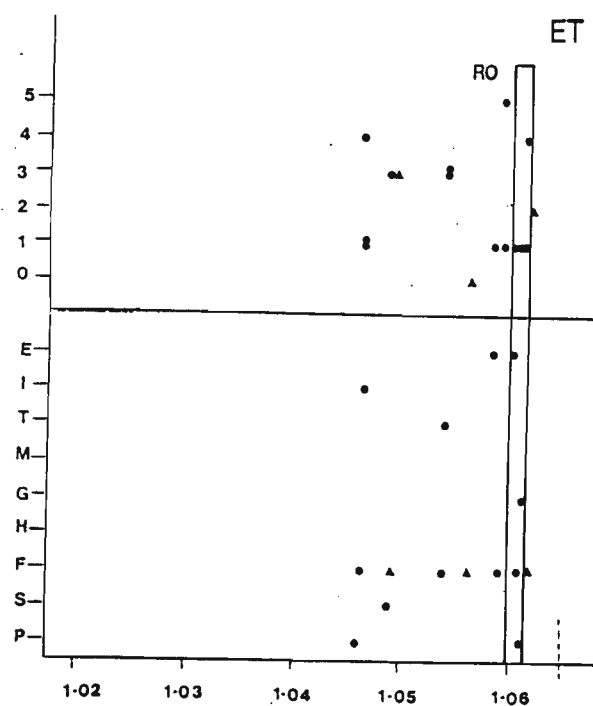
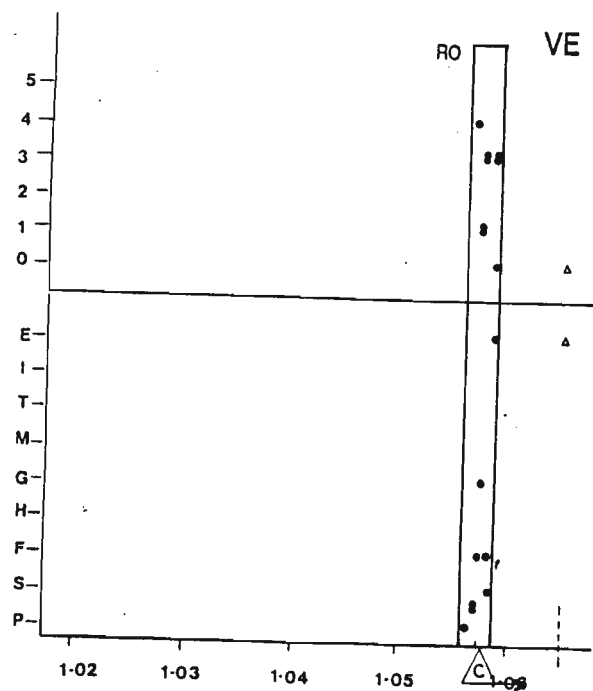
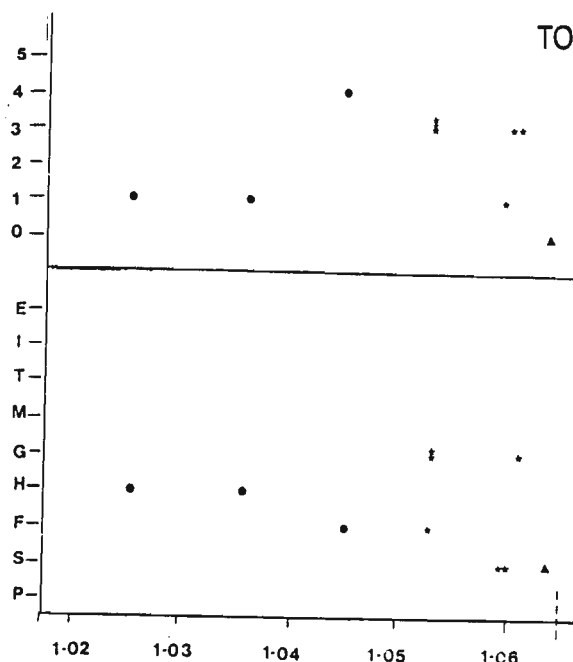
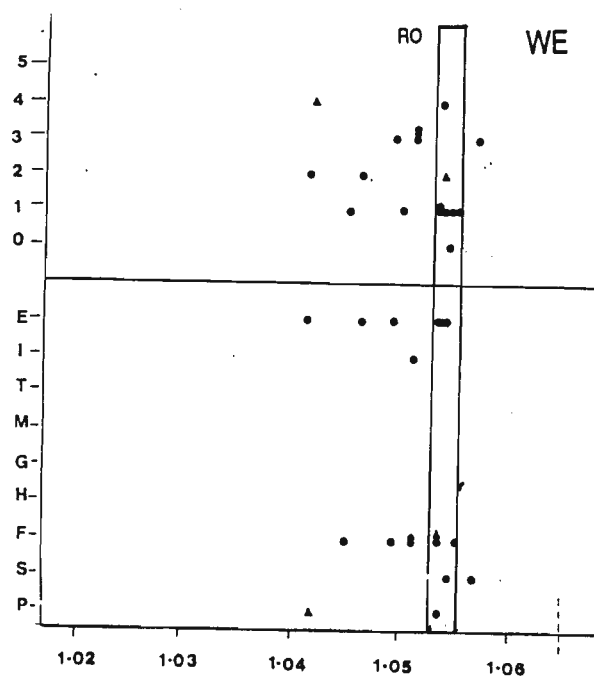
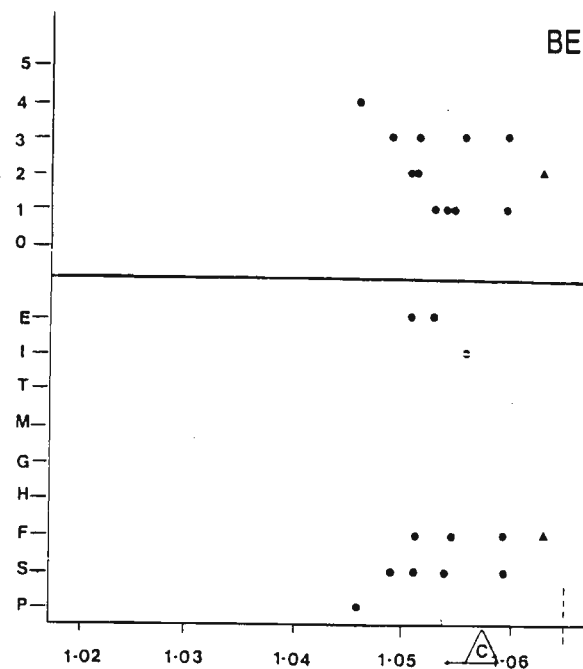
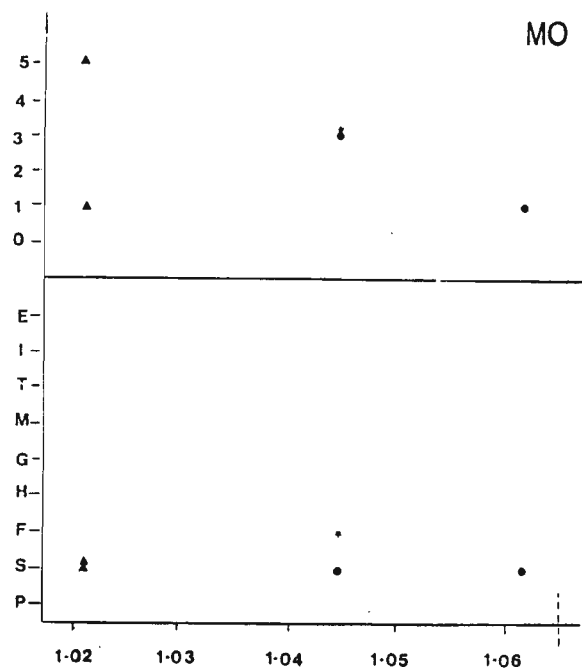


Figure 7.1 (continues in next page)

Sociosexual behaviour observed in the Windy Ridge troop. (P: sexual presenting; S: genital inspection; F: following; H: hand on shoulders; G: grabbing of hips; M: mounting (no thrusting); T: pelvic thrusting (not regular); I: with insertive, regular thrusts and E: when ejaculatory pause is observed. Responsibility (0: Unknown; 1: male starts and female accepts sexual approach; 2: female starts and male accepts; 3: male starts and female rejects male; 4: female starts and male ignores and 5: male inspects surface where female has just been sitting). The triangle at the bottom corresponds to the date of estimated conception (163 days: Johnson *et al.* 1973; Bramblett *et al.* 1975) or whether it had to occur prior or after that date. The adult males (RO●), (LE▲), (GRΔ) and subadult male (TI★) as partners. Vertical bars show the periods of sexual consortship.



There are no grounds for determining if the alpha male of this troop mated selectively with females at midcycle (see Fig. 7.1). Yet, some females only interacted with this male for a few consecutive days.

In Windy Ridge, the subadult male (TI) showed the highest proportion of sociosexual behaviour in series (18.2%), the subordinate male (LE) slightly less (13.3%) and the dominant adult male (RO) the least (5.6%) (RO/LE + TI: Fisher's exact test; NS). The second lowest ranking female (VE) accounted for 3 sequences out of the 4 found for RO (Table 7.5).

During the field study, although no significant differences in rates of friendly behaviour preceding a male-female sociosexual bout could be detected (RO: 19.4%; LE: 26.7% and TI: 36.4%;  $\chi^2$ ; NS), the trend was comparable to that found for the caged males. If the proportion of times the free-living males groomed females prior to a sexual bout are analysed separately, the subadult male (TI) tended to be responsible more often than the adult males (TI: 36.4%; LE: 6.7% and RO: 9.7%), although statistical significance cannot be tested because of the very low number of observations.

From the 21st of April 1988 until the 6th of June 1988, the dominant male (RO) visually monitored the subordinate male's actions and his locality (unpublished results). RO herded females away from LE on 5 of the total 16 times he was seen herding females, all of which took place during the mating season. RO herded LE on 10 occasions (in at least 4 of these LE was in the vicinity of females). When a general progression was about to start, RO would approach LE in the same manner he would herd females, possibly to show him the way (the remaining 10 observations of herding LE). This behaviour was understood as the dominant male's concern with not allowing the subordinate male go out of his sight.

RO's alternative strategy was to position himself between the other adult male and the rest of the troop, although LE was mostly within 50 m of the females (therefore not considered peripheral in this study). The indirect cost of this behaviour to RO was quite obvious at the end of the study, by which time his physical condition had clearly deteriorated.

Towards the end of May, when LE was badly wounded on his left foot and ankle, RO's efforts to control LE's access to the main body of the troop were less evident. LE would spend hours at 50-100 m from the rest of the troop (peripheral) only joining them in general progressions, and always at the tail of the group. RO would approach LE and display his genitalia, the subordinate would then perform a series of submissive behaviour and finally follow RO.

On the 5th of November 1988 only HI and BE (the dominant and middle ranking female respectively) had black infants with them (new born). The young females SM and VE (2nd and 7th ranking) looked very pregnant. Pregnancy was not detected for the lowest ranking and very old female (ET), although she looked as if she had gained some weight. No apparent pregnancies were reported for the other adult females. On the 8th of January 1989, SM and VE had black infants probably conceived after the 25th of May.

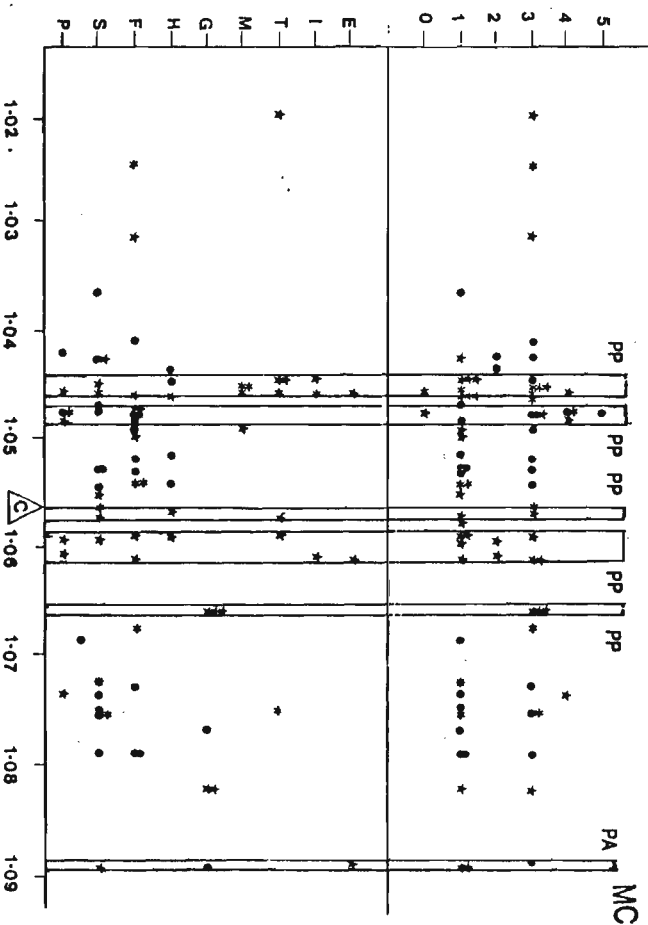
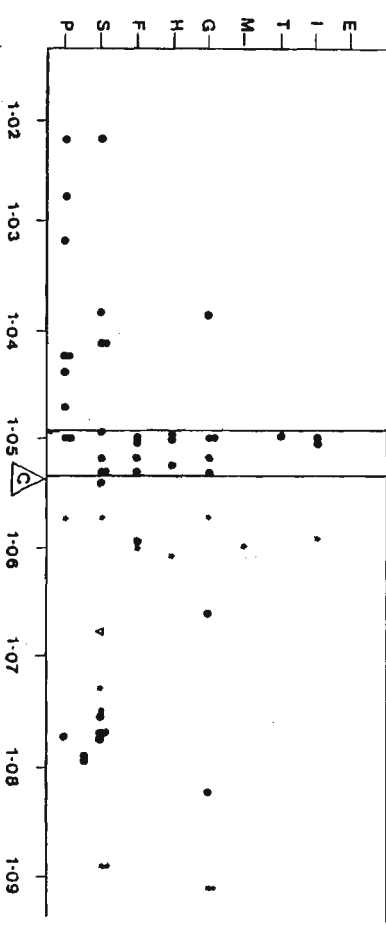
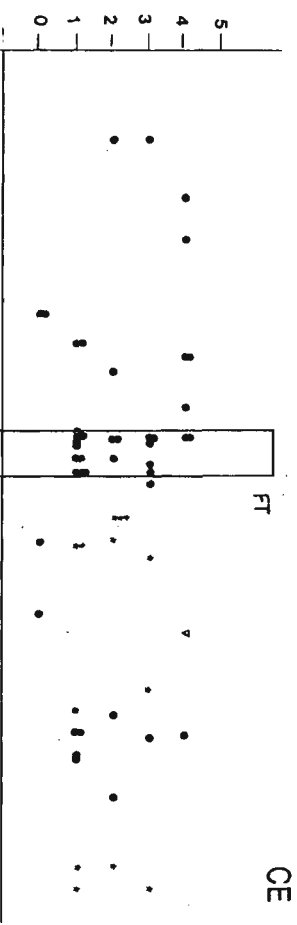
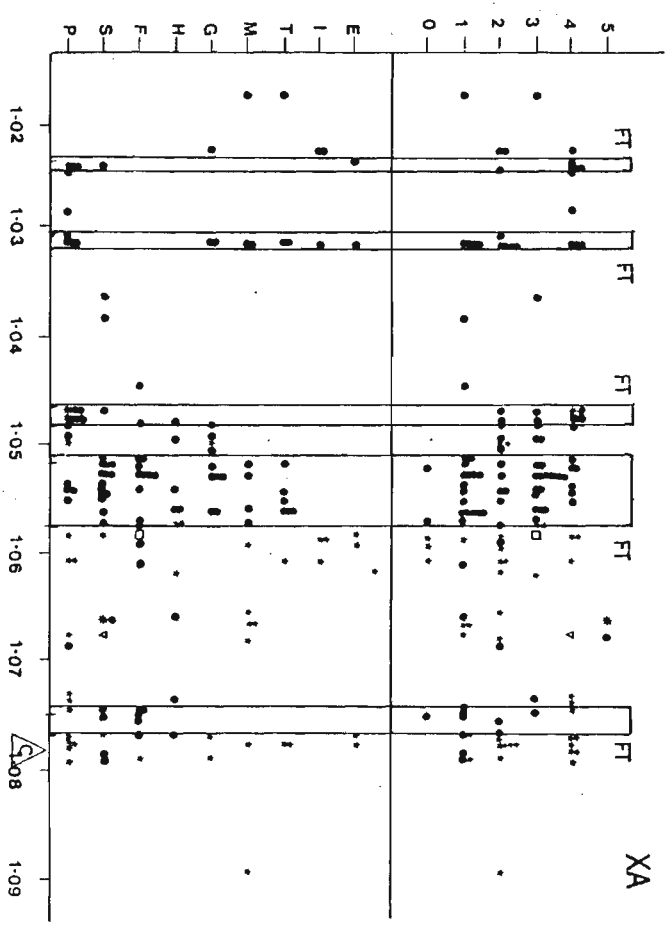
## 7.2. HETEROSEXUAL INTERACTIONS IN A CAGED TROOP

The dominant adult male (FT) was involved in 367 sociosexual bouts while the high ranking subadult male (PP) participated in 242 bouts and the lowest ranking subadult male (PA) in 91 bouts. There were significant differences in participation in heterosexual behaviour by those three males ( $X^2=164.0$ ; 2df;  $p<0.001$ ) in relation to their respective ranks (FT>PP>PA). The two adult subordinate males RN (11 bouts) and FY (19 bouts) did not differ ( $X^2=2.133$ ; 1 df; NS) and both were hardly ever observed interacting with an adult female. A more detailed analysis of the number of mounts in which each pair participated in will be done in the next section.

In the Cage, the middle ranking adult male RN directed 2 out of 11 instances of sociosexual behaviour towards an adult female of the free-ranging troop (AT) (following her). Of the rest, only once did a female (XA) sexually present to RN and he responded by avoiding her. On 7 occasions RN approached a female (6 times the lowest ranking female and once the middle ranking female) and inspected her genitalia. In his interaction with a middle ranking female (MC), RN inspected her genitalia and his testes abducted. Finally, RN once smelled where a female (XA) had been sitting after a sexual interaction with PP.

Figure 7.2 (next two pages).

Sociosexual behaviour observed for each female in the Cage Troop with adult males FT (●), RN (★) and FY (★), subadult males PP (★) and PA (★) of the same troop and preliminary behaviour that involved adult males MD (▽) and MO (Δ) or juvenile males (□) of the neighbouring free-ranging troop(AT) (the rest as for Figure 7.1),



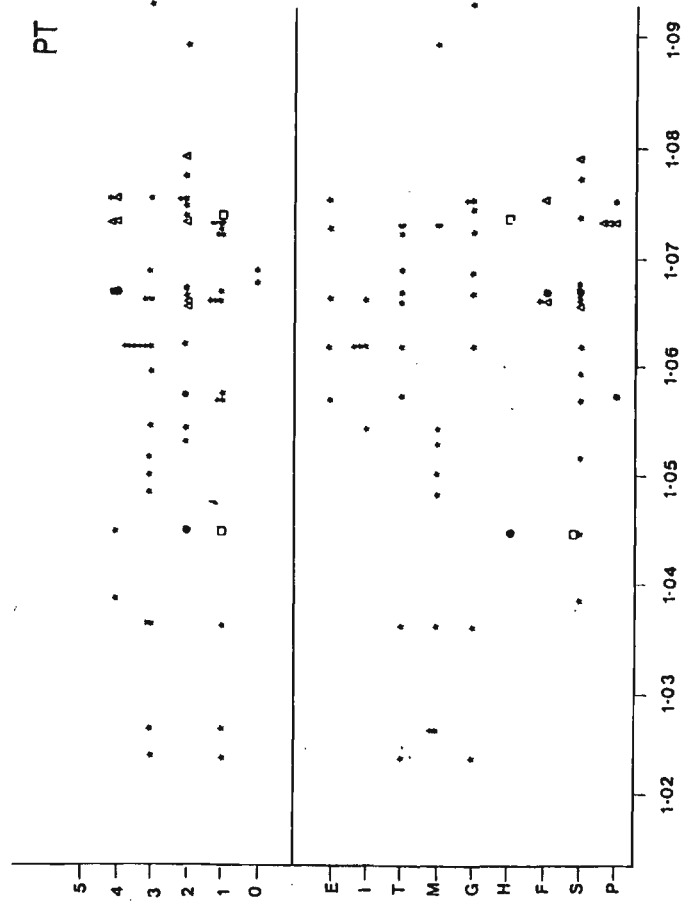
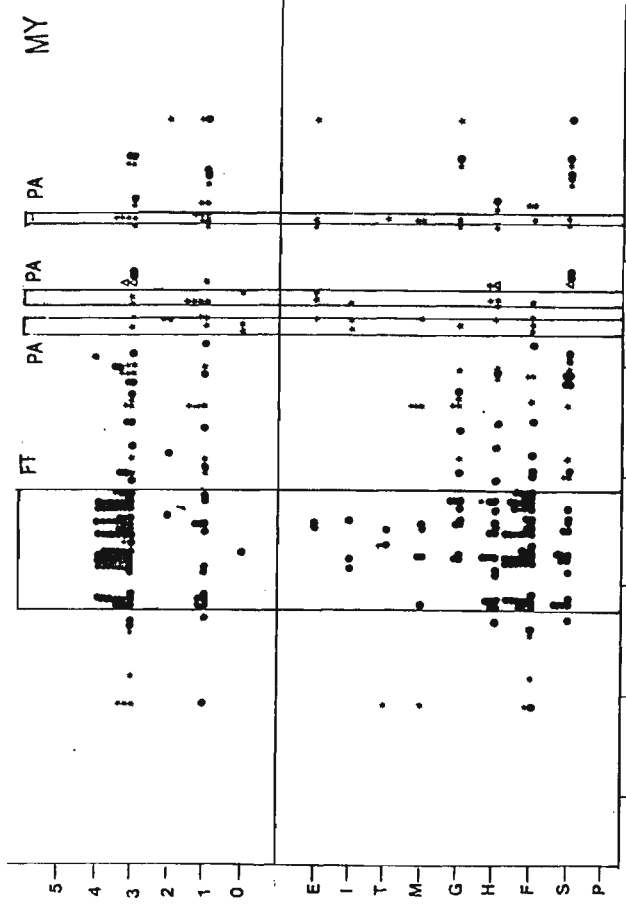
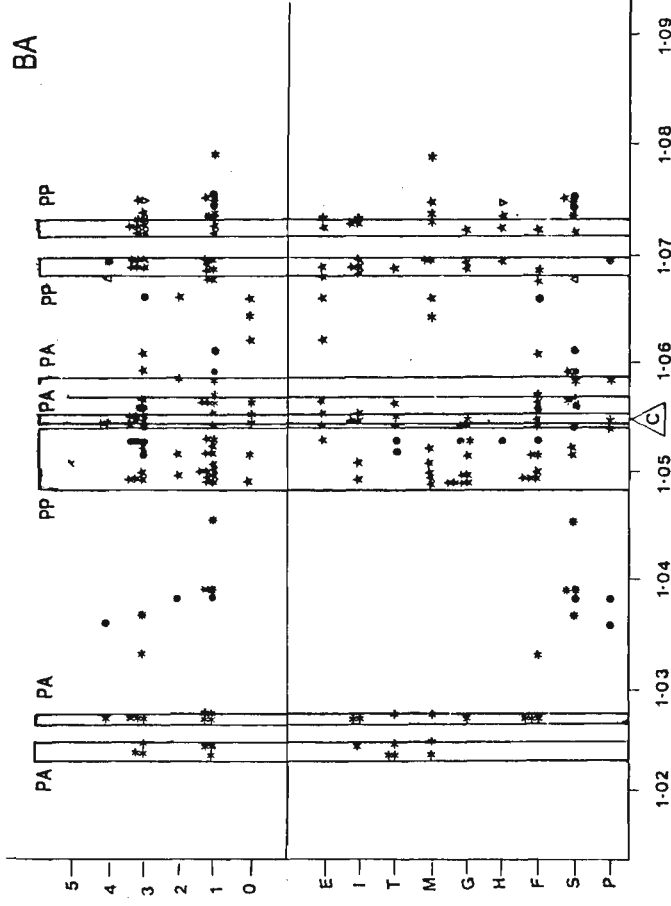


Table 7.1

Responsibility for initiating and maintaining sociosexual relationships for each heterosexual dyad of the caged vervet monkeys. Female (FF) versus male (MM) initiated bouts of sociosexual interaction. The Binomial test was used to determine significant differences (two-tailed test; probability set at 0.5; \*\*  $p < 0.001$ ; \*  $p < 0.05$  and NS: non significant). Pairs of animals that seldom interacted in a sexual context or interactions involving a male of the free-ranging troop (AT) have only been included in the total.

FEMALE	MALE	FF	MM	
XA	FT	44	57	NS
	PP	28	10	**
	total	75	68	NS
CE	FT	15	24	NS
	PP	5	7	NS
	total	21	32	NS
MC	FT	3	26	**
	PP	5	31	**
	PA	1	12	*
	total	9	70	**
MY	FT	2	166	**
	PP	1	32	**
	PA	2	23	**
	total	6	223	**
BA	FT	3	13	*
	PP	4	29	**
	PA	3	24	**
	total	11	73	**
PT	FT	3	0	?
	PP	12	29	*
	PA	3	9	NS
	total	26	38	NS

In the case of FY (the lowest ranking adult male), 15 out of 19 sociosexual bouts involved a female from the other troop (AT) and consisted of persistent following of her and inspection of her genitalia. Once after FY touched the spot where the female had been sitting and smelled his finger, he began jerking his penis, which was quite a rare event for him. On another occasion when MY approached FY and touched his genitalia, FY began jerking his scrotum. When the nulliparous female (PT) approached FY and sexually presented to him, FY developed a mild erection and did not proceed further than grooming her genitalia. Both MY and PT groomed FY afterwards. Thereafter, FY approached an adult female of his troop only twice (BA and CE) and merely inspected her genitalia.



The two highest ranking adult females of the captive troop initiated as many sociosexual bouts as their male partners (Binomial test; two-tailed probability of 0.5; NS). The exception was XA's interactions with the highest ranking subadult male (PP); here the dominant female initiated more bouts than the subadult male (see Fig. 7.2). In contrast, middle and low ranking females were more often approached by males than *vice versa* (Binomial test; two-tailed probability set at 0.5; all  $p < 0.001$  except for BA/FT:  $p < 0.05$ ) (Table 7.1).

The nulliparous female (PT) presumed to be the top ranking female's daughter mainly interacted with the highest ranking subadult male (PP), who was mostly responsible for their sexual interactions (Binomial test: two-tailed probability set at 0.5;  $p < 0.05$ ). This young female showed a great deal of interest (7 out of her 26 self initiated bouts) in the leader of the neighbouring free-ranging troop (MD). PT persistently followed MD (once), sexually presented ( $N=3$ ) and did a visual-tactile inspection of MD's genitalia ( $N=3$ ). MD merely inspected PT's genitalia on two occasions (tactile and olfactory) and completely ignored her the rest of the time.

### 7.3. MALE AND FEMALE MATE CHOICE

Responsibility for initiating sociosexual bouts in the Cage Troop has been analysed above (Table 7.1). The focus in this section will be on emphasising individual male and female differences in attractivity, receptivity and proceptive behaviour.

The Chi-square test was used to detect differences between the observed and expected frequencies of interaction for each male with the females. This was undertaken for: i) female receptivity, *i.e.* female started or willingly accepted a male's sexual approach that culminated in a complete mount; ii) female attractivity, *i.e.* male sexually approached the female (successfully or not) or accepted female's sexual presenting; and iii) female proceptive behaviour *i.e.* when the female spontaneously presented to the male (see Johnson & Phoenix, 1977; Blaffer Hrdy & Whitten, 1987).

#### 7.3.1. Female receptivity

When analysing individual differences in female receptivity, it was found that PP was the preferred male sexual partner (FT/PP/PA:  $X^2=44.4$ ; 2 df;  $p < 0.001$  and FT/PP:  $X^2=21.429$ ; 1 df;  $p < 0.001$ ). This was true for the middle ranking (MC), lowest ranking (BA), postreproductive (MY) and nulliparous (PT) females (see Fig. 7.3 and Table 7.2).

The top ranking female (XA) shared an equivalent number of complete mountings with PP and FT, and none with PA (Fig. 7.3). The second ranking female (CE) was only observed being mounted (with the male performing regular pelvic thrusts) three times, twice with FT and once with PP.

FT's sexual success was comparable to that of PA ( $X^2=1$ ; 1 df; NS) with at least the three lowest ranking and the nulliparous females (Fig. 7.3), but the highest ranking female (XA) preferred FT to PA. The second ranking and primiparous female (CE) was only observed being mounted by PA, who performed irregular pelvic thrusts and intromission was not clearly seen.

The only receptive females FT mated with were the two highest ranking females (XA and CE). However, all the females were equally receptive to the high ranking subadult male (PP) ( $X^2=9.333$ ; 5 df; NS). The lower ranking subadult male PA's receptive female mate partners were the middle ranking (MC) and the post-reproductive female (MY). Finally, the other two subordinate adult males (RN and FY) never attempted to mount females.

### **7.3.2. Female attractivity**

To assess the attractiveness of each female, the number of times a male initiated a copulation or accepted the sexual present by a female and mounted her were analysed. This measure partly reflects male's preferences for individual females.

Overall, a similar pattern to the one obtained for female receptivity was found for attractivity. The three males that expressed sexual interest in the females of their own troop ( $X^2=44.136$ ; 2 df;  $p<0.001$ ) differed. The high ranking subadult male PP was more attracted to females than the dominant adult male FT ( $X^2=22.345$ ; 1 df;  $p<0.001$ ) and FT showed the same interest in mounting females as the low ranking male PA ( $X^2=0.889$ ; 1 df; NS). The other remaining two adult males were sexually inactive.

Female differences in attracting males were found for almost all the females of CT. The top ranking female's attractivity did not differ for PP and FT, although PA never attempted to mount her (Fig. 7.4). The middle ranking (MC) was more attractive to PP than to other males and differences between the other two males were not noted. The lowest ranking female (BA) was more attractive to the subadult males (more to PP than to PA), while the nulliparous female was a source of sexual interest only to

PP. Therefore MC, BA and PT were more attractive to PP than to the other males. The highest ranking female was attractive to both FT and PP. Finally, the post-reproductive female (MY) was attractive to all of them (Fig. 7.4).

The three sexually active males preferred some females to others: FT ( $X^2=12.5$ ; 5 df;  $p<0.05$ ) was inclined to mount the post-reproductive female (MY) and the reproductive XA and CE were the only other females he was attracted to and successful with. The subadult PP was attracted to all the females of his group, and special attention was paid to the lowest ranking (BA) and nulliparous female (PT). The dominant female (XA) was next and finally, the post reproductive (MY) and middle ranking (MC) females were more attractive than the second ranking - primiparous- female (CE) ( $X^2=20.876$ ; 5 df;  $p<0.001$ ). PA, the lowest ranking of the three males observed mating, was sexually interested in the lowest ranking female (BA), and some effort was made to mate with the two next ranking females (MY and MC) ( $X^2=10.5$ ; 2 df;  $p<0.05$ ).

### **7.3.3. Proceptive behaviour**

The concepts of female receptivity and attractiveness can be better understood if female proceptive behaviour are analysed separately. A female is defined as proceptive when she tries to initiate copulation by sexually presenting to the male.

Differences among females in initiating a complete sexual mounting were found ( $X^2=13.33$ ; 5 df;  $p<0.05$ ). The highest ranking female (XA) was the female that showed more self-initiated successful mountings. XA initiated 4 sexual interactions with FT and 11 with PP ( $X^2=3.125$ ; 1 df;  $p=0.08$ ). PT was the second female most responsible for initiating sexual mounting (see Fig. 7.5). The other females did so very seldom and statistical analysis was not possible.

Additionally, female choice was found to be apparent: i) the two top ranking females presented to FT and PP but not to PA; ii) the lowest ranking and the nulliparous to PP only; and iii) the post-reproductive female to FT and PA only.

When considering all the females from the Cage Troop together, male individual differences were obtained for female solicitation of males ( $X^2=10.600$ ; 2 df;  $p<0.05$ ). Although FT (4 times) and PP (11 times) did not differ as female elected male partners ( $X^2=3.125$ ; 1 df; NS), nor did PA (once) and FT ( $X^2=1.667$ ; 1 df; NS), but the 2 subadult males differed ( $X^2=8.333$ ; 1 df;  $p<0.05$ ).

Table 7.2

Female differences between observed and expected frequencies of mount with insertive thrusts for the adult (FT) and subadult males (PP and PA) of the Cage troop. The other two adult males have not been included because they were never observed involved in heterosexual mountings. The rest is as for table 7.1. AA: male attracted to the female; RR: female receptivity.

MALE		N	$\chi^2$
FT	AA	11	12.5 (2) *
	RR	6	12.0 (2) *
PP	AA	47	20.9 (5) **
	RR	36	9.3 (5) NS
PA	AA	7	10.5 (2) *
	RR	3	??

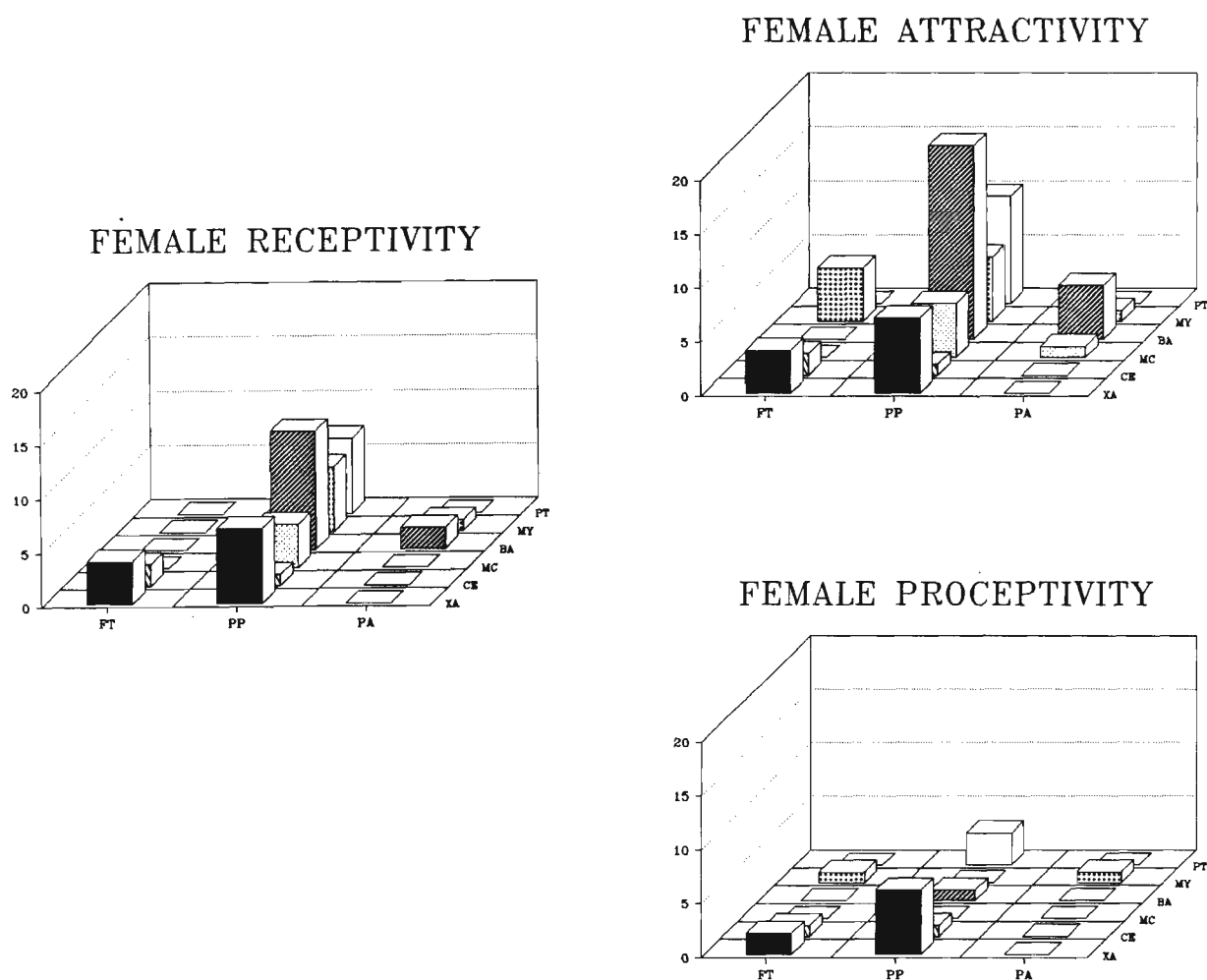


Figure 7.3. Female receptivity, attractivity and proceptive behaviour directed towards the adult male (FT) and subadult males (PP and PA) of the Cage Troop. Reproductive females are ordered in decreasing rank, the post-reproductive female (MY) and the nulliparous female (PT) are next.

## 7.4. GENITAL INSPECTION

All the observations of genital inspection obtained in the Cage have been related to the total number of sociosexual contacts. Unfortunately, data from the Windy Ridge was too scarce to allow any analysis.

### 7.4.1. Female differences in genital inspection by males

As has been mentioned above, subordinate females do not initiate the same proportion of sexual bouts with males as do more dominant females (see Table 7.1). It can be inferred, therefore, that when females do not show any signs of proceptivity, males must rely on other non-behavioural cues and inspect the females' genitalia more often in order to assess their reproductive state.

*Visual:* Males closely looked at some of the females' genitalia during a higher proportion of sociosexual bouts than at others (all females:  $X^2=38.994$ ; 5 df;  $p<0.001$ ). The differences remained when the nulliparous female (PT) was excluded ( $X^2=38.977$ ; 4 df;  $p<0.001$ ), but no differences were found when the two lowest ranking and apparently oldest females (MY and BA) were excluded (XA/CE/PT/MC:  $X^2=4.030$ ; 3 df; NS). Therefore, males visually inspected MY and BA's perineum less often than expected during their sexual encounters (Fig. 7.6).

*Tactile:* Males touched some of the females' genitalia more often than others ( $X^2=31.237$ ; 5 df;  $p<0.01$ ) per sociosexual bout. This is also significant when the nulliparous female (PT) is excluded from the analysis ( $X^2=30.609$ ; 4 df;  $p<0.01$ ). On the other hand, if the two lowest ranking females are not considered, there were no differences amongst the other females (XA/CE/PT/MC:  $X^2=7.548$ ; 3 df; NS). As was found for visual inspection, males in general did not touch (inspect or stimulate) MY and BA's perineum as often as they did those of other females (Fig. 7.6).

*Olfactory:* Smelling of the perineal area by males (without establishing contact with their muzzle) was observed more often when males sexually interacted with some of the females than with others ( $X^2=20.300$ ; 5 df;  $p<0.001$ ). This was still true when excluding the two lowest ranking females (XA/CE/PT/MC:  $X^2=15.259$ ; 3 df;  $p<0.05$ ). The second ranking primiparous female (CE) accounted for a higher proportion of olfactory genital inspection than any other female (All except CE:  $X^2=8.365$ ; 4 df; NS), while the nulliparous (PT) accounted for the lowest

proportion (Fig. 7.6). Finally, the argument that certain olfactory cues in the female's perineum exist, is reinforced by observations of males smelling the spot where the female had been sitting and having done so, becoming sexually aroused.

*Muzzling*: The same female individual differences in genital inspection that obtained for tactile and visual modalities were repeated for muzzling (all females:  $X^2=31.445$ ; 5 df;  $p<0.001$ ; only adult females  $X^2=29.612$ ; 4 df;  $p<0.001$ ). When the two lowest ranking females are excluded (XA/CE/PT/MC:  $X^2=2.785$ ; 3 df; NS) no differences were detected (Fig. 7.6).

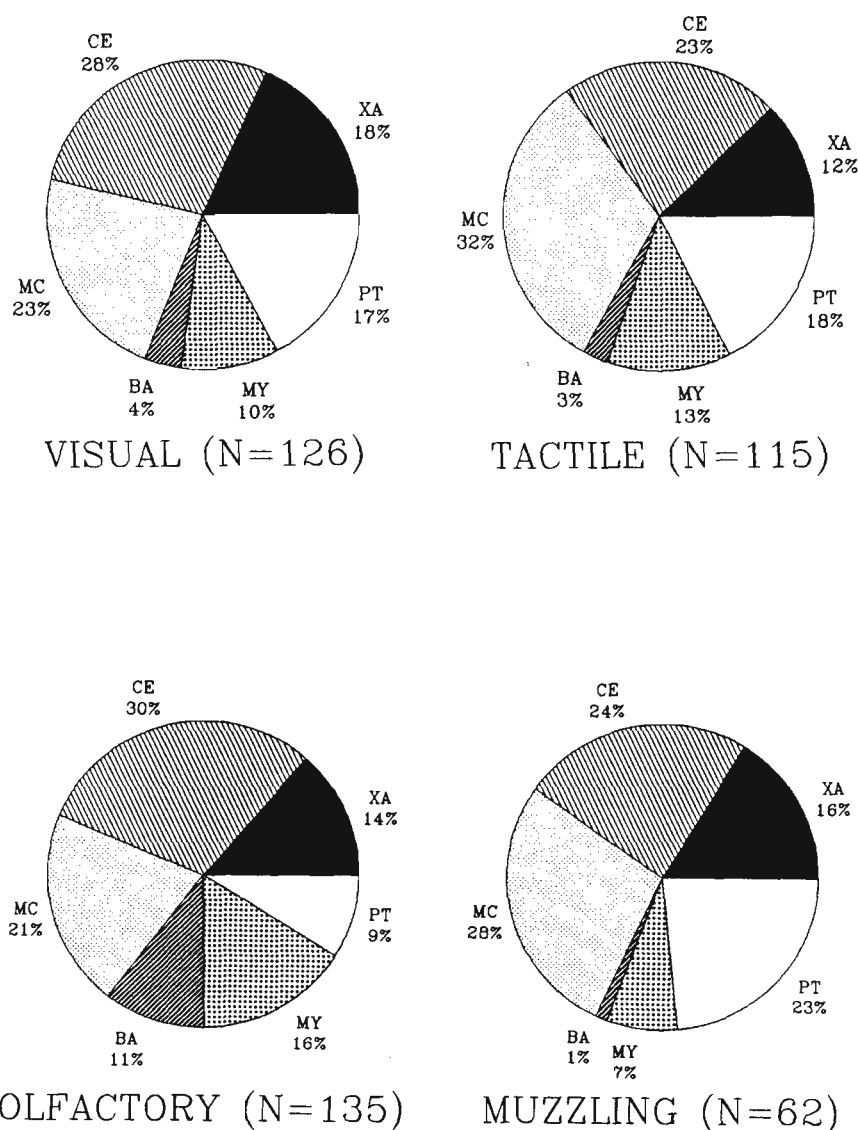


Figure 7.4. Male inspection of female genitalia. The reproductive females rank order was  $XA>CE>MC>BA$  and MY was a post-reproductive and PT a nulliparous female. The slices represent the proportional contribution of each female (corrected by total number of sociosexual bouts she was involved in) to the total genital inspection performed by males. The total number of bouts that involved visual, tactile, olfactory inspection and/or muzzling are given (N).

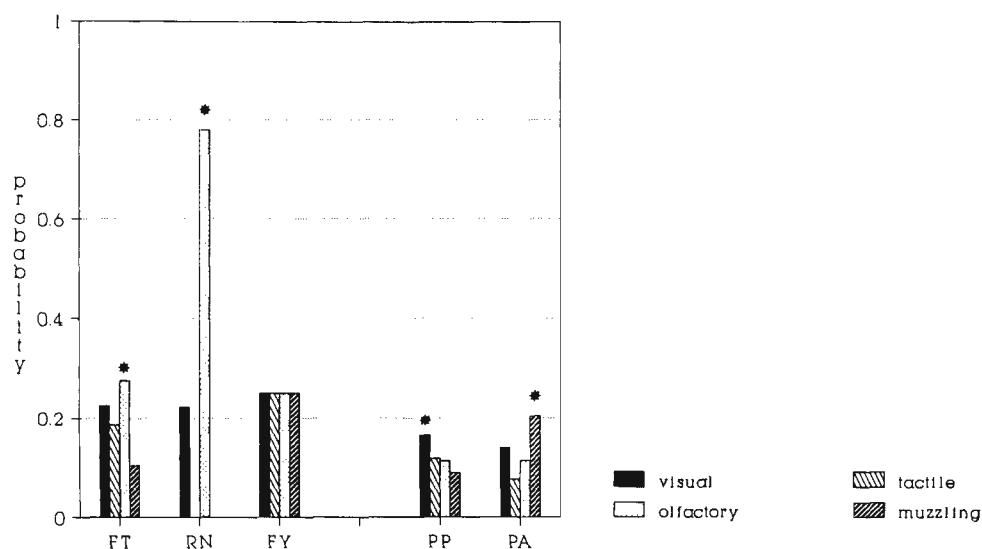


Figure 7.5. Probability that a male sociosexual bout involved visual, tactile, or olfactory inspection or muzzling of the female's genitalia. The most common form of genital inspection used by the adult male FT and the subadult males PP and PA is shown. Differences were tested with the Chi-square test, with the probability set at 0.05. FT and RN used olfactory inspection the most, PP visual and PA muzzling.

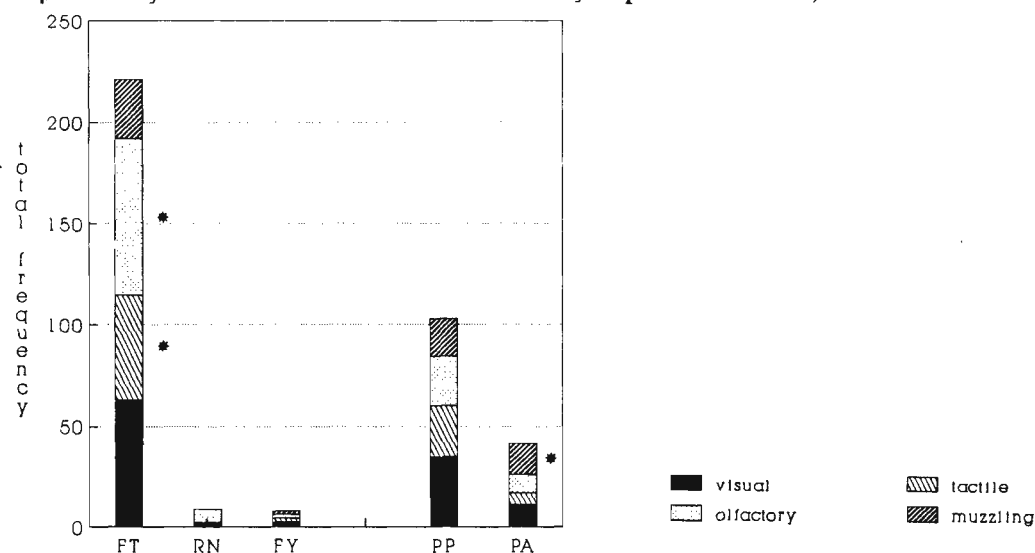


Figure 7.6. Total frequency of visual, tactile, olfactory and muzzling inspection of the female's genitalia performed by the adult male (FT) and subadult males (PP > PA). Intra-male differences tested with the Chi-square test ( $P < 0.05$ ) showed that there were not significant for visual inspection; tactile and olfactory inspections were more common for FT; and muzzling more frequently shown by PA than by other males.

Although low ranking females initiated fewer sociosexual bouts than their male partners, the results obtained for visual, tactile and muzzling inspection show that males did not check their genitalia more intensively than that of their higher ranking counterparts. In addition, the young, second ranking female was the female who received more olfactory inspection per sociosexual contact. A complicating factor is that the lowest ranking females were also the oldest females, so that age-related attractiveness cannot be excluded.



When looking at the proportion of sociosexual bouts that involved visual, tactile, olfactory and/or muzzling for each female, it was found that the highest ranking female (XA) received less muzzling than any other form of genital inspection ( $X^2=8.290$ ; 3 df;  $p<0.05$ ) and no differences were noted for the other three patterns ( $X^2=3.518$ ; 2 df; NS). The post-reproductive female (MY) also received less muzzling than expected ( $X^2=23.658$ ; 3 df;  $p<0.001$ ; muzzling excluded:  $X^2=4.164$ ; 2 df; NS). The second ranking female showed the same tendency, although without significant differences ( $X^2=7.539$ ; 3 df;  $p=0.056$ ). The nulliparous (PT:  $X^2=3.724$ ; 3 df; NS) and the middle ranking (MC:  $X^2=2.786$ ; 3 df; NS) females received the same amount of each type of genital inspection. In contrast, the lowest ranking female's genitalia were mainly inspected by smelling ( $X^2=19.841$ ; 3 df;  $p<0.001$ ) and the same proportion of bouts involved any of the other patterns of inspection ( $X^2=3.558$ ; 2 df; NS).

Therefore, it can be concluded though even that behavioural and other signals may complement each other, they do not exclude each other.

#### **7.4.2. Male differences in inspection of females' genitalia**

Individual male differences in the proportion of sociosexual interactions that involved visual, tactile, olfactory and muzzling of the female's genitalia (see Fig. 7.4) will be analysed in this section. The participation of the two lowest ranking adult males (RN and FY) in heterosexual activities was so small (9 and 4 bouts respectively) that they will only be included in the general comparison. When significant differences among males were found, a more detailed analysis was carried out in order to distinguish between the rates obtained for the top adult male (FT) and the two subadult males (PP dominant to PA).

*Visual:* Males did not differ in the proportion of sociosexual bouts that involved visual inspection of the female genitalia and no differences in the rate of male sociosexual behaviour that involved visual inspection of the females' genitalia were found (22.6% of FT's; 16.6% of PP's and 14.1% of PA's sociosexual bouts:  $X^2=6.700$ ; 4 df; NS).

*Tactile:* Some males showed a higher tendency towards touching the females' perineum than others ( $X^2=285.69$ ; 4 df;  $p<0.001$ ). The dominant male engaged in tactile inspection in a higher proportion of his sociosexual bouts (18.6%) than the subadult males (11.8% and 7.7%) (FT/PP:  $X^2=3.685$ ; 1 df;  $p<0.05$ ). The subadult males did not differ ( $X^2=0.639$ ; 1 df; NS).



*Olfactory*: Intermale differences were highly significant ( $X^2=43.533$ ; 4 df;  $p<0.001$ ). Smelling the females' genitalia occupied a higher percentage of FT's sexual contacts (27.6%) than those of the subadult males (11.4% for PP and 11.5% for PA) (FT/PP:  $X^2=18.347$ ; 1 df;  $p<0.001$ ). However, PP and PA did not differ ( $X^2=0$ ; 1 df; NS).

*Muzzling*: Direct contact between the male's muzzle and the female's genitalia was more commonly found for PA when engaged in sociosexual behaviour with females (20.5%) than for either PP (9.0%) or FT (10.4%) ( $X^2=14.995$ ; 4 df;  $p<0.05$ ). This pattern of genital inspection was as common for FT as for PP ( $X^2=0.129$ ; 1df; NS).

It can be established from this data that males do show considerable interest in the female's genitalia. Whether they obtain sufficient information from it to determine the reproductive state of the female is not yet known. Some of the males rely more heavily on one or some of their senses during inspection of the female's genitalia (Fig. 7.5).

The dominant adult male (FT) used certain patterns of genital inspection more than others ( $X^2=27.822$ ; 3 df;  $p<0.001$ ). FT used muzzling the least (10.4%) and smelling the most (27.6%). No differences were obtained for visual and tactile inspection (22.6% and 18.6% respectively:  $X^2=1.095$ ; 1 df; NS).

The differences obtained for the second ranking adult male (RN) were not statistically very reliable ( $N=9$ ), although they were significant ( $X^2=19.407$ ; 3 df;  $p<0.001$ ). Smelling prevailed over visual inspection and no touching or muzzling of the female's genitalia were ever observed. His reaction to an approaching female was generally fear and uneasiness (looking around).

The higher ranking subadult male (PP) visually inspected (16.6%) slightly more than muzzled (9%) the female's genitalia ( $X^2=4.778$ ; 1df;  $p<0.05$ ). However, when comparing the above with tactile inspection (11.8%) and smelling (11.4%), no statistical significance was obtained ( $X^2=5.960$ ; 3 df; NS).

Contrasting results were found for the second subadult male (PA). PA muzzled (20.5%) more often than touched (7.7%) the female's genitalia ( $X^2=4.286$ ; 1df;  $p<0.05$ ), although when comparing those to visual (7.7%) and olfactory inspection (11.5%), there were no differences ( $X^2=5.833$ ; 3 df; NS).

## 7.5. BEHAVIOUR PRIOR TO AND FOLLOWING A SOCIOSEXUAL BOUT

Sociosexual encounters that occur in sequence will be reviewed first. Repeated attempts to mate or inspect the partners genitalia is probably more frequently found among younger males or within a sexual consortship. Next, the frequency with which individual adult males interact in a friendly way with a female partner prior to attempting a sexual contact will be analysed. As female choice might be overridden when the males are aroused for other reasons, the sociosexual bouts preceded by an agonistic or alarm situation will be determined. The point is to analyse the main motivation for each male-female pair to be involved in a sexual interaction.

In the last section I will focus on the behaviour that follows a sexual bout for each male, and when enough data is available for each male-female dyad. Individual differences in affiliative behaviour could be explained as a result of consortship relationships.

### 7.5.1. Sociosexual behaviour in series

Sociosexual interactions consisted of a sequence of sexual bouts more often for the subadult male PP (41.1%) than for FT (29.5%) or PA (24.0%) (all:  $X^2=7.439$ ; 2df  $p<0.05$ ; PP/FT:  $X^2=4.820$ ; 1 df;  $p<0.05$ ; PP/PA:  $X^2=3.977$ ; 1 df;  $p<0.05$ ). However, no significant differences were found when comparing FT and PA ( $X^2$ ; NS).

When looking at the data on the sequences of sociosexual behaviour for FT, clear differences were observed in his relationships with MY (48.1%) when compared with the adult females XA (12.5%), CE (17.4%), MC (5.3%), BA (22.2%) and primiparous PT (none out of 3) female (MY/other females:  $X^2=31.991$ ; 1 df;  $p<0.001$ ) (see Table 7.3). For PP, the proportion of bouts of sociosexual behaviour that followed another bout of the same nature when interacting with XA (43.3%), CE (16.7%), MC (35.0%), BA (53.7%), MY (40.9%) and primiparous female PT (29.6%) did not differ statistically ( $X^2$ ; NS) (see Table 7.3 for raw values). The subordinate subadult male (PA) showed a low proportion of sociosexual behaviour in series, and did not show significant female differences; MC (25%), BA (25%), MY (28.6%) and PT (14.3%) ( $X^2$ ; NS).

The dominant males of both study troops did not differ in the proportion of sociosexual behaviour that occurred in series (RO/FT:  $X^2$ ; NS; see Table 7.3).

### **7.5.2. Proportion of sociosexual bouts preceded by affiliative interactions**

When all friendly and sexual behaviour that involved a male-female pair prior to a sociosexual bout were combined (MG+FG+SF+SE: Table 7.3) no significant differences were found for FT, PP and PA ( $X^2$ : NS). If sociosexual behaviour is excluded from the analysis, FT (15.2%), PP (13.7%) and PA (34.0%) differed in time spent interacting (grooming included) with their mate ( $X^2=11.946$ ; 2 df;  $p<0.05$ ). In other words, the lowest ranking male (PA) of those showing heterosexual behaviour, dedicated more time to his sexual partner than the other two males prior to engaging in a sociosexual behaviour.

These differences were mainly reflected in the number of times PA interacted in a friendly way (grooming not included) with a female prior to attempting a sexual interaction (PA: 24%; PP: 5.5% and FT: 4.0% ;  $X^2=26.098$ ; 2 df;  $p<0.001$ ), though FT (9.4%), PP (6.2%) and PA (10%) groomed their female partners prior to the sociosexual bout at comparable rates ( $X^2$ : NS).

Female individual differences for each male could only be statistically tested for PA, who did not groom and/or interact in a friendly way with any one of his female sexual partners more often than others prior to being involved in a sociosexual behaviour ( $X^2$ : NS). PP groomed females at different rates; XA (never out of 30 recorded instances), CE (16.7%), MC (20%), BA (7.6%), MY (never out of 22 recorded instances) and PT (3.7%) ( $X^2=11.556$ ; 5 df;  $P<0.05$ ). The females also differed in the proportion of time they interacted (MG+FG+SF) with PP prior to a sexual interaction ( $X^2=16.906$ ; 5 df;  $P<0.05$ ), while MC and PT showed the highest proportions (30% and 29.6% respectively) and XA (none out of 30) the lowest (Table 7.3).

The dominant adult male of the Cage troop (FT) interacted in an affiliative fashion with the adult females MC (31.6%), MY (17%) and XA (14.1%) ( $X^2$ : NS) prior to being involved in a sexual context, but not with the other females. When considering grooming alone, the differences were still not significant for MC, MY and XA ( $X^2$ : NS).

The dominant adult male of the Windy Ridge troop was not engaged more often in an affiliative interaction (MG+FG+SF) with his female sexual partner prior to sociosexual behaviour (19.4%) than his caged counterpart (15.2%) or the dominant subadult male of the Cage troop (13.7%) ( $X^2=1.881$ ; 2 df; NS).

### **7.5.3. Do agonistic and alarm contexts prompt sex in some males more than in others?**

It was expected that the dominant male of each troop would be involved in more sexual activity when the level of arousal had peaked due to intra or intertroop agonism or other alarm situations.

In the Cage, no significant differences were found for FT (19.2%), PP (15.8%) or PA (8%) (all combinations:  $X^2$ ; NS). FT sexually approached XA (39.1%) more often than CE (21.7%), MC (21.1%), MY (8.5%) or any other female in a stressful situation ( $X^2=26.114$ ; 4 df;  $p<0.001$ ). During a stressful situation, PP mostly approached XA (30%) and BA (22%) rather than CE (16.7%), PT (11.1%), MC (5%) or MY (none out of 22 bouts) ( $X^2=12.073$ ; 5 df;  $p<0.05$ ). For PA no differences could be tested (there were only 4 bouts).

In Windy Ridge, alarm and agonistic contexts prompted sexual behaviour only for the dominant male (31.9% of all his sexual bouts; 23 out of 72). The exception which involved LE (once in 15 bouts), occurred when the female had been threatening an infant (Table 7.3). Moreover, the chances for each female of being involved in a sociosexual bout with the dominant male in these situations, were the same ( $X^2$ ; NS, considering their total number of sexual bouts with RO).

The dominant adult male of the wild troop was more often sexually prompted by agonism or alarm situations (31.9%) than the dominant adult male of the confined troop (19.2%) ( $X^2=26.767$ ; 1 df;  $p<0.001$ ).

### **7.5.4. Does a sexual interaction incite sex among others?**

The alpha male of the Windy Ridge Troop only showed sexual behaviour after another sexual bout had occurred involving at least one other member of the troop, on three occasions: twice when the top ranking adult female interfered with his ongoing sexual interaction and sexually presented to him (once she was successful and he achieved ejaculation, on another occasion RO ignored HI and they fed together) and once after RO interrupted his subordinate LE who was following WE (middle ranking female) RO then followed her in turn.

The subadult male TI was once seen grooming HI's perineum and muzzling it. TI then approached TO and grabbed her hips TO did not assume the adequate mounting position and TI was forced to leave her. Finally, TI approached the 2 year-old male (FE) and mounted him.

In the Cage, where visibility was excellent, it was difficult for a male-female pair to conceal their activities. The proportion of time that the dominant male (18.8%), the higher ranking subadult male (14.4%) and the lowest ranking subadult male (24%) expressed a sexual interest in females, either after interaction with another female, or after the female was the source of sexual interest by another male, were similar ( $X^2$ ; NS) (see OS in Fig. 7.3).

FT mostly interacted with BA (55.6% of the times) in a sexual context involving at least another male or another female; CE (39.1%), MC (26.3%) and XA (20.3%) showed intermediate values and MY (7.5%) the lowest ( $X^2=24.420$ ; 4 df;  $p<0.001$ ). The fact that BA accounted for most of those interactions, emphasises the low level of sexual interest FT had in this particular female.

Similar results were obtained for PP. The post-reproductive female MY (27.6%) was the female PP approached more often in those occasions; MC (20%), PT (18.5%), XA (10%) and on BA (2.4%) less often ( $X^2=9.447$ ; 4 df;  $p<0.05$ ).

Finally, no female individual differences in proportion of sexual bouts initiated after a sexual interaction involving at least one other animal, were found for PA ( $X^2$ ; NS).

In summary, it seems that PA invested more time 'being friendly' with his sexual partner, while PP spent more time involved in sociosexual behaviour and FT was primarily involved in maintenance activities (not shown in the Table 7.3). The exception was FT's interaction with MY (MY/other females:  $X^2=31.991$ ; 1 df;  $p<0.001$ ), the post-reproductive female for whom FT showed 48.1% of sociosexual behaviour in series and 17% preceded by affiliative behaviour (see MG,FR and SF in Table 7.3).

Table 7.3

Context preceding sociosexual activities for male (MM) and female (FF) in the Cage Troop (CT) and in Windy Ridge Troop (WT). N: number of sociosexual bouts where the context could be determined: (MG) male grooms female; (FG) female grooms male; (SF) other social friendly behaviour or remaining in proximity; (AR) agonistic or alarm context; (SE) sociosexual behaviour with the same mate; (OS) sex involving one of them prior to interaction. Male differences were estimated with the Chi-square test (NS: non-significant; \*  $p < 0.05$  and \*\*  $p < 0.001$ ; ? not determined).

MM	FF	N	MG	FG	SF	AR	SE	OS
CT)								
FT	XA	64	6	1	2	25	8	15
	CE	23	0	0	0	5	4	9
	MC	19	2	2	2	4	1	5
	MY	106	13	0	5	9	51	12
	BA	9	-	-	-	-	2	6
	PT	3	-	1	-	-	-	2
	all	224	9.4	1.8	4.0	19.2	19.2	21.9
PP	XA	30	0	0	0	9	13	4
	CE	6	1	-	-	1	1	2
	MC	20	4	1	1	1	7	5
	MY	22	0	0	2	0	9	7
	BA	41	3	0	0	9	22	4
	PT	27	1	2	5	3	8	8
	all	146	6.2	2.1	5.5	15.8	41.1	20.6
PA	XA	1	-	-	-	1	-	-
	CE	0	-	-	-	-	-	-
	MC	8	3	-	1	-	-	3
	MY	14	1	0	4	1	4	3
	BA	20	1	0	4	2	5	7
	PT	7	-	-	3	-	1	3
	all	50	10.0	-	24.0	8.0	20.0	32.0
Male differences			NS	?	**	NS	*	**
WT)								
RO	all	72	7	0	7	23	4	3
LE	all	15	1	2	1	1	2	0
TI	all	11	4	0	0	0	2	2
Male differences			?	?	?	**	NS	?

### **7.5.5. Behaviour that commonly follows a male-female sexual interaction**

The behaviour which immediately followed a male-female sociosexual bout is analysed here to determine if male-female pairs form consort relationships, groom and/or maintain proximity after a sociosexual bout more often than other pairs (Table 7.6).

Females might threaten their male partners after the occurrence of a sociosexual bout. The subadult male PP (28.4%) was threatened more often by the female he had been interacting with, and the dominant male less often than expected (17.3%) while the lowest ranking subadult male PA showed intermediate values (21.4%) ( $X^2=7.547$ ; 2 df  $p<0.05$ ). On the other hand, males hardly if ever threaten their female partners after these bouts; FT, 4 times out of 248 sociosexual bouts; PP twice out of 183; PA never after 56 bouts.

For the Windy Ridge males, significant differences in the rate of female aggressive behaviour after a sociosexual interaction were found ( $X^2=9.970$ ; 2 df;  $p<0.05$ ). However, when the subadult male was excluded, there were no differences (RO/LE: Fisher's exact test; NS). The tendency found for the dominant male of the Cage Troop was repeated. The dominant adult male was less threatened by females than the subordinate and subadult considered together (Fisher's exact test:  $p<0.05$ , two-tailed test). Only once was a male (RO) of this troop observed threaten a female after a sexual interaction.

The female walking or running away from the male could also be classified as a negative reaction. In the Windy Ridge troop, RO (9.7%) did not elicit this reaction more often than the other two males (none after LE's 15 bouts and 3 times after TI's 11 bouts) (RO/LE+TI:  $X^2$ ; NS).

Similar results were found for the Cage Troop; FT's sexual approaches ended with the female walking or running away (10.9%) as often as for PP (7.1%) and PA (3.6%) (Table 7.4).

Affiliative behaviour occurring after a sexual interaction (genital inspection and other preliminary sexual behaviour included), denote a friendly attitude for both participants, which together with high rates of proximity are characteristic of sexual consortships.

Table 7.4

Behaviour that follows sociosexual activities for male (MM) and female (FF) caged (CT) and free-ranging (WT) vervet monkeys. N: number of sociosexual bouts where the context could be determined. The rest as for Table 7.3, except for (FA) female walks or runs away; (FT) female threatens male.

	MM	FF	N	MG	FG	SF	AR	FA	FT	OS
<b>CT)</b>										
FT	XA		73	11	0	8	7	4	13	26
	CE		23	3	1	4	1	2	4	6
	MC		19	5	3	0	1	0	3	4
	MY		121	32	3	6	8	19	23	48
	BA		9	1	0	3	1	2	0	1
	PT		3	0	3	0	0	0	0	0
	all		248	52	10	21	18	27	43	84
PP	XA		31	5	1	2	4	1	6	10
	CE		9	2	0	0	1	0	3	2
	MC		27	5	0	2	2	3	5	9
	MY		30	2	0	2	2	3	9	10
	BA		54	7	1	2	1	0	18	18
	PT		32	0	3	3	0	6	11	8
	all		183	21	5	11	10	13	52	57
PA	XA		0	-	-	-	-	-	-	-
	CE		0	-	-	-	-	-	-	-
	MC		8	4	0	0	0	0	2	2
	MY		18	6	0	4	1	0	5	1
	BA		23	9	0	4	2	0	3	3
	PT		7	3	0	0	0	2	2	0
	all		56	22	0	8	3	2	12	6
Male differences				**	?	**	?	NS	*	*
<b>WT)</b>										
RO	all		72	5	3	13	11	7	2	7
LE	all		15	3	0	4	0	0	1	1
TI	all		11	1	0	0	0	3	3	4
Male differences				NS	?	NS	?	NS	?	**

Inter-male differences were not obtained in affiliative behaviour that followed a sexual bout in Windy Ridge (RO/LE/TI and RO/LE:  $X^2$ ;NS), nor for male grooming of the female partner (RO/LE/TI and RO/LE:  $X^2$ ;NS). However, very clear differences were obtained for the caged males post-sexual affiliative interactions ( $X^2=24.066$ ; 2 df;  $p<0.001$ ). The dominant adult male (33.5%) was involved more often than the high ranking subadult (20.2%) and less than the low ranking subadult male (53.6%) (FT/PP:  $X^2=8.553$ ; 1 df;  $p<0.05$  and FT/PA:  $X^2=7.069$ ; 1df;  $p<0.05$ ).



### **7.5.6. Sexual consortships**

Sexual consortships are defined in this study in terms of frequent sociosexual contact, following, visual monitoring of the partner and proximity (see p. 219).

#### *Windy Ridge troop*

The dominant adult male was observed on 6 occasions copulating with the dominant female HI from the 5th of April until the 14th of the same month (Fig. 7.1 p.234). Although they were often seen grooming each other and in proximity, when comparing proximity rates at that time with those found for the rest of the mating season statistical significance was not obtained ( $X^2=102.9$ ; 1 df;  $p=0.09$ ). Therefore, if a consort relation existed was for only a few hours per day.

RO consorted with the middle ranking female WE during the 10 and 11th of May and from the 14th until the 16th of the same month. Their proximity relationships were significantly more intense than at other times during the mating season ( $X^2=9.535$ ; 1 df;  $p<0.01$ ) (see Fig. 7.1 p.235). In this case it was apparent that the dominant male was responsible for the consort relation and groomed WE often and approached her immediately whenever the subordinate male was in her vicinity.

An overlap in RO's sexual interest for WE and BE was apparent to the author. On the 12th and 14th of May RO mated with BE and rested in her proximity. However, when analysing the time they spent within 10 m with that found for the rest of the mating season, no differences were found (1.286; 1df;  $p=0.3$ ). Therefore, if a consort relation existed, it only lasted for a few hours. Actually, RO was usually located between BE and LE while resting and moving. BE had spontaneously solicited RO one month earlier which could correspond to the middle of her previous cycle (see p. 223).

The young, low ranking female VE was often approached by RO during resting periods during the 19th-22nd and 25th of May. Although only once they were observed mating, numerous times the dominant male followed the female down a gully and on they return she would autogroom her genitalia while nervously looking around. Often, the lowest ranking female would approach VE and groom her genitalia. An increase in proximity between RO and VE during these days was found ( $X^2=16.931$ ; 1df;  $p<0.001$ ).

Finally, shortly before the study ended, RO was attracted to the lowest ranking female ET, their behaviour was similar to that observed for RO and VE ( $X^2=23.760$ ; 1 df;  $p<0.001$ ).

The subordinate male appeared to maintain a concealed consort relation with ET, the duration of which is difficult to determine but it must be emphasised that RO was unsuccessful in herding LE away from ET on the 19th and 28th of April (see p. 165). The last day RO opted for performing a tree display apparently to ET and other females, away from LE. RO remained between them and LE, shortly afterwards LE paid homage to RO and sat at 5 m of him with his hands covering his own genitalia. Another example was obtained in the 4th of May when ET as well as LE had not been seen with the troop for the whole morning. On their return RO herded ET towards the rest of the females and after displaying his genitalia to LE, he stayed between LE and the rest of the troop. On the 9th of May, RO was seen 'guarding' LE almost all the observation time and this behaviour continued for the period when WE and BE were sexually receptive.

### *Cage troop*

The highest ranking female in the Cage troop was the first one to show signs of sexual behaviour (towards the end of January). On these occasions the dominant male mounted her without ejaculation. Two weeks later, FT showed more sexual interest in her (penile intromission and ejaculation were achieved) although this time she was responsible for maintaining a sexual consortship with him. This relationship lasted for a couple of days at least and another short bout of sexual interaction between FT and XA occurred (see Fig. 7.2 p.238). XA was mostly responsible for initiating this sexual interactions through sexual presenting. About two weeks later when XA was very sick (gastrointestinal disease) FT simply inspected her genitalia a couple of times. After that FT's sexual interest shifted towards MY (see above) and he consorted with her for approximately one month, when they were closer together than at other times during the mating season ( $X^2=10.182$ ; 1 df;  $p<0.001$ ) (Fig. 7.1). Although FT was rather unsuccessful, he constantly followed and attempted to mount MY.

During the last third of April, XA often presented to FT and his sexual approaches towards MY stopped almost completely until the intensive study terminated at the end of July. At the beginning of May, FT consorted with XA's daughter CE ( $X^2=16.760$ ; 1 df;  $p<0.001$ ). After CE's estimated date of conception, FT lost all sexual interest in CE and accepted XA's persistent following and sexual presenting. FT and XA maintained an almost constant sexual consortship from the 5th until the 25th of May. Initially it was the female who was more responsible for the association but after FT stopped his interactions with CE, FT followed XA more often than she followed him. In the middle of July FT and XA formed a pair bond that lasted for six days. In the beginning he was more responsible for maintaining the sexual association but after a couple of days XA mostly initiated their sociosexual interactions. On the estimated date of conception, that is 163 days backdated from the time of birth of her infant (Johnson *et al.* 1973; Bramblett *et al.* 1975), XA shifted her sexual interest from FT to PP (Fig. 7.2. p.226). XA's strategy of switching from one male to another at the time of ovulation could have been an attempt to conceive (she was the last one, possibly due to her long sickness that lasted well into April).

These observations show that the top ranking male of the Cage (FT) maintained sexual consortships with the first ranking female (XA) a few times and for quite a long duration, including a period around the time of conception. The time they spent at 2 m of each other during their consort relations was more than during the rest of the mating season ( $X^2=30.390$ ; 1df;  $p<0.001$ ).

The second ranking female (CE)'s consortship with FT lasted for about 8 days and stopped after conception. It is possible that FT fathered CE's infant and she was never seen interacting with another male; yet 10 days into her pregnancy, she copulated with PP. FT was preferentially closer to XA and CE during the non-mating season, *i.e.* proximity and grooming; these females were suspected to be mother and daughter (see also Melnick & Pearl, 1987, p.131).

Numerous episodes of consort activity were observed for the subadult male PP with the middle ranking female MC and they ranged from 1 to 6 days of duration; during that time they were closer than expected ( $X^2=4.440$ ; 1df;  $p<0.05$ ). PP was the most likely father of her next infant. PP usually accepted PA's presence, possibly to deter the dominant male from interfering. PP mainly associated with MC during the non-mating season (special friendly relationship).

PP also consorted with the lowest ranking female BA and they were the male-female pair that were most often observed mating with ejaculation. PP and BA consorted from the 28th of April until the 13th of May that was around conception time. Once BA was pregnant, PP formed a four days consort relation towards the end of June, and for a two day period during 7-8th of July ( $X^2=6.396$ ; 1 df;  $p=0.01$ ). PA was unsuccessful in his attempts to interrupt their relationship around the time of conception, but successfully stopped a mounting sequence which occurred in November. Meanwhile, PP succeeded the three times he tried to stop PA from mounting or consorting with BA.

The low ranking subadult male (PA) consorted with MY, who never bore an infant, a few times for 2 to 3 days ( $X^2=6.436$ ; 1df;  $p=0.01$ ). PA also associated with MC and PP, with an interplay between mate competition and homosexual behaviour, this association could not be classified as a consort relationship ( $X^2=0.190$ ; 1 df; NS). Finally, PA spent more time following, grooming and attempting copulation with the lowest ranking female (BA), the first bouts of consortship were observed in February and the last in July when BA was almost two months pregnant ( $X^2=22.668$ ; 1df;  $p<0.001$ ). If any, BA was the only female impregnated by PA. BA was also the female PA groomed more often throughout the study.

Finally, no adult or subadult showed a consort relationship with the juvenile female (PT). The subadult male PP copulated with her a few times, but they never remained in contact afterwards. The typical interaction was followed by the young female threatening PP or PP running away before it happened. PA never went further than pelvic thrusting and no penile intromission was observed. The yearling male (MS) mounted PT incompletely a couple of times on his own initiative. A juvenile male from the free-ranging troop inspected PT's genitalia once and a second time he put his hands on PT's shoulders while showing penile erection. PT even sexually presented to the dominant male of the other troop (MD) and to the lowest ranking male of her own troop (FY), who later ran away.

No attempts were made by the two lowest ranking males of the Cage troop to form any sexual consortships (not even of copulation) with females of their troop. It is important to emphasise that the lowest ranking of the two was sexually aroused and often followed one of the low ranking females of the other troop (AT).

### **7.5.7. Sexual interference**

Sexual interference is an element of mate competition. In general, adult females in the Cage were more successful in interfering with an ongoing sexual interaction (Binomial test:  $<0.001$ ) than males were (Binomial test: NS). It can be argued then, that vervet females rely more strongly on sexual interference than males.

The female MC was prevented from mating by others most often (33.7% of her sociosexual behaviour was met with attempted or successful intervention) and BA, the lowest ranking female was next (23.2%) with similar rates for MY. It is significant that these females were the low ranking male's consort partners.

Table 7.5.

Matrix of male interference in sociosexual behaviour involving other males of the caged troop or neighbouring free-ranging troop (AT). Subadult males (PP and PA) are placed just below FT (the dominant adult male), because they showed a higher sexual rank than the subordinate adult males (RN and FY).

#### **a) successful**

	FT	PP	PA	RN	FY	(AT)	TOTAL
FT	-	1	2	0	0	2	5
PP	9	-	6	0	0	0	16
PA	3	9	-	0	0	0	12
RN	0	0	0	-	0	0	0
FY	0	0	0	0	-	0	0
(AT)	0	0	0	0	0	-	
TOTAL	12	10	8	0	0	2	33

#### **b) unsuccessful**

	FT	PP	PA	RN	FY	(AT)	TOTAL
FT	-	1	0	0	0	0	1
PP	0	-	0	0	0	0	0
PA	3	10	-	0	0	0	13
RN	0	0	0	-	0	0	0
FY	0	0	0	0	-	0	0
(AT)	0	0	0	0	0	-	0
TOTAL	3	11	0	0	0	0	14

Among captive animals, sexual interference against the female dominance hierarchy involved closely related females (PT and CE were XA's daughters) or females with at least similar ranks (ranking immediately below), who might also have been related (Baldellou, in prep.).

Unexpected results were found for the two subadult males. They were successful in interrupting the top ranking male's sociosexual behaviour on 12 occasions (PP 9 and PA 3 times), while the dominant male only stopped such interaction on 3 occasions (PP once and PA twice). Moreover, PA (subordinate to PP) stopped PP's sexual interactions 9 times (Table 7.5).

FT tried only twice to stop PP's interactions with females (on one occasion he did not succeed). PP was always successful in stopping FT's sociosexual behaviour (9 times) and twice interrupted PA's. FT equally succeed or not in interrupting PA's sexual approaches to females (3 times each). It is understood that FT was less interested in stopping the two subadult males' sexual approaches towards females of their natal group than *vice versa*, possibly because interference by males was more successful when it was directed towards a male attempting an approach on the former's consort (Baldellou, in prep.).

## 7.6. DISCUSSION

### 7.6.1. Birth and mating seasons

Vervet monkeys in Natal are seasonal breeders (Basckin & Krige, 1973; Henzi & Lucas, 1980) as has been found in other study sites (Struhsaker, 1967 a; Cheney *et al.* 1986). In this study, all the infants were born between the middle of September and the beginning of January. That the birth season in Natal is somewhat shorter than the one reported for vervets in Kenya, could be attributed to the quality of the habitat (Butynski, 1988).

As has been pointed out, sexual behaviour in male Old World monkeys is released in the presence of behaviourally receptive females (Wilson, 1980). It is also not surprising that mating is restricted to a certain period of time in species with a clear birth season.

Nevertheless, copulatory behaviour may be unaccompanied by ovulation in the Japanese monkey (Takahata, 1980; Nigi *et al.* 1990) and the vervet monkey (Gartlan, 1969; Andelman 1986; Butynski, 1988) and among other species (review: Blaffer Hrdy & Whitten, 1987). This findings have been corroborated here although the physiological state of the female could not be determined, copulation was observed three months into pregnancy. In agreement with the above, Andelman and co-workers (1985) found that free-ranging vervet female copulatory behaviour starts about 2 months before physiological estrus and corresponds to an increase in estrogen that was not associated with ovulation. They also point out that copulatory behaviour can continue for a similar period of time after conception. Andelman (1987) also discussed the adaptive significance of copulation outside the female's fertile period and suggested that they conceal the time of ovulation as a strategy to reduce infanticide (see also Blaffer Hrdy, 1974 for langurs).

Nigi and collaborators (1980) studied seasonal changes and sexual maturation in free-ranging male Japanese monkeys (*Macaca fuscata*). They concluded that plasma testosterone levels and activity of the testes drop during the birth season, and rise again before the beginning of the next mating season. However, some adult males (no mention of rank) still present physiologically active testes (seminiferous tubules with less noticeably regressive changes) during the birth season.

That vervet males (at least some) may be fertile outside the mating season is demonstrated by the presence of new born infants (<3 months old) in the middle of the mating season (Butynski, 1988 p.370,311; personal observation). The fact that masturbation also occurs outside the mating season also suggests that males are potentially active in a sexual way during this period (Struhsaker, 1967 a; Baldellou in prep.). The question that still remains unanswered is whether all the males are physiologically fertile during the mating season.

#### **7.6.2. Frequency and distribution of sociosexual behaviour**

It has been reported that either the highest ranking adult male accounted for all the copulations of a troop of vervet monkeys (Struhsaker, 1967b) or that the highest ranking adult males mated more than the subordinate males (*e.g.* Andelman, 1987). On the other hand, natal males are generally of lower rank than immigrant males and copulate less often (Cheney *et al.* 1986). When natal males are excluded, dominant males do not achieve more copulations than subordinate males (Cheney *et al.* 1986; see also Cowlshaw & Dunbar, 1991).

The subordinate male remaining in the Windy Ridge troop during the mating season only participated in a few sociosexual bouts with females and was only observed mounting a female in the absence of the alpha male, and after the female presented to him (see Gouzoules, 1974 for clandestine mounts in stumptail macaques). The peripheralise and attract strategy described for bonnet macaques could be the one used by the subordinate male of the Windy Ridge troop (see Taub, 1980 p. 297).

Striking differences in male sociosexual behaviour have been found in this study. The alpha males of both the Windy Ridge Troop and the Cage Troop were the ones more involved in male-female sociosexual behaviour. In the Cage however, when looking at the number of copulations, the dominant adult male was less successful than the high ranking subadult male. The low ranking subadult did not participate to such a degree in sexual intercourse but he displayed many more sexually related behaviour towards the females than the remaining two adult males (RN and FY). RN and FY hardly ever interacted in a sociosexual manner with females of their own troop, yet showed some interest in the females of their neighbouring free-ranging troop.

The high levels of sexual performance achieved by the subadult male are parallel to those seen in rhesus monkeys by Smith (1981) which indicates that males achieved a high reproductive rank prior to achieving a higher dominance rank. Besides, Glick (1980, p.359) concluded that sexual activity was not correlated to testosterone but high ranking males with high levels of testosterone mated more and high ranking males in general showed greater sexual arousal.

When the two most successful male mate partners of the Cage Troop are compared, it is seen that there were some qualitative differences in sexual behaviour. First, the younger male displayed sociosexual behaviours in series (see Carpenter, 1942b for rhesus monkeys) more often than the older dominant male; keeping the female in close proximity seems *a priori* a very powerful strategy to ensure fertilisation. Second, the dominant male lost interest in most of the females after the time of estimated conception. Third, the subadult male copulated with all the females of the troop (the nulliparous female included) while the top ranking adult male was more selective mating with only the two highest ranking females and the post-reproductive female.

The lowest ranking subadult male's sexual interactions were restricted to the three lowest ranking females and BA, and his efforts to copulate with females extended over a longer period, which could be at least partly explained as a lower level of selectivity for cycling females. PA also spent more time interacting in a friendly way with females prior to attempting sexual behaviour.



MY, the post-reproductive female of the Cage group, behaved in a non-receptive manner despite the dominant adult male's constant sexual approaches. It was only in this particular couple that a few instances of apparent 'rape' were observed. In Windy Ridge peri-menstrual estrus (see Takahata, 1980) was only detected for the post-reproductive female. In fact, it was the only time she was seen presenting and took place in a context where submissive behaviour seemed a more appropriate term than sexual presenting. Although accounts in the literature of old-age females are not common, Takahata (1980) points out that Japanese monkey females may continue to show estrus behaviour a few years after giving birth.

Evidence has been presented in this chapter on the responsibility of males and females for the initiation of sociosexual bouts. Only the top-ranking adult females and the related primiparous female were more responsible than or as responsible as the males for the maintenance of sexual relationships. The rest of the females were mainly the receptors of sociosexual approaches by males. Whether lower ranking females avoid proximity to adult males (due to their differing social rank), or whether they prevent an agonistic contest with the higher ranking females (female mate competition) remains unknown. Therefore, Andelman's (1987) argument that females are not more receptive to males around the time of conception than at other times could be the result of the influence of rank on female receptivity (see also Johnson & Phoenix, 1977).

Analysis of the rates of genital inspection and female solicitations in relation to the moment of ovulation has not been attempted because it is conceivable that ovulation may have occurred once or more before the estimated moment of conception. In fact, it is apparent that females initiate sexual behaviour mostly according to their rank, and this pattern does not seem to change throughout the mating period.

Presenting in a non-sexual context has been viewed as an appeasement behaviour to divert attack (e.g. Zuckerman, 1932; Richards, 1974). In female bonded primates sexual presenting by females towards newly arrived males can also be a strategy to prevent infanticide (Andelman, 1987). It is worth noting that in non-female bonded primates, in which females might commit infanticide, presenting occurs more often amongst females (Wrangham, 1986).

Finally, the argument that females are slightly more attractive to males during the week of conception (Andelman, 1987) agrees with the results in this study, at least for the highest ranking adult male of both the caged and the free-living troops.

### **7.6.3. Genital inspection**

Most female primates living in multi-male troops present a clear visual genital signalling system that facilitates the detection of their reproductive status by the males (for baboons: Rowell, 1967; Clutton-Brock & Harvey, 1976; Shaikh *et al.* 1982; Blaffer Hrdy & Whitten, 1987), but this is not the case for vervets. Adult male baboons initiate copulation with females at or near maximal swelling more often than at other times (Chalmers & Rowell, 1971, p.9). Estradiol treatment enlarged the sexual skin swellings of talapoin monkeys, making them more attractive to males (Keverne, 1983 p.88).

How do vervet males determine the reproductive state of the females? There is evidence that in Cercopithecine monkey estrogen increases female attractivity. On the other hand, progesterone decreases male sexual interest in the female (in ovariectomised rhesus monkeys: Keverne, 1983 p.84).

I suggest that adult male vervet monkeys use some visual and/or olfactory cues to identify the female's reproductive state. Muzzling is mostly used by less experienced males and may also serve to sexually arouse the female. The same could occur with tactile inspection of the female's perineum or vagina. A few observations of the male approaching the female from behind, grabbing her hips and inserting a finger into her vagina, were followed by the male smelling the finger and the female adopting a sexual presenting position (see also Gouzoules, 1974 for stumptail macaques).

Keverne (1983 p.85-86) proposed that non-behavioural cues (mainly olfaction) are the most important factor regulating male rhesus monkeys' sexual behaviour. He found that anosmia prevented males from recognising the onset of female attractiveness, but ejaculation could be prompted by female proceptive behaviour (for another view see Goldfoot, 1981). Oral contact (muzzling) with the perineal area can facilitate the detection of long chained aliphatic acids providing some information about the reproductive state of the female (Keverne, 1983 p.83).

In the meantime, muzzling of the female genitalia may arouse the female and/or act as an aphrodisiac for the male. The above arguments seem to agree with the results found in this study; the subadult male PA mostly muzzled the female's genitalia and was as successful as the dominant adult male in his sexual interactions.

In addition, tactile and olfactory inspection was more commonly found in sociosexual interactions involving the top ranking adult male. This could be a case of discriminating between physiological and behavioural estrus. FT, a fully grown adult male, and PP, a subadult male with high levels of sexual performance, could obtain the same information through more visual, olfactory or tactile cues and/or female behaviour. PA's high interest in muzzling the female's genitalia could be explained in this way. That the dominant adult male mostly smelt the female's genitalia agrees with Meredith's (1983 pp.241-242 suggestion that more experienced animals might use finer sensory or behavioural distinctions.

The observations reported of the lowest ranking males smelling and muzzling the ground where females had been sitting emphasise the importance of the olfactory-muzzling system in the detection of the female reproductive cycle. A similar occurrence in the free-ranging troop was recorded for the third ranking male just before he emigrated at the end of the pre-mating season. The low ranking males responded to their extended penes by either jerking the scrotum or by handling and looking at it, and then proceeding to conceal their genitalia with their hands or body.

For females, differences in the proportion of sociosexual bouts that involved any of the forms of genital inspection seemed more related to rank and/or age. The two lowest ranking and older looking females were less often inspected visually, by tactile means, or by muzzling than others. While smelling of the perineum occurred proportionately more often with the second ranking and very young female (CE) and least with the nulliparous (PT) and lowest ranking (BA) than with any other females. Finally, the females that received less muzzling than any other form of genital inspection were the highest ranking (XA and CE) and the post-reproductive (MY). Yet the lowest ranking female (BA) received more olfactory inspection of her genitalia than any other pattern, which could be related to the preferences shown by their mates (see below).

It still remains to be analysed whether changes in vervet females' perineum are correlated to cyclical changes or with the timing of male copulations. Although Andelman (1987) and other authors have not detected cyclical changes in the female's perineum, I observed female vervets with clearly visible clitoris and reddening of their vulva when males were muzzling and/or grooming their genitalia during a sexual context.

#### **7.6.4. Male and female mate preferences**

Here, I simply draw attention to the fact that male reproductive success depends largely on what the female's attitude is, both in initiating and accepting sexual approaches that lead to sexual intercourse with the male.

Apart from sexual presenting, no other ways of soliciting copulation have been described for vervet females (review for other species in Blaffer Hrdy & Whitten, 1987). Vervet females may attract the male's attention towards them from a distance. This was very obvious when the middle ranking female (BE) raced across the canopy and approached the area where the dominant male of the troop (RO) was; the rest of the troop was left behind and only one other adult male was in the area. BE started feeding but was immediately approached by RO, who without any obvious genital inspection proceeded to copulate.

The top ranking female XA initiated most of her interactions with PP and a comparable amount with FT. The young, second ranking female (CE) was more interested in interacting with FT and PP than they were, and she never attempted to interact with the low ranking subadult male (PA). PA was more responsible than any of the adult females for initiating sexual contacts.

In general, the subadult male PP was the most successful male sexual partner in the Cage having mated with all the receptive females. Moreover, MC, BA and MY initiated and/or accepted PP more often than any other male and the nulliparous female PT was only ever mounted by PP. FT, the dominant adult male persistently followed and attempted to mate with MY, but only the top ranking females (XA and CE) copulated with him when they were sexually receptive. At the other end of the scale, the low ranking subadult male PA copulated with middle (MC) and low ranking (MY and BA) receptive females. The subordinate subadult PA's degree of sexual acceptance by females did not differ from the dominant adult FT's, but the rank of their female mate partners was parallel to their own.

The attractivity of females was also higher for PP than it was for FT and PA and no differences were found for FT and PA. PP was mostly attracted to MC and BA while FT to XA and possibly to CE. Finally no male differences existed for MY, in spite of FT constantly following her.

It can be concluded that high ranking females were more responsible for initiating sociosexual contacts and in particular complete mountings with the dominant male than the lower ranking females were. No significant differences were found when comparing FT and PP, or FT and PA, although the high ranking subadult male PP did awaken more proceptive behaviour in females than the lowest ranking subadult male, PA.

The manner in which the middle and low ranking females avoided being seen interacting with the alpha male of their troop and the higher success of female rather than male sexual interference, emphasises the existence of intense female mate competition in vervet monkeys (Mori, 1979, p. 187 for geladas).

A wide range of immature and adult vervets might try to or might successfully abort a mating sequence (see Hall, 1967 for patas monkeys; Gouzoules, 1974 for stump-tail macaques; Young, 1981 for howler monkeys). Ruiz de Elvira and Herndon (1986) argue that concealed copulation occurs to prevent sexual interference.

Females were in general more successful than males at interfering in ongoing sexual interactions. Female interference was mostly directed towards lower ranking females -the exceptions occurred between individuals of adjacent rank (probably related). In the field study, subordinate males never attempted to interfere in the alpha male's sexual approaches, but in the Cage, the subadult male (PP) who was lower ranking than the adult male (FT) attempted and often succeeded in stopping FT's sociosexual contacts, especially when one of PP's consort partners was involved. Gouzoules (1974) argued that sexual harassment in stump-tail macaques had the effect of redirecting the high levels of aggression of the adult males away from the female sexual partner and toward the harasser. For vervets, in contrast, the female is the only one that typically displays aggression towards the male during mating or shortly afterwards.

It is predicted that 'concealed ovulation' in vervet monkeys (Andelman, 1987): i) increases the probability of female mate choice while reducing male-male competition; ii) reduces the risk of infanticide (Andelman, 1987); iii) serves to reinforce male-female bonds. However, there was an evident reduction of sexual behaviour by the dominant male of both the field and caged troops towards females after their estimated time of conception (but see Andelman, 1987), although the subadult males retained sexual interest in them. The above results suggest an increased selection for females in midcycle as the male grows older.

The fact that dominant males select high ranking females may result in an increase in their inclusive fitness because high ranking females reproduce more successfully than lower ranking females (Cheney *et al*, 1986, Fairbanks & McGuire, 1986; Baldellou, in prep.). Although the males generally interacted in a sexual way with females of a similar rank, some exceptions were found that can only be explained in terms of individual preferences (Michael & Zumpe, 1990 for rhesus) and age-related mate choice (Silk & Boyd, 1983 for macaques)

### *Sexual consortship*

Sexual consortship in vervet monkeys is described here for the first time in a qualitative way. It is suggested that the duration of the consortship would be related to the total number of females available, male competitive power and mate choice. The fact that sexual consortships in vervets vary in duration could have produced statements like that they do not form sexual consortships Andelman (1987). Actually, other researches have described sexual consortships in baboons and macaques that may last for only a few minutes up to more than one week (Hausfater, 1975; Lindburg, 1980; Bercovitch, 1987).

Not all successful and attempted copulations occurred within a consort relationship. They were more common for the highest ranking male and the subadult males of the Cage troop (4 reproductive, 1 post-reproductive and 1 nulliparous female to 3 adult and two subadult males).

The highest ranking male (FT) constantly followed, groomed and inspected the post-reproductive female (MY)'s genitalia, without the female showing the slightest interest. However, the most dominant females (XA, CE and the nulliparous PT) constantly interfered in their consort relationship. The constant (one-sided) sexual consortship between FT (alpha male of the caged troop) and MY (post-reproductive female), was followed by FT engaging in a consort relationship with CE (the second ranking female) and XA (the highest ranking female) during late April. In those cases the females were almost as responsible as FT for the sexual consortship. MY was then followed by PP (the subadult male).

In the Cage, the alpha male did not consort with the adolescent female who was the most responsible for maintaining sexual interactions with other males.

The highest ranking subadult male consorted with a middle ranking female although occasionally both engaged in sexual contacts with the lower ranking subadult male. Although actual agonistic coalition of adult or subadult males for access to a sexually receptive female has never been observed in vervets (see DeVore, 1965 for baboons), the closeness of the two subadult males may have deterred the dominant male from interfering in the sexual interactions. Even though the subadult male was alone, he was generally successful in sexual interference with the dominant adult male when the latter was attempting copulation with his consort females.

The top ranking female showed two clear periods of sexual arousal. During the first she constantly followed and sexually presented to the dominant male of her troop and they were frequently involved in grooming (sexual consortship). During her second 'behavioural estrus' XA mainly presented to the subadult male PP (although there was no sexual consortship). She was in general, more responsible than the males for initiating sociosexual interactions. That an ejaculatory pause was only observed for PP and not for FT at around XA's date of conception, supports the possibility that it was PP and not FT (who had just been consorting with XA) who fathered her offspring. Unfortunately no tests on paternity were done and the success of sexual consortship versus sporadic sexual interaction cannot be tested. The subadult male PP was responsible for maintaining sexual consortships with middle and low ranking females.

The low ranking subadult male PA was the most unsuccessful male consort, he spent more time grooming females and in proximity to females consorted by the other subadult male. In addition, PA was successfully supplanted by PP when attempting copulation with the middle and low ranking females. The close relationship found for the two subadult males may have made possible their high levels of participation in sexual behaviour.

In contrast, in the Windy Ridge troop (7 reproductive and 1 post-reproductive female to 2 adult males and one subadult male) consort relationships were not quite so evident, or rather, they were of shorter duration. It is important to note that the low ranking females of this troop were the only ones that showed a significant increase in proximity to the dominant male when they were the source of sexual interest by him. This finding may be partially explained by female mate competition and the fact that the only potential male competitor within his troop showed a tendency to be near middle and low ranking females but not in the vicinity of higher ranking females (see Fig. 6.1 p. 175). Eventually, the strategy adopted by the dominant male was to 'guard' the only potential mate competitor he had and herd him away from females.

Therefore, sexual consortships in vervets can last from a few hours (the minimum time required to record a sexual consortship was one hour by definition) to almost a month. What appears interesting is that the male-female pairs involved in consort relationships more often were also those pairs of animals that groomed and were found in close proximity outside the mating season more often than expected. In addition, the subadult male's 'passive' agonistic interference mostly benefited the two lowest ranking females with whom he consorted during the mating season (review in other multi-male species in Smuts, 1987).

Even in species where sexual consortships are commonly described, they only partially describe male-female sexual relationships. The animals that participate in consort relations were neither exclusively high ranking individuals (but see Wilson *et al.* 1982 rhesus monkeys) nor only adult males (but see Glick, 1980, p.358 bonnet macaque).

#### *Context of sociosexual behaviour*

Andelman (1987) reported that most copulation attempts (94%) were initiated by males, that no preliminary interaction except the occasional smelling of the female's genitalia occurred, and that they terminated with either the male or the female running away (>50%). The results for this study differ somewhat. First, initiation of sexual behaviour seems more related to the rank of the female than to the sex of the subject. Second, grooming and female genital inspection were quite common, at least among the caged animals.

However, following an intertroop encounter or alarm situation, the alpha male of the Windy Ridge Troop would seek a female and mate with her. This type of sexual intercourse was not preceded by any genital inspection or affiliative behaviour towards the female. The females normally adopted a submissive crouch while sexually presenting to him. An increase in copulatory behaviour during alarm or agonistic situations was not as evident for the males of the Cage troop.

#### *Behaviour after copulation*

In the Cage about one third of the sociosexual bouts observed for the two most successful male partners were followed by the pair getting involved in a grooming interaction or by remaining in proximity. The values for the lowest ranking subadult male approached the 50% mark. In general, these results are comparable to those found by Gartlan (1969).



In Windy Ridge the probability that a male would direct or receive any affiliative behaviour from the female was lower. This can be better understood by the almost total monopoly of the females held by the dominant male of the troop and the very low levels of acceptance of the subadult male by the females. Gartlan (1969 p.137) stated that the vervet populations in Uganda and Kenya differed in reproductive behaviour, therefore the differences reported above could be due primarily to the variability amongst populations.

#### **7.6.5. Male reproductive success**

It is suggested that the alpha male of the Windy Ridge was the most probable father of 3 of the 4 infants born into the troop. Because the second lowest ranking female mated with a newly immigrated male, this male is a potential father of her offspring. The reason why WE and ET failed to conceive successfully may be related to social stress (see Goldman, 1981, p.11) and MO could have been in the process of becoming post-reproductive as was TO.

Of the 9 females present in the Windy Ridge troop at the beginning of the study, 8 became pregnant in the next mating season; one of these was a primiparous female that was estimated to have conceived at 2.5 years and another was presumably killed by a leopard just before giving birth. Only 4 out of the surviving 7 females with yearlings gave birth to an infant that was still alive 3 months later. The remaining female was considered post-reproductive because she did not produce an infant in at least 4 consecutive years.

The strategy of the high ranking male was to consort females for a few days (1-4), especially those low ranking females that did not attempt to initiate sexual contacts with him. An alternative strategy was that of controlling the movements of his potential competitor for most of the mating season.

The proportion of females producing an infant every year appeared to be lower for the free-ranging troop than the Cage Troop. Whether this difference was due to food scarcity or to RO's strategy of maintaining LE under control is not known (see Takahata, 1980 for Japanese monkeys).

Four out of five captive females reproduced consecutively (during the first season the lowest ranking female (HH) could not attend her new born infant and they both had to be put down. The fifth female has been classified as post-reproductive because she did not have an infant for at least 3 years.

The subadult males in the Cage were apparently less selective in choosing the right time to consort with the females. The potential costs of maintaining these pairs bonds were at least partially outweighed when considering that subadult males were more successful than expected preventing the highest ranking dominant male from mating with their female consorts. Therefore, it can also be concluded then that sexual consortship in vervets enhances mating frequency of low ranking males (see Hausfater, 1975, p. 116 for baboons) and females.

The key elements to investigate in future research are the relationship between behavioral measures of mating success and actual paternity and the efficiency of forming sexual consortships to improve vervet male reproductive success. In addition, the benefits consort males may provide to females seem to play an important role in the success of sexual interference by other females.

The main difference with sexual consortships in baboons and macaques is that in free-ranging undisturbed vervets it is not possible to assume when ovulation is more likely to occur. Attempts to determine the moment of most probable ovulation have been carried out analysing urine of free-ranging vervets to determine hormonal levels (Andelman *et al.* 1985). Although no mention is made on the influence of female choice and mate competition on male reproductive success, it is stated that male rank does not influence frequency of mating during the week of most probable conception (Andelman, 1987).

## **8. ADAPTIVE SIGNIFICANCE OF THE VERVET MULTI-MALE SYSTEM**

The semi-terrestrial slightly dimorphic vervet monkey lives in female-bonded groups which typically include more than one adult male. All-male groups and isolated males have not been described as permanent structures for this species, where they occur, they have been interpreted as a transition stage during migration between two troops (Henzi & Lucas, 1980) or when environmental conditions prompt group fission (Hauser, 1986; Isbell *et al.* 1990).

A question which remains to be answered is why congeneric species *i.e.* arboreal guenons (Rowell, 1988) and the terrestrial patas monkeys (Hall, 1965) typically live in uni-male groups and extragroup males may be solitary or live in all-male bands.

Taking into account that in polygynous species the limiting resource for males is females (Emlen & Oring, 1977), it can be argued that additional male vervet monkeys remain in the troop outside the mating season primarily to improve their mating opportunities (but see Henzi, 1988). By staying in the troop adult males are forced to coexist with unrelated males and compete for food resources with other members. As it has been pointed out that females in female-bonded groups tolerate adult males only if they provide some benefits that offset the costs of their presence in the troop (Wrangham, 1987; van Schaik & van Noordwijk, 1989), the potential costs and benefits of male association in troops of vervets monkeys will be reviewed.

### **8.1. HOW UNRELATED MALES HAVE 'ADAPTED' TO COEXISTENCE**

Dominance hierarchies can be viewed as a mechanism which benefits both the dominant and subordinate animals and maximises the 'benefits to cost ratio' of social dispersion, because the costs of open aggression are reduced (Jones, 1981; Slobodchikoff & Schulz, 1988 p.18).

Different behaviour patterns have been reported from a wide variety of non-human primates that have the effect of stopping or preventing overt aggression. For low ranking individuals avoidance is the simplest way (e.g. mountain gorilla: Schaller, 1963 p.255) and submissive acts are normally accompanied by lipsmacking (Chalmers & Rowell, 1971).

It appears that homage or self-initiated displays of submission (Henzi, 1982, 1985) may function to demonstrate the sender's submissiveness and appease the higher ranking male. Henzi (1982) suggests that by showing submission, subordinate males may benefit by being accepted by the most dominant male of the troop.

Scrotal adduction, the 'down-and-out' tail carriage (Henzi, 1982) and other behavioural means to keep the genitalia out of sight, *i.e.* hands or body concealing the male's genitalia, occur during displays of submission and during stressful situations, *i.e.* attacks, threats, alarm in general (Henzi, 1982; 1985). A physiological consequence of displays of dominance and open aggression directed towards low ranking males can be that the retraction of the scrotum into the inguinal canal could result in a rise in the temperature of the testis affecting the viability of the sperm (Henzi, 1981; see also Waites, 1970).

The vivid genital colouration of most cercopithecine species (see Napier & Napier, 1967; Kingdon, 1980) has been the source of much speculation (Darwin, 1876; Wickler, 1967) and assertive hypotheses (Struhsaker, 1967a; Henzi, 1982; 1985).

Male vervet monkeys have evolved sophisticated visual signals which may facilitate the coexistence of unrelated adult males in multi-male, multi-female troops. Visual genital signalling systems such as the display of male dominance towards other males of the same troop; *e.g.* the Red-White and Blue Display (Struhsaker, 1967a), and Broadside (Henzi, 1985), are not the only examples.

These displays of dominance are almost exclusive to the top ranking male although second ranking males have been observed displaying their genitalia towards other lower ranking males in a more rudimentary way: by standing bipedally close to him and/or putting his hand on his shoulders ('penile display': Struhsaker, 1967a; cf. Henzi, 1982). The response of the recipient may be one of fear or subordination accompanied by scrotal adduction (see Henzi, 1982). The finding that these displays of dominance are generally directed at closely ranked males can be understood when considering that between two males of widely disparate rank there is no need to reinforce dominance relationships (see Johnson, 1989 for olive baboons).

The dominant male's genitalia are also clearly visible during the 'confident walk' which is also listed as an expression of dominance (see Struhsaker, 1967a). This 'assertive walk' is mostly used by anubis baboons, drills and patas monkeys to gather all the members of the troop and is a mild form of herding behaviour that does not involve either threats or attacks (Bolwig, 1978). A version which is directed towards a specific individual and which can be more aggressive (cf. 'herding of females' Cheney, 1983a, p.235) was used by the free-living alpha male when he was 'herding' his rival during the mating season both to position himself between the group of females and his subordinate and to 'call him back' when the troop was about to start a general progression ('notifying' for hamadryas baboons: Abegglen, 1984).

During agonistic interference the adult male stands on his hindlegs and exposes his white chest (slightly blue) and genitalia, which are clearly visible to those animals involved in ongoing agonism. It has previously been suggested that the ventral area is used in vervet communication, but only during inter-troop interactions (Harrison, 1983a).

Other displays which involve showing off male genitalia have been described for vervet males during inter-troop interactions. The 4 legs-up and the splayleg displays ('open posture' common among Old World monkeys: Wickler, 1967) are typical of vigilant males and are directed towards external males (Henzi, 1985). In addition, the 'tree display' also emphasises the male's genitalia and is directed towards other troops or external disturbances (Henzi, 1985) and occasionally is used by the dominant male to herd females away from other males of the same troop. All the displays of dominance and 'keep out signals' mentioned above emphasise the male's genitalia, can be accompanied by penile extension (Henzi, 1982).

The finding that male vervet monkeys may sometimes form agonistic coalitions with other males has not been recorded in other studies (Henzi, 1985; review in Smuts, 1987). Agonistic coalition of males against other males was only observed in the Cage troop and were mostly subadult males forming coalitions against adult males, especially the top ranking male (see also Keddy, cited in Cheney & Seyfarth, 1990).

It is concluded that adult male vervet monkeys employ visual and/or auditory systems to establish and maintain their social structure and that, as suggested by Zeller (1987), visual communication is strongly affected by past social experience and interactions with other individuals within the social group.

## 8.2. THE SOCIAL POSITION HELD BY VERVET MALES

Closely ranked males spend more time together than males whose rank difference is greater. The lower ranking males avoid proximity to the alpha male, mostly during the mating season when open aggression is more common (rhesus monkeys: Kaufmann, 1967; patas monkeys: Hall, 1967; vervets: this study). However, the relative number of 'homage paid' to 'displays received' by a male pair does not vary between seasons. That the production of testosterone could drop radically after direct threat or attack (rhesus monkeys: Rose *et al.* 1971; Bernstein, *et al.* 1979; squirrel monkeys: Gonzalez, *et al.* 1981) could explain why the dominant male in Windy Ridge troop was more openly aggressive towards his subordinate during the mating season.

Males do not participate in grooming as often as females and male-male grooming is rare. Young, middle ranking males groom other males, especially higher ranking males, more than other males (see also Tsukahara, 1990 for Japanese monkeys).

In general, vervet males are spatially closer to other males than to individual females; this is more apparent during the birth season and for the young and low ranking males. During the mating season the captive subadult males in this study were closer to females than expected, suggesting that subadult males are socially protected (see Dessi-Fulgheri *et al.* 1981 for Japanese macaques) although the effects of relatedness to the dominant male of the troop cannot be ruled out.

Dominant male vervets associate with females more often than subordinate males do (see also Raleigh & McGuire, 1990), which indicates their central position in the troop. In addition, male-female proximity, grooming and other social behaviour are regulated by competitive interactions based on the attractiveness of high ranking individuals (see Tsukahara, 1990 for Japanese monkeys), with the result that the very low ranking males are socially isolated. As a consequence, the degree to which adult females interact with adult males is constrained by their respective rank, with female competition to associate with the alpha male being most evident during the mating season. It is also during the mating season when the alpha male grooms females as often as they groom him; this is especially true for the highest ranking females (see also O'Brien, 1991 for capuchin monkeys; Zumpe & Michael, 1985 for cynomolgus monkeys).

Therefore, the prediction that unrelated adult male vervet monkeys have weak social bonds with each other and with other members of the troop is corroborated in this study. The characteristic patterns are to supplant, avoid and make agonistic coalitions, behaviours which do not normally end in attack and which explains the lower frequency of wounding among females.

Preliminary observations of male-female monkeys in multi-male troops maintaining long lasting close associations, special bonds or special friendly relationships (Altmann, 1962; Kaufmann, 1965; Enomoto, 1974), were later confirmed and analysed in detail by Seyfarth (1978 b), Smuts (1983; 1985), Hamilton (1984) and Strum (1987) among others. In contrast, male-female special friendly relationships (*sensu* Smuts, 1985) in vervet monkeys outside the reproductive period have been overlooked in other studies (review in Smuts, 1987, but see Keddy Hector *et al.* 1989).

### 8.3. ADAPTIVENESS OF VERVET SOCIAL STRUCTURE.

The consequences of male presence in the troop throughout the year can be understood in terms of the costs and benefits to adult males, adult females and immatures.

#### *Potential costs and benefits to females and immatures by males remaining in the troop*

1. The importance of optimal foraging and predator defence strategies in regulating primate social behaviour, especially inter-individual distances in vervets has been discussed in this study (see also Fairbanks & Bird, 1978; Cheney & Seyfarth, 1987). Resident adult males contribute towards reducing predation risk through detection of predators and affording general protection more than females (see also van Schaik & van Noordwijk's, 1989). Although the alpha male contributed disproportionately to these differences and behaved as the resident adult male in one-male groups (*e.g.* Cheney & Wrangham, 1987), the presence of dominant and subordinate sentinel males when the troop forages or during general progressions is noteworthy and may outweigh the costs of food competition. Males in general also spend noticeably more time in hazardous positions, such as at the head or tail of progressions, while the most vulnerable members of the troop remain in the centre (but see Cheney & Seyfarth, 1981). These results agree with van Schaik and van Noordwijk's (1989) theory that besides the potential a male has in monopolising a group of females, predator avoidance determines the adult sex ratio in groups of primates.

The frequency of female submissive behaviour prompted by feeding competition was minimal during the mating season, a period when females showed submission in other contexts more often than at any other time of the year. It is clear that when food was scarcest during this study, females did not perform a greater proportion of submissive behaviour or avoidance activity than when food was plentiful. Unfortunately, systematic data was not obtained after the mating season ended, a period when male-female competition for food resources is expected to peak in Natal.

2. Adult males participate more often than females in territorial displays, *e.g.* keep out signals, tree displays and overt aggression towards males of other troops. Although the main proximate cause seems to be to maintain exclusive access to the females (Cheney, 1983a p.236), it may still benefit the females by keeping other groups away from their food resources.

3. The killing of infants has been observed in a number of Old World monkeys. In female-bonded multi-male groups it is typically performed by newly immigrated adult males (Dunbar, 1984, p.209; Smuts, 1985; review in Fairbanks & McGuire, 1987). Even though accounts of vervet males committing infanticide are rare, isolated cases have been cited (Andelman, 1987) and in this study the alpha male of the free-ranging troop was observed twice attacking one of the lowest ranking females with her young infant for no apparent reason.

In uni-male societies infanticide seems to be more common and occurs when males gain control of a harem of females (Carpenter, 1974; Blaffer Hrdy, 1977; Fry, 1980 p. 83) or when extragroup males enter the troop (Struhsaker, 1977 for redtail monkeys). It has been pointed out that females use resident males to evade invaders (Smuts, 1985 for baboons) and they may remain with long-term resident males to avoid infanticide by invading males (Hausfater & Hrdy, 1984).

4. Another possible benefit to females and immature animals by having permanent male membership is male agonistic interference during intratroup agonism as found for other species (review in Smuts, 1987). Likewise, Tollman (1975) reported a marked increase in agonistic encounters during feeding, when the dominant male was not in the vicinity of the troop. On the other hand, males rarely direct aggression towards females; when it occurs, the defence strategy used by females is to form coalitions with other females and occasionally immatures to supplant or chase away the offending male (*cf.* Camberfort, 1981).



5. Social bonds in great apes (excluding the solitary orangutan) are believed to reduce intraspecific lethal aggression. Female chimpanzees seek male company to stop female infanticide and rape by males not belonging to the same community (Wrangham, 1986). In contrast, for the slightly dimorphic vervet monkey, the dependence of females on males is not as obvious as it is for other species with weaker female-female relationships (see Dunbar, 1983b) and with greater sexual dimorphism (Hamilton, 1984). However it is still necessary to investigate to what extent female vervets benefit from close proximity to the adult males in terms of increased protection for their infants (see Gartlan, 1969) or access to preferred food resources.

*Potential costs and benefits male vervets derive from remaining in the troop*

1. Predator detection is a major advantage of living in groups in diurnal primates (van Schaik, 1983; Terborgh, 1983). In Windy Ridge the dominant male of the troop invested more time in vigilance (every month) and he was the only one that participated in active defence of the troop against predators. That this occurred at the expense of time feeding was evident and was reflected by its detrimental effects on his physical condition (see also Glick, 1979 for *Macaca radiata*). The subordinate males might benefit from the protection against predators by the top ranking male. The dominant male was also the male that had more chance of fathering offspring (see below). Interestingly, vervets in Amboseli do not show either of those trends (Cheney et al. 1988; Andelman *et al*, 1985; Cheney & Seyfarth, 1990, p.190).

2. Location and defence of food resources is easier for animals living in a troop than it is for solitary individuals. Vervet females remain in the same area throughout their lives and have a better knowledge of where to find preferred resources and better sleeping places, knowledge which may benefit males. It may be hypothesised that male arboreal guenons do not benefit enough to outweigh the cost of direct food competition with other members of the troop. In addition, samango females reproduce once every two years while vervet females may potentially do so every year (Henzi & Lawes, 1988).

3. By settling and maintaining a well structured male dominance hierarchy long before the mating season starts, dominant adult males can direct more effort towards stopping extra-group males from mating with females. The advantage for resident subordinate males is that they receive less open aggression when receptive females are present than in other closely related species (cf. Slobodchikoff & Schulz, 1988, p.18).

When the results of other studies are taken into account, it can be concluded that displays of dominance occurring throughout the year serve to lower both the level of testosterone (see Bernstein *et al.* 1979; Dessi-Fulgheri *et al.* 1981) and the 'psychological' level, thereby excluding (to a certain extent) less dominant males from the social network of the troop (Gordon *et al.*, 1979) and depleting their sexual behaviour (Keverne, 1983). However, subordinate vervet males appear to minimise the costs of staying in the troop while maintaining the potential for reproduction whenever the opportunity arises (Henzi, 1982; see also Keverne *et al.*, 1982, p.92).

4. Vervet males, non-dominant males in particular, benefit from familiarity with females and the maintenance of friendly relationships with particular adult females outside the breeding season (see also Keddy Hector *et al.* 1989; Dittus, 1979 for toque monkeys). There is a tendency for vervet male-female pairs who are in contact more often during the non-mating season to be involved in sexual relationships during the mating season as it is found among baboons and macaques (Seyfarth, 1978b; Smuts, 1983; 1985; 1987; Strum, 1987). Therefore, a benefit males derive from close relations with females is increased mating opportunities. In addition, the acquisition of female allies by subordinate males, although very rare, this was observed on a few occasions during intragroup agonism.

That females form coalition against males mostly when they arrive into the troop and when the male hierarchy is unstable (unpublished results) suggests that females may decide whether an adult male takes over the group. This has been found in several highly dimorphic primates (Dunbar, 1984; Smuts, 1987) and emphasises the importance of males maintaining special relationship with the females of their group.

5. Although dominant males have been reported to father a greater proportion of infants than subordinate males (vervets: Struhsaker, 1967b; Andelman, 1987; baboons: Hausfater, 1975; Seyfarth, 1978 a,b; Packer, 1979b; rhesus: Kaufmann, 1967; stump-tail macaques: Gouzoules, 1974; Japanese macaques: Sugiyama, 1976), low ranking and newly immigrated males may also mate with estrus females (Henzi, 1982; Cheney *et al.*, 1988).

Results obtained in this study suggest that apart from agonistic rank, attention can be drawn to several features which may have a general significance for male reproductive success in vervets as it is common in other multi-male species. First, dominant males may refrain completely from copulating with a particular female (for baboons: Saayman, 1970; Hausfater, 1975; Seyfarth, 1978 a), especially nulliparous

females. Second, previous social experience may prompt females to choose lower ranking males (see also Raleigh & McGuire, 1990; for baboons: Saayman, 1971; Seyfarth, 1978 b; Smuts, 1985; Strum, 1987). Third, when the most dominant male is away from the troop, females have been observed copulating with subordinate males (for baboons: Bercovitch, 1987) or subordinate animals may separate from the rest of the troop for concealed mating (for stump-tail macaques: Gouzoules, 1974). Finally, although enough evidence was not obtained in this study, there may be more females cycling than the most dominant male can maintain with exclusive access (for rhesus: Altmann, 1962).

By remaining in the troop after the infants are born, males may also increase the chances of survival for their offspring (see Dittus, 1979; and above). In brief, remaining in the troop is a strategy used by males living in multi-male societies to maximise their reproductive success (cf. Dunbar, 1988a,c for geladas).

#### **8.4. MALE AND FEMALE SEXUAL STRATEGIES**

Vervet female morphological genital characters are in marked contrast to baboons, mangabeys and macaques where reproductive state is easily predicted by changes in colour and perineal swelling (Rowell, 1971).

A positive correlation between male dominance rank and mating success in polygamous primate groups is found amongst animals of the same age class. This relationship appears to be a function of the number of adult males and in highly dimorphic species to the number of females (Cowlislaw & Dunbar, 1991). It is a result of male-male competition (Fairbanks, *et al.* 1978) and their capacity to influence female choice (Chapais, 1983a). However, breeding synchrony among females makes it more difficult for high ranking males to monopolise receptive females in seasonally breeding species such as the vervet monkey (Emlen & Oring, 1977; Ridley, 1986; Dunbar, 1988).

Andelman's (1987) findings on vervet monkeys in Amboseli (Kenya) that males in the top, middle and bottom third of the hierarchy, participated in an equivalent number of copulations with females in the week of most probable conception and also that most males copulated with most females, are not supported by data presented in this study.

First, in the Cage the adult males in the bottom third of the dominance hierarchy, which were classified as socially inactive, did not attempt to interact in a sexual way with females of their own troop. When approached by females, these males would adduct their testes or cover them with their hands and walk away (see also Loy *et al.*, 1978; Bielert *et al.* 1980). Whereas, the observed subordinate male's sexual attraction to females of other troops could be one of the proximate causes for male migration (see Cheney & Seyfarth, 1983; cf. Henzi & Lucas, 1970). Second, in both study troops middle ranking males preferentially mated with middle or low ranking females. Finally, dominant males were the preferred sexual partner of high ranking females.

Variations between the sexual behaviour observed in the Cage and in the Windy Ridge troops, could be explained by the situation of extreme contrast in ecological and demographic variables, which may also explain differences with Andelman's (1987) study. Consort relations were somehow shorter in the Windy Ridge troop where the number of subadult and adult males to females was on average 1:2.67 than in the Cage troop where the ratio was 1:1.25. In the former troop, sexual harassment by subordinate males was never observed and may have resulted in less mate selectivity by the dominant male (for baboons: Saayman, 1970; Hausfater, 1975; Seyfarth, 1978a).

In fact, male-male competition for females is more intense when there are only two adult males, and the high ranking male may opt to condition his subordinate. Besides, when dominance hierarchies are less stable, the high ranking males have more difficulty monopolising estrus females (Cowlshaw & Dunbar, 1991).

The dominant adult male's attitude of not interfering with the subadult male's sexual advances towards females may have been the reason why all four reproductive females in the Cage produced an infant in the next birth season. It is possible that being a provisioned troop may have decreased stress from shortage of natural resources and it might be that these males were related. In the free-ranging troop, the dominant male's strategy of constantly following his male competitor reduced his own chances of impregnating some of the females of his group (only 4 of the 7 reproductive females gave birth). It is likely that the alpha male fathered most of the infants that season and that those potential infants did not have to compete for resources with infants fathered by his competitor (see also Wasser, 1983 for yellow baboons).

Therefore, the attitude of the dominant adult male of the troop can severely impair the mating opportunities for the younger or more subordinate males. Although no clear agonistic coalition by the two subadult males against a dominant male was seen in a sexual context (Smuts, 1987) the fact that these young males remained in proximity, might have been sufficient to deter the adult male from interfering in their sexual relationships. Certainly, his attempts to do so were unsuccessful.

It is postulated that vervet monkey sexual consortships are more common among male-female pairs that have 'special friendly' relationships during the non-mating season, *i.e.* they are generally closer and/or groom more often (for baboons: Seyfarth, 1978 b, Smuts, 1983; 1985; Strum, 1987). In addition, preliminary observations suggest that in vervets, male defence of females and immatures during the non-reproductive period influences the preference of these females for the next breeding season (see Saayman, 1971; Seyfarth, 1978b for baboons). The free-ranging dominant male invested more time in maintaining exclusive sexual access to middle and low ranking females than to high ranking females, possibly because those females showed a tendency to remain closer to his subordinate competitor.

The key strategies for improving male reproductive success are to mate when females are more likely to conceive and with females that can produce offspring with high survivorship rates (Bercovitch & Goy, 1990). That high ranking males tend to mate selectively with high ranking females is common (Hausfater, 1975; review in Berestain & Wade, 1983) and has already been found for vervets (Keddy, cited in Cheney & Seyfarth, 1990). Preferential selectivity to mate with females that have already produced an infant has also been observed (Smuts, 1987). Finally, in vervets the dominant males' sexual interest in females appears to fall more often with the presumed ovulation periods (see also Chapais, 1983a for rhesus; Janson, 1984 for capuchin monkeys) and declines sharply after they have conceived.

In conclusion, if the highest ranking adult males cannot completely stop other males from mating with females of the group, they may still mate with females at the right time, that is when ovulation is most probable (Chapais, 1983a for rhesus; Hausfater, 1975 p.110; Packer, 1979b but see Bercovitch, 1987 for baboons) and with the females that have more chances of having infants that will survive to adulthood (see Wrangham, 1980; Krebs & McCleery, 1984; Bercovitch, 1987) than other males. Similar results were found for vervets in this study.

Whether the differences in mate selectivity result from demographic ratios or are facultative responses to differing patterns of relatedness cannot be addressed with only two study populations. More data are necessary to determine the degree of promiscuity for vervets compared to baboons and macaques.

To assess male responsibility for maintaining sexual consortships with females when the chances of conception are higher (for baboons: Saayman, 1970; Hausfater, 1975; Seyfarth, 1978a) could not be determined in this study because no clear visual cues to signal the period of maximum receptivity in vervet females have been found (Andelman, 1987). It is thought that, as is the case for vervets, the low predictability of ovulation reduces the chances for a single male to control access to females. However, the contribution of chemosensory input through olfactory and other systems acting synergistically with visual or tactile cues cannot be ruled out for vervets.

The top ranking females sexually approached males as often or more than males approached them and were more successful than males during sexual interference. Together with the fact that low ranking females do not often initiate interactions with males (see also O'Brien, 1991), this suggests that female rather than male mate competition works as a short-term strategy to regulate male reproductive success (see also Hausfater, 1975 for baboons; Enomoto, 1974; Ruiz de Elvira & Herndon, 1986 for rhesus monkeys; Taub, 1980 for Barbary macaques; Silk & Boyd, 1983 for Japanese macaques; Pereira & Weiss, 1991 for lemurs). Therefore, it must not be overlooked that female mate choice acting concurrently with female mate competition has serious effects on male reproductive success (Lindburg, 1980 p. 361). This is in accordance to the theory of sexual selection which states that female mammals will show more mate selectivity than males and males would mate more indiscriminately (Emlen & Oring, 1977).

Consequently, females may influence male mating success and preference to mate with 'special friends', proved to be one of the determinants of mate choice for this study (see also Smuts, 1985; 1987). However, high dominance rank for males is in itself a mechanism which improves mating opportunities because it influences female mate choice. The herding of females may also serve to bias female preference for a particular male (for Japanese monkeys: Enomoto, 1981). In this study, the alpha male of the free-ranging troop herded females during both the mating and non-mating seasons, suggesting that it works as a long-term strategy. However, the finding that in vervets female choice of males, especially by the dominant female, may influence which male became dominant during a period of instability (Raleigh & McGuire, 1990), suggests that females may select helpful or non-aggressive males.

It is concluded that in general, subadult and subordinate male vervets rely more heavily on social friendly behaviour and consort relationships than do more dominant adult males. Its function may be to alter female preference for higher ranking males and at the same time females may benefit from close proximity to those males.

While the conclusions on sexual consortships drawn in this study are admittedly preliminary, similarities emerge with other studies on macaques (Lindburg, 1980) and baboons (Smuts, 1985; Bercovitch, 1987), and surprisingly not with other studies done on vervets (Andelman, 1987).

By using telemetry techniques to determine temperature changes in the female's internal genitalia as suggested by Hausfater (1975 p. 79) as a correlate of the moment of most probable ovulation, it would be possible to determine the distribution of male consorting activity and sporadic mating activity according to day cycle. Together with paternity tests (*e.g.* Burke, 1989) it would provide a better estimate of the reproductive success in a particular vervet monkey.

Although physiological processes are regulated by genes that pass from generation to generation, proximate mechanisms may vary between populations of the same species. Alternative strategies may arise and vary in accordance with specific needs, and generalisations must be made carefully (Dunbar, 1988 p.26). Thus, vervet males living in multi-male multi-female groups can display a number of different strategies in order to increase their reproductive output.

The importance of learning and social influence in sexual behaviour may separate behavioural from hormonal reasons to a greater extent in primates than in other species (Rose *et al.* 1974 p. 282; Lindburg, 1980 p.365). Among vervet monkeys in particular, it is argued that the physiological concomitants of reproductive behaviour are less important than behavioural differences in male-female interactions (Raleigh & McGuire, 1990).

### 8.5. THE EXTENT TO WHICH VERVET SOCIETIES DIFFER FROM OTHER MULTI-MALE SOCIETIES.

The use of infants during inter-male agonism has been extensively commented upon for baboons and macaques (review in Smuts, 1987). Non-dominant males rely on infants for agonistic buffering more heavily and they also provide more care for infants than dominant males *Papio cynocephalus* (Altmann *et al.* 1988). This point may also help to clarify why vervet males do not show much direct care of infants. When it occurs it is directed towards potential infants, especially when the male is the most dominant of the troop (Hauser, 1986; Keddy Hector *et al.* 1989). It has been argued that low ranking vervet males sometimes care for infants they certainly did not father, which suggests a strategy to improve mating opportunities with the mother (Keddy Hector *et al.* 1989) or an inability to distinguish their own infants. That females show preferences for those males exhibiting paternal care has also been reported for typically multi-male species (*e.g.* Smuts, 1987).

The fact that vervet females do not rely on male assistance as heavily as other Cercopithecines do, ought to be understood in terms of first, their slight sexual dimorphism that enables some females to be dominant over males more often than it is found among macaques and baboons (Kaplan, 1987, p. 140); second, female-female strong affiliative relationships reflected by small inter-individual distances and high frequencies of grooming (Seyfarth, 1977; Bernstein, 1980; Lopez-Lujan *et al.* 1989) regulates frequent agonistic coalition among females (Seyfarth, 1976; 1980; Fairbanks, 1980; Cheney, 1983b).

Female bonds and female philopatry have been related to the need of defending food resources (Mitchel *et al.* 1991) suggesting that agonistic coalition and remaining in the troop are correlated to the need of different members allying to defend discrete resources and increasing infant survivorship (*e.g.* Fairbanks, 1982b). However, this is not the case for males; vervet male social relationships are based on their genital signalling system which is likely to have evolved as an adaptive mechanism ensuring a reduction in reproductive success for resident subordinate males while maintaining low levels of open aggression.

The fact that male-male agonistic coalition, male-female sexual consortships and particularly social bonds that continue outside the mating period and involving male interference in female agonism have been described in this study, indicating that vervet society is more similar to other typically multi-male species than was previously understood (see review Smuts, 1987).



Vervet monkeys are highly adaptable and live in a wide range of demographic and environmental conditions. As an epiphenomenon of demography, vervet monkeys may be in one-male or multi-male groups (Lee, 1984) as it occurs for the spider monkey (*Ateles geoffroyi*) and the hanuman langur (*Presbytis entellus*), or in some cases age-graded groups as in the case of the gorilla (see Napier & Napier, 1985 tables 4 and 5) when only one adult male reproduces and subadult males may also participate in copulations (e.g. Struhsaker, 1967b, the Cage troop). This is possible because social systems are determined by behavioural interactions between individuals which reflect behavioural strategies that tend to maximise an individual's inclusive fitness (Silk, 1987).

The highly developed visual signalling system that regulates male-male interactions in vervets (Henzi, 1982) emphasises the multi-male nature of their societies. The evolution of ritualised displays of dominance and subordination facilitate the coexistence of unrelated adult males throughout the year and are rare or non-existent among non multi-male species (Young, 1983 for *Allouatta palliata*). The reason is that they require a high capacity for communication only possible because of the degree of neocortex development characteristic of the most complex multi-male multi-female societies (Sawaguchi & Kudo, 1990).

## REFERENCES

- Abegglen, J.J. 1984. *On socialization in hamadryas baboons: A field study*. Cranbury, New Jersey: Associated University Press, Inc.
- Albert, D.J., Petrovic, D.M., Jonik, R.H. & Walsh, M.L., 1990. Decline in testosterone-dependent aggression of male rats following replacement of intact female cagemate with ovariectomized female. *Psychobiology*, 18: 215-219.
- Alexander, R.D., 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics*, 5: 325-383.
- Altmann, J., 1974. Observational study of behaviour. *Behaviour*, 49: 227-265.
- Altmann, J., 1980. *Baboon mothers and infants*. Harvard University Press.
- Altmann, J., Hausfater, G. & Altmann, S.A., 1985. Demography of Amboseli baboons, 1963-1983 *American Journal of Primatology*, 8: 113-125.
- Altmann, J., Hausfater, G. & Altmann, S.A., 1988. Determinants of reproductive success in savannah baboons, *Papio cynocephalus*. *Reproductive success*. T.H. Clutton-Brock (ed.). pp.403-418. Chicago: The University of Chicago Press.
- Altmann, S.A., 1962. A field study of the sociobiology of rhesus monkeys *Macaca mulatta*. *Annual Review of the Academy of Science* (N.Y.), 102: 338-345.
- Altmann, S.A., 1979. Baboon progressions: order or chaos? A study of one-dimensional group geometry. *Animal Behaviour*, 27: 46-80.
- Andelman, S.J., 1986. Ecological and social determinants of Cercopithecine mating patterns. *Ecological aspects of Vertebrate social evolution*. D.I. Rubenstein and R.W. Wrangham. pp. 201-216. Princeton: Princeton University Press.
- Andelman, S.J., 1987. Evolution of concealed ovulation in vervet monkeys (*Cercopithecus aethiops*). *American Naturalist*, 129: 179-183.
- Andelman, S.J., Else, J.G., Hearn, J.P. & Hodges, J.K., 1985. The non-invasive monitoring of reproductive events in wild vervet monkeys (*Cercopithecus aethiops*) using urinary pregnanediol-3alpha-glucuronide and its correlation with behavioural observations. *Journal of Zoology* (Lond.), 205: 467-477.
- Anderson, C.M., 1986. Predation and primate evolution. *Primates*, 27:15-39.
- Bachmann, C. & Kummer, H., 1980. Male assessment of female choice in hamadryas baboons. *Behavioral Ecology and Sociobiology*, 6: 315-321.
- Bartecki, U., 1986. The social position of male barbary macaques (*Macaca sylvanus*) in a semifree-ranging population. *Primates*, 27:173-183.

- Basckin, D.R. & Krige, P.D., 1973. Some preliminary observations on the behaviour of an urban troop of vervet monkeys (*Cercopithecus aethiops*) during the birth season. *Journal of Behavioural Science*, 1(5):287-296.
- Bercovitch F.B., 1987. Reproductive success in male savanna baboons. *Behavioral Ecology and Sociobiology*, 21: 163-172.
- Bercovitch F.B. & Goy, R.W., 1990. The socioendocrinology of reproductive development and reproductive success in macaques. *Socioendocrinology of primate reproduction*. Monographs in primatology (Vol. 13). T.E. Ziegler & F.B. Bercovitch (eds.). pp. 59-93. New York: Wiley-Liss.
- Berenstain, L. & Wade, T.D., 1983. Intrasexual selection and male mating strategies in baboons and macaques. *International Journal of Primatology*, 4 (Review article): 201-235.
- Bernstein, I.S., 1980. Activity patterns in a stumptail macaque group. *Folia Primatologica*, 33:2-45.
- Bernstein, I.S. & Ehardt, C., 1986. The influence of kinship and socialization on aggressive behaviour in rhesus monkeys (*Macaca mulatta*). *Animal Behaviour*, 34: 739-747
- Bernstein, I.S., Rose, R.M., Gordon, T.P. & Grady, C.L., 1979. Agonistic rank, aggression, social context, and testosterone in male pigtail monkeys. *Aggressive Behaviour*, 5: 329-339.
- Bielert, C., Howard-Tripp, M.E. & Van der Walt, L.A., 1980. Environmental and social factors influencing seminal emission in chacma baboons (*Papio ursinus*). *Psychoneuroendocrinology*, 5: 287-303.
- Bielert, C. & Van der Walt, A., 1982. Male chacma baboon (*Papio ursinus*) sexual arousal: mediation by visual cues from female conspecifics. *Psychoneuroendocrinology* 7: 31-48.
- Blaffer Hrdy, S., 1974. Male-male competition and infanticide among langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica*, 22: 19-58.
- Blaffer Hrdy, S., 1977. *The langurs of Abu*. Cambridge, Massachusetts: Harvard University Press.
- Blaffer Hrdy, S. & Whitten, P.L., 1987. Patterning of sexual activity. *Primate societies*. B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, T. Struhsaker (eds.), pp. 370-383. Chicago: University of Chicago Press.
- Bolwig, N., 1978. Communicative signals and social behaviour of some African monkeys: A comparative study. *Primates*, 19: 61-99.
- Bramblett, C.A., 1978. Sex differences in the acquisition of play among juvenile vervet monkeys. *Social play in Primates*. pp 33-48. E.O. Smith (ed.). London: Academic Press.
- Bramblett, C.A., 1980. A model for development of social behaviour in vervet monkeys. *Developmental Psychobiology*, 13: 205-223.
- Bramblett, C.A. & Coelho, Jr., M., 1987. Development of social behavior in vervet monkeys, Sykes' monkeys, and baboons. *Comparative Behaviour of African monkeys* (pp.67-79). *Monographs in Primatology* (Vol 10) E.L. Zucker (ed.) New York: Alan R. Liss, Inc.

- Bramble, C.A., Pejaver, L.D. & Drickman, D.J., 1975. Reproduction in captive vervet and Sykes' monkeys. *Journal of Mammalogy* 56(4): 940-946.
- Burke, T., 1989. DNA Fingerprinting and other methods for the study of mating success. *Tree*, 4(5): 139-144.
- Butynski, T.M., 1988. Guenon birth seasons and correlates with rainfall and food. *A primate radiation: Evolutionary biology of the African guenons*. A.Gautier-Hion; F. Bourliere, J.P. Gautier & J. Kingdon (eds.). pp.284-322. Cambridge University Press.
- Byrne, R.W., Whiten, A. & Henzi, S.P., 1989. Social relationships of mountain baboons: Leadership and affiliation in a non-female bonded monkey. *American Journal of Primatology*, 18: 191-207.
- Cambeport, J.P., 1981. A comparative study of culturally transmitted patterns of feeding habits in the chacma baboon *Papio ursinus* and the vervet monkey *Cercopithecus aethiops*. *Folia primatologica*, 36:243-263.
- Carpenter, C.R., 1942a. Societies of monkeys and apes. *Biol. Sym.* 8:177-204.
- Carpenter, C.R., 1942b. Sexual behavior of free ranging rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, 33: 113-142.
- Carpenter, C.R., 1974. Aggressive behavioural systems. *Primate aggression, territoriality and xenophobia*, New York: Academic Press,
- Chalmers, N.R. & Rowell, T.E., 1971. Behaviour and female reproductive cycles in a captive group of mangabeys. *Folia Primatologica*, 14: 1-14.
- Chance, M.R.A., 1959. *What makes monkeys sociable?* New Scientist, 5: 520-523.
- Chance, M.R.A. & Jolly, C.J., 1970. *Social groups of monkeys, apes and men*. London: Thames and Hudson.
- Chapais, B., 1983a. Reproductive activity in relation to male dominance and the likelihood of ovulation in rhesus monkeys. *Behavioural ecology and sociobiology*, 12: 215-228.
- Chapais, B., 1983b. Matriline membership and male rhesus reaching high ranks in their natal troops. *Primate social relationships: An integrated approach*. R.A.Hinde (ed.). pp. 171-175. Oxford: Blackwell Publications.
- Chapais, B., 1986. Why do adult male and female rhesus monkeys affiliate during the birth season? *The Cayo Santiago macaques: History, behavior and biology*. R.G. Rawlins & M.J. Kessler (eds.). pp.173-200. Albany: State University of New York Press.
- Chapman, C.A., 1990. Ecological constraints on group size in three species of neotropical primates. *Folia Primatologica*, 55: 1-9.
- Chapman, C. & Fedigan, L.M., 1984. Territoriality in the St. Kitts vervet, *Cercopithecus aethiops*. *Journal of Human Evolution*, 13: 677-686.
- Cheney, D.L., 1978. Interactions of immature male and female baboons with adult females. *Animal Behaviour*, 26: 389-408.

- Cheney, D.L., 1981. Intergroup encounters among free-ranging vervet monkeys. *Folia primatologica*, 35: 124-146.
- Cheney, D.L., 1983a. Intergroup encounters among Old World monkeys. *Primate social relationships*. R.A. Hinde (ed.). pp.233-241. Oxford: Blackwell Scientific Publications.
- Cheney, D.L., 1983b. Extrafamilial alliances among vervet monkeys. *Primate social relationships*. R.A. Hinde (ed.). pp.278-286. Oxford: Blackwell Scientific Publications.
- Cheney, D.L., 1984. Category formation in vervet monkeys. *The meaning of primate signals*. R. Harre and V. Reynolds (eds.). pp. 58-74. Cambridge University Press. Great Britain.
- Cheney, D.L., Lee, P.C. & Seyfarth, R.M., 1981. Behavioral correlates of non-random mortality among free-ranging female vervet monkeys. *Behavioral Ecology and Sociobiology*, 9: 153-161.
- Cheney, D.L. & Seyfarth, R.M., 1981. Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour*, 76: 25-61.
- Cheney, D.L. & Seyfarth, R.M., 1982a. How vervet monkeys perceive their grunts: field playback experiments. *Animal Behaviour* 30: 739-751.
- Cheney, D.L. & Seyfarth, R.M., 1982b. Recognition of individuals within and between groups of free-ranging vervet monkeys. *American Zoologist*, 22: 519-529.
- Cheney, D.L. & Seyfarth, R.M., 1983. Non random dispersal in free-ranging vervet monkeys: Social and genetic consequences. *American Naturalist*, 122: 392-412.
- Cheney, D.L. & Seyfarth, R.M., 1987. The influence of intergroup competition on the survival and reproduction of female vervet monkeys. *Behavioral Ecology and Sociobiology*, 21: 375-386.
- Cheney, D.L. & Seyfarth, R.M., 1990. *How monkeys see the world: Inside the mind of another species*. Chicago: University of Chicago Press.
- Cheney, D.L., Seyfarth, R.M., Andelman, S.J. & Lee, P.C., 1988. Reproductive success in vervet monkeys. *Reproductive success*. T.H. Clutton-Brock (ed.). pp. 384-402. Chicago: The University of Chicago Press.
- Cheney, D.L. & Seyfarth, R.M. & Smuts, B., 1986. Social relationships and social cognition in nonhuman primates. *Science*, 234: 1361-1366.
- Cheney, D.L. & Wrangham, R.W., 1987. Predation. *Primate societies*. B.Smuts, D.Cheney, R.Seyfarth, R.Wrangham, T.Struhsaker (eds.), pp. 227-239. Chicago: University of Chicago Press.
- Chism, J. & Olson, D., 1982. Reproductive strategies of male patas monkeys. IX congress of the International Primatology Society. June 1982. Atlanta, Georgia.
- Chism, J. & Rowell, T.E., 1988. The natural history of patas monkey. *A primate radiation*. A.Gautier-Hion, F.Bouliere, J.P.Gautier and J.Kingdon, (eds.). pp. 412-438. Cambridge: Cambridge University Press.

- Clutton-Brock, T.H., 1974. Primate social organization and ecology. *Nature* (London), 250: 539-542.
- Clutton-Brock, T.H., 1977. Some aspects of intraspecific variation in feeding and ranging behaviour in primates. *Primate Ecology*. T.H.Clutton-Brock, (ed.). pp. 539-556. London: Academic Press.
- Clutton-Brock, T.H., 1989. Female transfer and inbreeding avoidance in social mammals. *Nature*, 337 (Letters to Nature).
- Clutton-Brock, T.H. & Harvey, P.H., 1976. Evolutionary rules and primate societies. *Growing points in ethology*. P.P.G. Bateson & R.A. Hinde (eds.). pp.195-237. Cambridge University Press.
- Clutton-Brock, T.H. & Harvey, P.H., 1977a. Primate ecology and social organization. *Journal of Zoology* (Lond.), 183: 1-39.
- Clutton-Brock, T.H. & Harvey, P.H., 1977b. Species differences in feeding and ranging behaviour in Primates. *Primate Ecology*. T.H.Clutton-Brock, (ed.). pp.557-583. London: Academic Press.
- Collins, D.A., 1986. Interactions between adult male and infant yellow baboons (*Papio c. cynocephalus*) in Tanzania. *Animal Behaviour*, 34: 430-443.
- Cords, M., 1990. Vigilance and mixed-species associations of some East African forest monkeys. *Behavioural Ecology and Sociobiology*, 26: 297-300.
- Cords, M., Mitchell, B.J., Tsingalia, H.M. & Rowell, T.E., 1986. Promiscuous mating among blue monkeys in the Kakamega forest, Kenya. *Ethology*, 72: 214-226.
- Cowlshaw, G. & Dunbar, R.I.M., 1991. Dominance rank and mating success in male primates. *Animal Behaviour*, 41: 1045-1056.
- Crook, J.H. & Gartlan, J.S., 1966. Evolution of primate societies. *Nature*, 210: 1200-1203.
- Curie-Cohen, M., Yoshihara, D., Blystad, C., Luttrell, L., Benforado, K. & Stone, W.H., 1981. Paternity and mating behavior in a captive troop of rhesus monkeys. *American Journal of Primatology*, 11335 (Abstracts): 335.
- Darwin, C., 1876. Sexual selection in relation to monkeys. *Nature*, 15, 18-19.
- Datta, S.B., 1983. Patterns of agonistic interference. *Primate social relationships: An integrated approach*. R.A. Hinde (ed.). pp. 289-297. Oxford: Blackwell Scientific Publications.
- Davies, N.B. & Houston, A.I., 1984. Territory economics. *Behavioural Ecology. An evolutionary approach* (2nd edition). J.R. Krebs and N.B. Davies (eds.). pp. 148-169. London: Blackwell Scientific Publications.
- Dawkins, R., 1976. *The Selfish Gene*. Oxford University Press.
- Deag, J.M. & Crook, J.H., 1971. Social behaviour and "agonistic buffering" in the wild barbary macaque *Macaca sylvana* L. *Folia primatologica*, 15:183-200.
- Dessi-Fulgheri, F., Messeri, P. & Lupo di Prisco, C., 1981. A study of testosterone, estradiol, cortisol and prolactin in a socially intact group of japanese macaques. *Antropologia Contemporanea*, 4(1-2): 123-127.

- DeVore, I., 1963. Mother-infant relations in free-ranging baboons. *Maternal behavior in Mammals*. H. Rheingold (ed.), pp. 305-335. New York: John Wiley.
- DeVore, I., 1964. The evolution of social life. *Horizons of Anthropology*. S. Tax (ed.), pp. 25-36. Chicago: Aldine.
- DeVore, I., 1965. Male dominance and mating behavior in baboons. *Sex and behavior*. F. Beach (ed.). New York: Wiley.
- Dittus, P.J., 1977. The social regulation of population density and age-sex distribution in the toque monkey. *Behaviour*, 63: 281-322.
- Dittus, P.J., 1979. The evolution of behaviors regulating density and age-specific sex ratios in a primate population. *Behaviour* 69: 265-302.
- Dittus, P.J., 1980. The social regulation of primate populations: A synthesis, Wolfgang. *The macaques: Studies in ecology, behavior and evolution*. Primate behavior and development series. D.G. Lindburg (ed.). pp. 203-286. New York: Van Nostrand Reinhold Company.
- Dixon, A.F., 1983. Observations on the evolution and behavioral significance of "sexual skin" in female Primates. *Advances in the Study of Behavior*, 13: 63-106
- Dixon, A.F., Hastie, N., Patel, I. & Jeffreys, A.J., 1988. DNA 'fingerprinting' of captive family groups of common marmosets (*Callitrix jacchus*). *Folia Primatologica*, 51: 52-55.
- Drickamer, L., 1974. A ten-year summary of reproductive data for free-ranging *Macaca mulatta*. *Folia Primatologica*, 21: 61-80.
- Drickamer, L., 1975. Patterns of space utilization and group interactions among free ranging *Macaca mulatta*, *Primates*, 16: 23-33.
- Dunbar, R.I.M., 1983a. Life story tactics and alternative strategies of reproduction. *Mate choice*. P. Bateson (ed.). pp. 423-433. London: Cambridge University Press.
- Dunbar, R.I.M., 1983b. Structure of gelada baboon reproductive units. II. Social relationships between reproductive females. *Animal Behaviour*, 31(parts 1 and 2): 556-564.
- Dunbar, R.I.M., 1983c. Structure of gelada baboon reproductive units. III. The male's relationships with his females. *Animal Behavior*, 31: 565-575.
- Dunbar, R.I.M., 1983d. Relations and social structure in gelada and hamadryas baboons. *Primate social relationships: An integrated approach* R.E. Hinde (ed.). pp. 299-307. Oxford: Blackwell.
- Dunbar, R.I.M., 1984. *Reproductive decisions: An economic analysis of gelada baboon social strategies*. Monographs in Behavior and Ecology. J.R. Krebs & T. Clutton-Brock (eds.). Princeton: Princeton University Press.
- Dunbar, R.I.M., 1985. Monogamy on the rocks. *Natural History*, 94 (11): 40-47.
- Dunbar, R.I.M., 1988. *Primate social systems*. Kent, England: Croom Helm Ltd.
- Dunbar, R.I.M. & Dunbar, P., 1988. Maternal time budgets of gelada baboons. *Animal Behaviour* 36: 970-980.



- Eaton, G.G., 1976. The social order of Japanese macaques. *Scientific American*, 235: 97-106.
- Eisenberg, J.F., 1981. *The mammalian radiations*. Chicago: Chicago University Press.
- Eisenberg, J.F., Muckenhirn, N.A. & Rudran, R., 1972. The relation between ecology and social structure in primates. *Science*, 176: 863-874.
- Emlen, S.T., 1973. *Ecology: An evolutionary approach*. Reading, Massachusetts: Addison-Wesley Publications.
- Emlen, S.T. & Oring, L.W., 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, 197: 215-223.
- Enomoto, T., 1974. The sexual behavior of Japanese monkeys. *Journal of Human Evolution*, 3: 351-372.
- Enomoto, T., 1981. Male aggression and the sexual behavior of Japanese monkeys. *Primates*, 22: 15-23.
- Fairbanks, L.A., 1980. Relationships among adult females in captive vervet monkeys: Testing a model of rank-related attractiveness. *Animal Behaviour*, 28: 853-859.
- Fairbanks, L.A., 1988a. Mother-infant behaviour in vervet monkeys: Response to failure of last pregnancy. *Behavioural Ecology and Sociobiology*, 23: 157-165.
- Fairbanks, L.A., 1988b. Vervet monkey grandmothers: Effects on mother-infant relationships. *Behaviour*, 104: 176-188.
- Fairbanks, L.A. & Bird, J., 1978. Ecological correlates of interindividual distance in the St. Kitts vervet (*Cercopithecus aethiops ascanius*). *Primates*, 19: 605-614.
- Fairbanks, L.A. & McGuire, M.T., 1984. Determinants of fecundity and reproductive success in captive vervet monkeys. *American Journal of Primatology*, 7: 27-38.
- Fairbanks, L.A. & McGuire, M.T., 1985. Relationships of vervet mothers with sons and daughters from one through three years of age. *Animal Behaviour*, 33: 40-50.
- Fairbanks, L.A. & McGuire, M.T., 1986. Age, reproductive value, and dominance-related behavior in vervet monkey females: Cross-generational influences on social relationships and reproduction. *Animal Behaviour*, 34: 1710-1721.
- Fairbanks, L.A. & McGuire, M.T., 1987. Mother-infant relationships in vervet monkeys: Response to new adult males. *International Journal of Primatology*, 8: 351-366.
- Fairbanks, L.A., McGuire, M.T. & Page, N., 1978. Social roles in captive vervet monkeys (*Cercopithecus aethiops sabaeus*). *Behavioural Processes* 3: 335-352.
- Feder, H.H., 1981. Estrus cyclicity in Mammals. *Neuroendocrinology of Reproduction*. N.T. Adler (ed.), pp. 279-248.
- Fedigan, L. & Fedigan, L.M., 1988. *Cercopithecus aethiops*: A review of field studies. *A primate radiation: Evolutionary biology of the African guenons*. A. Gautier-Hion, F. Boulière, J.P. Gautier & J. Kingdon (eds.). pp. 389-411. Cambridge University Press.



- Fedigan, L.M., Fedigan, L., Gouzoules, S. & Gouzoules, H., 1986. Lifetime reproductive success in female Japanese macaques. *Folia Primatologica*, 47: 143-157.
- Fleagle, J.G., 1988. *Primate adaptation and evolution*. New York: Academic Press.
- Forbes, H.O., 1896. A Handbook of the primates (I Vol.) *Lloyd's Natural History*. R.B. Sharpe (ed.). London: Edward Lloyd Limited.
- Forbes, H.O., 1897. A Hand-book of the Primates (II Vol.) *Lloyd's Natural History*. R.B. Sharpe (ed.). London: Edward Lloyd Limited.
- Fry, D.P., 1980. The evolution of aggression and the level of selection controversy. *Aggressive Behavior*, 6: 69-89.
- Gartlan, J.S., 1969. Sexual and maternal behaviour of the vervet monkey, *Cercopithecus aethiops*. *Journal of Reproduction and Fertility (Suppl.)*, 6: 137-150.
- Gartlan, J.S. & Brain, C.K., 1968. Ecology and social variability in *Cercopithecus aethiops* and *C. mitis*. *Primates: Studies in adaptation and variability*. P.C. Jay (ed.), pp 253-292. New York: Holt, Rinehart and Winston.
- Gautier, J.P. & Gautier-Hion, A., 1983. Comportement vocal des males adultes et organisation supraspecifique dans les troupes polyspecifiques de cercopitheques. *Folia Primatologica*, 40: 161-174.
- Gautier-Hion, A. & Tutin, C.E.G., 1988. Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. *Folia Primatologica*, 51: 149-151.
- Girolami, L., 1985. Steroid hormone influences on the mating behavior of vervet monkeys (*Cercopithecus aethiops*). *Hormones and Behavior*, 19: 1-13.
- Glick, B.B., 1979. Testicular size, testosterone level and body weight in male *Macaca radiata*: Maturational and seasonal effects. *Folia Primatologica*, 32: 268-289.
- Glick, B.B., 1980. Ontogenetic and psychological aspects of the mating activities of male *Macaca radiata*. *The macaques: Studies in ecology, behavior and evolution*. Primate behavior and development series. D.G. Lindburg (ed.) p.345-370. New York: Van Nostrand Reinhold Company.
- Goldfoot, D.A., 1981. Olfaction, sexual behavior, and the pheromone hypothesis in rhesus monkeys: A critique. *American Zoologist*, 21: 153-164.
- Goldman, B.D., 1981. Puberty. *Neuroendocrinology of reproduction*. N.T. Adler (ed.), pp. 229-241. New York: Plenum Press.
- Gonzalez, C.A., Hennessy, M.B. & Lewis, S., 1981. Subspecies differences in hormonal responses after group formation in squirrel monkeys, *American Journal of Primatology*, 1: 439-452.
- Goodall, A.G., 1977. Infant killing and cannibalism in free-ranging chimpanzees. *Folia Primatologica*, 28: 259-282.
- Gordon, T.P., Rose, R.M., Grady, C.L. & Bernstein, I.S., 1979. Effects of increased testosterone secretion on the behaviour of adult male rhesus living in a social group. *Folia primatologica*, 32: 149-160.

- Goss-Custard, J.D., Dunbar, R.I.M. & Aldrich-Blake, F.P.G., 1972. Survival, mating and rearing strategies in the evolution of primate social structure. *Folia Primatologica*, 17: 1-19.
- Gouzoules, H., 1974. Harassment of sexual behavior in the stump-tail macaque *Macaca arctoides*. *Folia Primatologica*, 22: 208-217.
- Hall, K.R.L., 1962. The sexual, agonistic, and derived social behaviour patterns of the wild chacma baboon, *Papio ursinus*. *Proceedings of the Zoological Society of London*, 139: 283-327.
- Hall, K.R.L., 1965. Behavior and ecology of the wild patas monkey, *Erythrocebus patas* in Uganda. *Journal of Zoology*, 14: 15-87.
- Hall, K.R.L., 1967. Social interactions of the adult male and adult females of a patas group. *Social communication among primates*. S.A. Altmann (ed.). pp.261-280. Chicago: Chicago University Press.
- Hall, K.R.L., 1968. Social organization of the Old-World monkeys and apes. *Primates: studies in adaptation and variability*. P.C. Jay (ed.). pp.7-31. Holt, Rinehart and Winston. New York.
- Hall, K.R.L. & DeVore, I., 1965. Baboon social behavior. *Primate behavior: Field Studies of monkeys and apes*. I. de Vore (ed.). pp.53-110. New York: Holt, Rinehart and Winston.
- Hall, K.R.L. & Gartlan, J.S., 1965. Ecology and behaviour of the vervet monkey, *Cercopithecus aethiops*, Lolui Island, lake Victoria. *Proceedings Zoological Society of London*, 145 (I): 37-56.
- Hamilton, W.D., 1964. The genetical evolution of social behavior, parts 1 and 2. *Journal of Theoretical Biology*, 7: 1-51.
- Hamilton III, W.J., 1984. Significance of paternal investment by primates to the evolution of adult male-female associations. *Primate paternalism*. D.M. Taub (ed.). pp. 309-335. United States of America: Van Nostrand Reinhold.
- Hanby, J., 1976. Sociosexual development in Primates. *Perspectives in ethology* (Vol. 2). P.P.G. Bateson and P.H. Klopfer (eds.). pp. 1-67. New York: Plenum Press.
- Harcourt, A.H., 1978. Activity periods and patterns of social interaction: a neglected problem. *Behaviour*, 66: 121-135.
- Harcourt, A.H. & Stewart, K.J., 1983. Interactions, relationships and social structure: the great apes. *Primate social systems: An integrated approach*. R.A. Hinde (ed.), pp. 307-313. Oxford: Blackwell Scientific Publications.
- Harding, R.S.O. & Olson, D.K., 1986. Patterns of mating among male patas monkeys (*Erythrocebus patas*) in Kenya. *American Journal of Primatology*, 11: 343-358.
- Harrison, M.J.S., 1983a. Territorial behaviour in the green monkey, *Cercopithecus sabaeus*: seasonal defense of local food supplies. *Behavioural Ecology and Sociobiology*, 12: 85-94.
- Harrison, M.J.S., 1983b. Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. *Animal Behaviour*, 31: 969-977.

- Hauser, M.D., 1986. Male responsiveness to infant distress calls in free-ranging vervet monkeys. *Behavioural Ecology and Sociobiology*, 19: 65-71.
- Hausfater, G., 1975. *Dominance and reproduction in baboons (Papio cynocephalus): A quantitative analysis*. Contribution to Primatology (Vol.7). Basel, Switzerland: S.Krager.
- Hausfater, G. & Hrdy, S.D., 1984. *Infanticide: Comparative and evolutionary perspectives*. Hawthorne, New York: Aldine.
- Henzi, S.P., 1981. Causes of testis-adduction in vervet monkeys. *Animal Behaviour (Short Communications)*, 29(3): 961-962.
- Henzi, S.P., 1982. Some aspects of visual signalling and social organization in the vervet monkey (*Cercopithecus aethiops pygerythrus*). Unpublished Ph.D. Durban: University of Natal.
- Henzi, S.P., 1985. Genital signalling and the coexistence of male vervet monkeys (*Cercopithecus aethiops pygerythrus*). *Folia Primatologica*, 45: 129-147.
- Henzi, S.P., 1988. Many males do not a multimale troop make. *Folia primatologica*, 51: 165-168.
- Henzi, S.P. & Lawes, M., 1987. Breeding season influxes and the behaviour of adult male samango monkeys (*Cercopithecus mitis albogularis*). *Folia Primatologica*, 48: 125-136
- Henzi, S.P. & Lawes, M., 1988. Strategic responses of male samango monkeys (*Cercopithecus mitis*) to a decline in the number of receptive females. *International Journal of Primatology*, 9: 479-495.
- Henzi, S.P. & Lucas, J.W., 1980. Observations on the intertroop movement of adult vervet monkeys (*Cercopithecus aethiops pygerythrus*). *Folia Primatologica*, 33: 220-235.
- Hill, D.A., 1986. Seasonal differences in the spatial relations of adult male rhesus macaques. *The Cayo Santiago macaques: History, behavior and biology*. R.G. Rawlins & M.J. Kessler (eds.). pp.159-172. Albany: State University Press.
- Hill, W.C.O., 1966. Superspecies *Cercopithecus aethiops* (IX). *Primates. Comparative Anatomy and Taxonomy (Vol.6) :Cercopithecoidea*. W.C.Oshan Hill (ed.). Edinburg University Press.
- Hinde, R.A., 1973. On the design of check-sheets. *Primates*, 14: 393-406.
- Hinde, R.A., 1977. On assessing the basis of partner preferences. *Behaviour*, 62: 1-9.
- Hinde, R.A., 1983. *Primate social relationships: An integrated approach*. Oxford: Blackwell Scientific Publications.
- Hooley, J.M. & Simpson, M.J.A., 1983. Influence of siblings on the infant's relationship with the mother and others. *Primate social relationships: An integrated approach*. R.A. Hinde (ed.), pp.139-141. Oxford: Blackwell Scientific Publications.
- Horrocks, J. & Hunte, W., 1983a. Maternal rank and offspring rank in vervet monkeys: an appraisal of the mechanisms of rank acquisition. *Animal Behaviour*, 31: 772-782.

- Horrocks, J.A. & Hunte, W., 1983b. Rank relations in vervet sisters: a critique of the role of reproductive value. *American Naturalist*, 122: 417-421.
- Horrocks, J.A. & Hunte, W., 1986. Sentinel behaviour in vervet monkeys: Who sees who first? *Animal Behaviour*, 34: 1566-1568.
- Huck, U.W. & Banks, E.M., 1982. Male dominance status, female choice and mating success in the brown lemming *Lemmus trimucronatus*. *Animal Behaviour*, 30: 665-675.
- Isbell, L.A., 1990. Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park, Kenya. *American Journal of Primatology*, 40: 41-52.
- Isbell, L.A., Cheney, D.L. & Seyfarth, R.M., 1990. Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. *Behavioural Ecology and Sociobiology*, 27: 351-358.
- Isbell, L.A., Cheney, D.L. & Seyfarth, R.M., 1991. Group fusions and minimum group sizes in vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology*, 25: 57-65.
- Iwamoto, T., 1982. Food and nutritional condition of free ranging Japanese monkeys on Koshima Islet during winter. *Primates*, 23: 153-170.
- Janson, C.H., 1984. Female choice and mating system of the brown capuchin *Cebus apella* (Primates: Cebidae). *Z. Tierpsychologie*, 65: 177-200.
- Jensen, G.D., Blanton, F.L. & Sassenrath, E.N., 1981. Sexuality of aging monkeys (*Macaca radiata*). *Primate behavior and sociobiology*. A.B. Chiarelli & R.S. Corruccini (eds.). pp.100-103. Heidelberg, Germany: Springer-Verlag.
- Johnson, D.F. & Phoenix, C.H., 1977. Hormonal control of female sexual attractiveness, proceptivity and receptivity in rhesus monkeys. *Journal of Comparative and Physiological Psychology*, 90: 4773-483.
- Johnson, J.A., 1989. Supplanting by olive baboons: Dominance rank difference and resource value. *Behavioural Ecology and Sociobiology*, 24: 277-283.
- Johnson, P.T., Valeiro, D.A. & Thompson, G.E., 1973. Breeding the African green monkey, *Cercopithecus aethiops*, in a laboratory environment. *Laboratory Animals Science*, 23: 355-359.
- Jolly, A., 1972. *The evolution of primate behavior*. New York: Macmillan.
- Jolly, A., 1985. *The evolution of primate behavior* (2nd. Edition). New York: McMillan Publishing Company.
- Jones, C.B., 1981. The evolution and socioecology of dominance in primate groups: A theoretical formulation, classification and assessment. *Primates*, 22: 70-83.
- Jouventin, P., 1975. Les roles des colorations du mandrill (*Mandrillus sphinx*). *Z. Tierpsychologie*, 93: 455-462.
- Kaplan, J.R., 1987. Dominance and affiliation in the Cercopithecini and Papionini: A comparative examination. *Comparative Behavior of African monkeys*. Monographs in Primatology (Vol.10). E.L.Zucker (ed.). New York: Alan R. Liss, Inc.

- Kaufmann, J.H., 1965. A three-year study of mating behavior in a free-ranging band of monkeys. *Ecology*, 46: 500-512.
- Kaufmann, J.H., 1967. Social relations of adult males in a free-ranging band of rhesus monkeys. *Social communication among primates*. S.A. Altmann (ed.). Chicago: University of Chicago Press.
- Kavanagh, M., 1980. Invasion of the forest by an african savannah monkey: Behavioural adaptations. *Behaviour*, 73: 238-260.
- Keddy Hector, A.C., Seyfarth, R.M. & Raleigh, M.J., 1989. Male parental care, female choice and the effect of an audience in vervet monkeys. *Animal Behaviour*, 38: 262-271.
- Keverne, E.B., 1983. Endocrine determinants and constraints on sexual behaviour in monkeys. *Mate choice*. P.Bateson (ed.). pp.407-420. Cambridge: Cambridge University Press.
- Keverne, E.B., Eberhart, J.A. & Abbott, D.H., 1984. Social influences on sex differences in the behaviour and endocrine state of talapoin monkeys. *Progress in Brain Research*, 61: 331-347.
- Keverne, E.B., Meller, R.E. & Eberhart, A., 1982. Dominance and subordination: Concepts or physiological states? *Advanced views in primatology*. A.B. Chiarelli & R.S. Corrucini (eds.). pp. 81-94. Berlin: Springer-Verlag.
- Kingdon, J., 1971. *East African Mammals (I)*. London: Academic Press.
- Kingdon, J. S., 1980. The role of visual signals and face patterns in African forest monkeys (guenons) of the genus (*Cercopithecus*). *Trans. Zool. Soc. Lond.*, 35: 425-475.
- Kingdon, J., 1988a. Comparative morphology of hands and feet in the genus *Cercopithecus*. *A primate radiation*. A.Gautier-Hion, F.Bouliere, J.P.Gautier and J. Kingdon (eds.). pp. 184-193. Cambridge University Press.
- Kingdon, J. S., 1988b. What are face patterns and do they contribute to reproductive isolation in guenons? *A primate radiation: Evolutionary biology of the african guenons*. A. Gautier-Hion, F. Bourliere, J.P. Gautier and J. Kingdon (eds.). pp. 227-245. Cambridge University Press.
- Krebs, J.R. & McCleery, R.H., 1984. Optimization in behavioural ecology. *Behavioural Ecology: An evolutionary approach* (2nd Edition). J.R.Krebs and N.B.Davies (eds.). pp 91-121. London: Blackwell Scientific Publications.
- Krige, P.D. & Lucas, J.W., 1974. Aunting behaviour in an urban troop of *Cercopithecus aethiops*. *Journal of Behavioural Science*, 2(2): 55-61.
- Krige, P.D. & Lucas, J.W., 1975. Behavioural development of the infant vervet monkey in a free ranging troop. *Journal of Behavioural Science*, 2(3): 151-160.
- Kummer, H., 1968. *Social organization of Hamadryas baboons*. Basel: Karger.
- Kurland, J.A., 1977. *Kin selection in the japanese monkey*. Contributions to primatology (Vol. 12).
- Lancaster, J.B., 1971. Play-mothering: The relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatologica*, 15: 161-182.

- Lee, P.C., 1983. Ecological influences on relationships and social structure. *Primate social relationships*. R.E. Hinde (ed.), pp. 225-229. Oxford: Blackwell Scientific Publications.
- Lee, P.C., 1984. Ecological constraints on the social development of vervet monkeys. *Behaviour*, 91: 245-262.
- Lernould, J.M., 1988. Classification and geographical distribution of guenons: a review. *A primate radiation*. A.Gautier-Hion, F.Bourliere, J.P.Gautier and J.Kingdon (eds.). pp 54-78. Cambridge University Press.
- Lindburg, D.G., 1969. Rhesus monkeys: mating season and mobility of adult males. *Science* (N.Y.), 166: 1176-1178.
- Lindburg, D.G., 1980. *The macaques: Studies in ecology, behavior and evolution*. New York: Van Nostrand Reinhold.
- Loizos, C., 1967. Play behaviour in higher primates: a review. *Primate Ethology*. O.Morris (ed.). pp 176-218. London: Weidenfeld and Nicolson.
- Lopez-Lujan, A.L., Ramirez Ochoa, I., Mayagoitia, L. & Mondragon-Ceballos, R., 1989. Sex differences in intra-group spacing behaviour in stump-tailed macaques (*Macaca arctoides*). *Folia Primatologica*, 52: 102-108.
- Lott, D.F., 1984. Intraspecific variation in the social systems of wild vertebrates. *Behaviour*, 88: 266-325.
- Loy, J., 1987. The sexual behaviour of African monkeys and the question of estrus. *Comparative Behavior of African monkeys*. Monographs in Primatology. E.L. Zucker (ed.). New York: Alan R. Liss, Inc.
- Loy, J., Loy, K., Patterson, D., Keifer, G. & Conaway, C., 1978. The behaviour of gonadectomized rhesus monkeys. I. Play. *Social Play in Primates* (pp. 49-78). E.O. Smith (Ed.). London: Academic Press.
- Machida, H. & Giacometti, L., 1967. The anatomical and histochemical properties of the skin of the external genitalia of the primates. *Folia primatologica*, 6:48-69.
- Martin, P. & Bateson, P., 1986. *Measuring behaviour. An introductory guide*. London: Cambridge University Press.
- McGuire, M.T., 1974. *The St. Kitts vervet*. Contributions to Primatology (Vol I). Basel: Karger.
- Meikle, D.B. & Vessey, S.H., 1988. Maternal dominance rank and lifetime survivorship of male and female rhesus monkeys. *Behavioural Ecology and Sociobiology*, 22: 379-383.
- Melnick, D.J. & Pearl, M.C., 1987. Cercopithecines in multimale groups: Genetic diversity and population structure. *Primate societies*. B.Smuts, D.Cheney, R.Seyfarth, R.Wrangham, T. Struhsaker (eds.), pp.121-134. Chicago: University Chicago Press.
- Meredith, M., 1983. Sensory physiology of pheromone communication. *Pheromones and reproduction in mammals*. J.G. Vandenberg (ed.). pp. 200-252. Orlando: Academic Press.

- Michael, R.P. & Herbert, J., 1963. Menstrual cycles influences grooming behaviour and sexual activity in rhesus monkeys. *Science*, 140: 500-501.
- Michael, R.P. & Zumpe, D., 1990. Sexual preferences during artificial menstrual cycles in social groups of rhesus monkeys (*Macaca mulatta*). *Primates*, 31: 225-241.
- Mitchel, C. L., Boinski, S. & van Schaik, C.P., 1991. Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedii* and *S. sciureus*). *Behavioral Ecology and Sociobiology*, 28: 55-60.
- De Moor, P.P. & Steffens, F.E., 1972. The movement of vervet monkeys (*Cercopithecus aethiops*) within their ranges as revealed by radio-tracking. *Journal of Animal Ecology* 41: 677-687.
- Mori, U., 1979. Reproductive behaviour. *Ecological and sociological studies of gelada baboons*. Contributions to Primatology. M. Kawai (ed.). pp.183-199.
- Moynihan, M., 1967. Comparative aspects of communication in New World primates. *Primate ethology*. D. Morris (ed.). pp. 236-265. London: Weidenfeld and Nicolson.
- Napier, J.R. & Napier, P.H., 1967. *A Handbook of Living Primates*. London: Academic Press.
- Napier, J.R. & Napier, P.H., 1985. *The natural history of the primates*. London: British Museum (Natural History) and the Cambridge University Press.
- Napier, P.H., 1981. *Catalogue of primates in the British Museum (Natural History) and elsewhere in the British Isles. Part II: Family Cercopithecidae, Subfamily Cercopithecinae*. London: Trustees of the British Museum (Natural History).
- Nigi, H., Hayama, S.I. & Torii, R., 1990. Copulatory behavior unaccompanied by ovulation in the japanes monkey (*Macaca fuscata*). *Primates*, 31: 243-250.
- Nigi, H., Tiba, T., Yamamoto, S., Floesheim, Y. & Ohsawa, N., 1980. Sexual maturation and seasonal changes in reproductive phenomena of male japanese monkeys (*Macaca fuscata*) at Takasakiyama. *Primates*, 21: 230-240.
- O'Brien, T.G., 1991. Female-male social interactions in wedge-capped capuchin monkeys: benefits and costs of group living. *Animal Behaviour*, 41: 555-567.
- Packer, C., 1977. Reciprocal altruism in *Papio anubis*. *Nature* (London), 265:441-443.
- Packer, C., 1979a. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Animal Behaviour*, 27: 1-36.
- Packer, C., 1979b. Male dominance and reproductive activity in *Papio anubis*. *Animal Behaviour*, 27: 37-45.
- Packer, C., 1980. Male care and exploitation of infants in *Papio anubis*. *Animal Behaviour*, 28: 512-520.
- Paul, A. & Kuester, J., 1987. Dominance, kinship and reproductive value in female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. *Behavioral Ecology and Sociobiology*, 21: 323-331.



- Pereira, M.E. & Macedonia, J.M., 1991. Ringtailed lemur anti-predator calls denote predator class, not response urgency. *Animal Behaviour*, 41: 543-544.
- Pereira, M.E. & Weiss, M.L., 1991. Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology*, 28: 141-152.
- Poirier, F.E., 1970. The Nilgiri langurs (*Prebytis johnii*) of South India. *Primate behaviour. Development in field and laboratory research*. pp.251-383. New York: Academic Press.
- Poirier, F.E., 1972. The St. Kitts green monkey (*Cercopithecus aethiops sabaeus*). Ecology, population dynamics, and selected behavioral traits. *Folia Primatologica*, 17: 20-55.
- Price, J.S., Burton, J.L., Shuster, S. & Wolff, K., 1976. Control of scrotal colour in the vervet monkey. *Journal of Medical Primatology*, 5: 296-304.
- Pulliam, H.R. & Caraco, T., 1984. Living in groups: Is there an optimal group size? *Behavioural Ecology: An evolutionary approach* (2nd Ed.). J.R.Krebs and N.B. Davies (eds). pp 122-147. London: Blackwell Scientific Publications.
- Pusey, A.E. & Packer, C., 1987. Dispersal and philopatry. *Primate societies*. B.Smuts, D.Cheney, R.Seyfarth, R.Wrangham, T.Struhsaker (eds.). pp.250-266. Chicago: University of Chicago Press.
- Raleigh, M.J., Brammer, G.L., Yuwiler, A., Flannery, J.W., McGuire, M.T. & Geller, E., 1980. Serotonergic influences on the social behavior of vervet monkeys (*Cercopithecus aethiops sabaeus*). *Experimental Neurology*, 68: 322-334.
- Raleigh, M.J. & McGuire, M.T., 1990. Social influences on endocrine function in male vervet monkeys. *Socioendocrinology of primate reproduction*. Monographas in primatology (Vol.13). T.E. Ziegler & F.B. Bercovitch (eds.). pp. 95-112. New York: Wiley-Liss.
- Ransom, T.W. & Rowell, T.E., 1972. Early social development of female baboons. *Primate socialization*. F.E. Poirier (ed.). New York: Random House.
- Rasmussen, K.L.R., 1983. Age-related variation in the interactions of adult females with adult males in yellow baboons. *Primate social relationships: An integrated approach*. R.A. Hinde (ed.), pp.47-52. Oxford: Blackwell Scientific Publications.
- Redican, W.K., 1975. Facial expressions in non-human primates. *Primate Behaviour* (Vol 4). L.A. Rosenblum (ed.), pp. 103-194. New York: Academic Press.
- Regal, P.J. & Connolly, M.S., 1980. Social influences on biological rhythms. *Behaviour*, 72(3-4): 171-199.
- Reinhardt, V., Dodsworth, R. & Scanlan, J., 1986. Altruistic interference shown by the alpha-female of a captive troop of rhesus monkeys. *Folia primatologica*, 46: 44-50.
- van Rhijn, J.G., 1980. Communication by agonistic displays: A discussion. *Behaviour*, 74: 284-293
- Richard, A.F., 1985. *Primates in nature*. New York: W.H.Freeman and Company.



- Richards, S.M., 1974. The concept of dominance and methods of assessment. *Animal Behaviour*, 22: 914-930.
- Ridley, M., 1986. The number of males in a primate troop. *Animal Behaviour*, 34: 1848-1858.
- Robinson, J.G., 1982. Intrasexual competition and mate choice in primates. *American Journal of Primatology (Suppl.)*, 1: 131-144.
- Rose, M.D., 1977. Positional behaviour of olive baboons (*Papio anubis*) and its relationship to maintenance and social activities. *Primates*, 18: 59-116.
- Rose, R.M., Gordon, T.P., Bernstein, I.S. & Catlin, S.F., 1974. Androgens and aggression: A review and recent findings in Primates. *Primate aggression, territoriality and xenophobia*. R.L. Halloway (ed.). New York: Academic Press.
- Rose, R.M., Holaday, J.W. & Bernstein, I.S., 1971. Plasma testosterone, dominance rank and aggressive behaviour in male rhesus monkeys. *Nature*, 231: 366-368.
- Rostal, D.C., Glick, B.B., Eaton, G.G. & Resko, J.A., 1986. Seasonality of adult male Japanese macaques (*Macaca fuscata*): Androgens and behaviour in a confined troop. *Hormones and Behaviour*, 20: 452-462.
- Rowell, T.E., 1967. Variability in the social organization of Primates. *Primate ethology*. D.Morris (ed.). pp. 219-235. London: Weidenfeld and Nicolson.
- Rowell, T.E., 1969. Longterm changes in a population of Ugandan baboons. *Folia Primatologica*, 11: 241-254.
- Rowell, T.E., 1971. Organization of caged groups of Cercopithecus monkeys. *Animal Behaviour*, 19: 615-645.
- Rowell, T.E., 1988. The social systems of guenons, compared with baboons, macaques and mangabeys. *A primate radiation: Evolutionary biology of the African guenons*. A.Gautier-Hion, F.Bourliere, J.P.Gautier & J.Kingdon (eds.). pp.439-451. Cambridge: Cambridge University Press.
- Rowell, T.E. & Hinde, R.A., 1963. Responses of rhesus monkeys to mildly stressful situations. *Animal Behaviour*, 11: 235-243.
- Rowell, T.E. & Richards, S.M., 1979. Reproductive strategies of some African monkeys. *Journal Mammalogy*, 60: 58-69.
- Ruiz de Elvira, M.C. & Herndon, J.G., 1986. Disruption of sexual behaviour by high ranking rhesus monkeys (*Macaca mulatta*). *Behaviour*, 96:227-240.
- Saayman, G.S., 1970. The menstrual cycle and sexual behavior in a group of free-ranging chacma baboons (*Papio ursinus*). *Folia Primatologica*, 12: 81-110.
- Saayman, G.S., 1971. Behaviour of the adult males in a troop of free-ranging chacma baboons (*Papio ursinus*). *Folia Primatologica*, 15: 36-57.
- Sade, D.S., 1965. Some aspects of parent-offspring and sibling relationships in a group of rhesus monkeys, with a discussion of grooming. *American Journal of Physical Anthropology*, 23:1-18.
- Sade, D.S., 1967. Determinants of dominance in a group of free-ranging rhesus monkeys. *Social communication among primates*. S. Altmann (ed.). Chicago: University of Chicago Press.

- Sade, D.S., 1972. A longitudinal study of social behavior of rhesus monkeys. *The functional and evolutionary biology of the primates*. R. Tuttle (ed.). Chicago: Aldine.
- Sade, D.S. Cushing, K., Cushing, p., Dunaif, J., Figueroa, A., Kaplan, J.R., Lauer, C. Rhodes, D. & Scheneider, J., 1977. Population dynamics in relation to social structure on Cayo Santiago. *Yearb Physical Anthropology*, 20: 253-262.
- Sawaguchi, T. & Kudo, H., 1990. Neocortical development and social structure in primates. *Primates*, 31: 283-289 (Short communication).
- van Schaik, C.P., 1983. Why are diurnal primates living in groups? *Behaviour*, 87: 120-144.
- van Schaik, C.P. & van Hooff, J.A.R.A.M., 1983. On the ultimate causes of primate systems. *Behaviour*, 85: 91-117.
- van Schaik, C.P. & van Noordwijk, M.A., 1989. The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. *Behavioural Ecology and Sociobiology*, 24:265-276.
- Schaller, G., 1963. *The mountain gorilla*. Chicago: University of Chicago Press.
- Schnell, G.D., Watt, D.J. & Douglas, M.E., 1985. Statistical comparison of proximity matrices: applications in animal behaviour. *Animal Behaviour*, 33: 239-253.
- Seyfarth, R.M., 1976. Social relationships among adult female baboons. *Animal Behaviour*, 24: 917-938.
- Seyfarth, R.M., 1977. A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65: 671-698.
- Seyfarth, R.M., 1978a. Social relationships among adult male and female baboons. I. Behaviour during sexual consortship. *Behaviour*, 44: 204-226.
- Seyfarth, R.M., 1978b. Social interactions among adult male and female baboons. II Behaviour throughout the female reproductive cycle. *Behaviour*, 44: 227-247.
- Seyfarth, R.M., 1980. The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behavior*, 28: 798-813.
- Seyfarth, R.M. & Cheney, D.L., 1982. How monkeys see the world: A review of recent reasearch on East African vervet monkeys. *Primate communication*. C.T. Snowdon, C.H. Brown & M.R. Petersen (eds.). pp. 239-252. London: Cambridge University Press.
- Seyfarth, R.M. & Cheney, D.L., 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, 308: 541-543.
- Seyfarth, R.M., Cheney, D.L. & Hinde, R.A., 1978. Some principles relating social interactions and social structure among primates. *Recent advances in primatology*. (Vol. I) D.J. Chivers & J. Herbert (eds.). LONDON: Academic Press.
- Seyfarth, R.M., Cheney, D.L. & Marler, P., 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, 28: 1070-1094.

- Shaikh, A.A., Celaya, C.L., Gomez, I. & Shaik, S.A., 1982. Temporal relationship of hormonal peaks to ovulation and sex skin deturgescence in the baboon. *Primates*, 23: 444-452.
- Sherman, P.W., 1977. Nepotism and the evolution of alarm calls. *Science*, 197: 1246-1253.
- Siegel, S. & Castellan, N.J. Jr., 1988. *Nonparametric statistics for the behavioural sciences*. United States of America: McGraw-Hill, Inc.
- Silk, J.B., 1987. Social behavior in evolutionary perspective. *Primate societies*. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, T.T. Struhsaker (eds.). pp. 318-329. Chicago: University of Chicago Press.
- Silk, J.B. & Boyd, R., 1983. Cooperation, competition, and mate choice in matrilineal macaque groups. *Social behaviour of female vertebrates*. S.K. Wasser (ed.). pp. 315-347. Academic Press.
- Silk, J.B., Clark-Wheatly, C.B., Rodman, P.S. & Samuels, A., 1981. Differential reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques. *Animal Behaviour*, 29: 1106-1120.
- Slobodchikoff, C.N. & Schulz, W.C., 1988. Cooperation, aggression, and the evolution of social behavior. *The ecology of social behavior*. C.N. Slobodchikoff (ed.). pp. 13-32. San Diego, United States of America: Academic Press.
- Smith, D.G., 1980. Paternity exclusion in six captive groups of rhesus monkeys (*Macaca mulatta*). *American Journal of Anthropology*, 53: 243-249.
- Smith, D.G., 1981. The association between rank and reproductive success of male rhesus monkeys. *American Journal of Primatology*, 1: 83-90.
- Smith, D.G., 1987. Generational bias in mating in captive groups of rhesus monkeys (*Macaca mulatta*). *Folia Primatologica*, 49: 212-215.
- Smuts, B.B., 1983. Special relationships between adult male and female olive baboons: selective advantages. *Primate social relationships*. R.A. Hinde (ed.). pp. 262-266. Oxford: Blackell Publications.
- Smuts, B.B., 1985. *Sex and friendship in baboons*. New York: Aldine Publishing Company.
- Smuts, B.B., 1987. Sexual competition and mate choice. *Primate societies*. Smuts, Cheney, Seyfarth, Wrangham & Struhsaker (eds.). pp. 385-399. Chicago: University Chicago Press.
- Sparks, J., 1967. Allogrooming in primates: A review. *Primate Ethology*. O. Morris (ed.). pp. 148-175. London. Weidenfeld & Nicolson.
- Stammbach, E. & Kummer, H., 1982. Individual contributions to a dyadic interaction: An analysis of baboon grooming. *Animal Behaviour*, 30: 964-971.
- Stein, D.M. & Stacey, P.B., 1981. A comparison of infant-adult male relations in a one-male group with those in a multi-male group for yellow baboons (*Papio cynocephalus*). *Folia Primatologica*, 36: 264-276.
- Strayer, F.F., 1976. Learning and imitation as a function of social status in macaque monkeys (*Macaca nemestrina*). *Animal Behaviour*, 24: 835-848.

- Struhsaker, T.T., 1967a. *Behaviour of vervet monkeys (Cercopithecus aethiops)*. Publications in Zoology: 82. University of California.
- Struhsaker, T.T., 1967b. Social structure among vervet monkeys (*Cercopithecus aethiops*). *Behaviour*, 29: 6-121.
- Struhsaker, T.T., 1967c. Auditory communication among vervet monkeys (*Cercopithecus aethiops*). *Social Communication among primates*. S.A. Altman (ed.). pp. 281-324. University of Chicago Press.
- Struhsaker, T.T., 1969. Correlates of ecology and social organization among African Cercopithecines. *Folia primatologica*, 11: 80-118.
- Struhsaker, T.T., 1977. Infanticide and social organization in the redbellied monkey (*Cercopithecus ascanius schmidtii*) in the Kibale forest. Uganda. *Z. Tierpsychologie*, 45: 75-84.
- Struhsaker, T.T. & Leland, L., 1979. Socioecology of five sympatric monkey species in the Kibale forest, Uganda. *Advanced studies of Behaviour*, 9: 159-228.
- Strum, S.C., 1982. Agonistic dominance in male baboons: An alternative view. *International Journal of Primatology*, 3: 175-202.
- Strum, S.C., 1983. Use of females by male olive baboons (*Papio anubis*). *American Journal of Primatology*, 5: 93-109.
- Strum, S.C., 1984. Why males use infants. *Primate paternalism*. D.M. Taub (ed.) pp. 146-185. United States of America: Van Nostrand Reinhold.
- Strum, S.C., 1987. *Almost human: A journey into the world of baboons*. New York: Random House.
- Sugiyama, Y., 1976. Life history of male Japanese macaques. *Advanced Study of Behavior*, 7: 255-284.
- Symons, D., 1978. Dominance and play. *Social play in primates*. E.O. Smith (ed.) pp. 193-230. New York: Academic Press.
- Takahata, Y., 1980. The reproductive biology of a free-ranging troop of Japanese monkeys. *Primates*, 21: 303-329.
- Tappein, N.C., 1960. Problems of distribution and adaptation of the african monkeys. *Current Anthropology*, 1(2): 91-120.
- Taub, D.M., 1980. Female choice and mating strategies among wild Barbary macaques (*Macaca sylvanus* L.). *The macaques*. D.G. Lindburg (ed.), pp. 287-344. New York: Van Nostrand Reinhold.
- Taub, D.M., 1984. Male caretaking behaviour among wild Barbary macaques (*Macaca sylvanus*). *Primate paternalism*. D.M. Taub (ed.), pp. 20-55. New York: Van Nostrand Reinhold.
- Taub, D.M. & Redican, W.K., 1984. Adult male-infant interactions in Old World monkeys and apes. *Primate paternalism*. D.M. Taub (ed.), pp. 377-404. New York: Van Nostrand Reinhold.
- Terborgh, J.W., 1983. *Five New World Primates: A study in comparative ecology*. Princeton: Princeton University Press.

- Thorington, R.W. & Groves, C.P., 1970. *Old World Monkeys. Evolution, systematics and behaviour*. J.R.Napier & P.H.Napier (eds.). New York: Academic Press.
- Timmermans, P.J.A., Schouten, W.G.P. & Krijnen, J.C.M., 1981. Reproduction of cynomolgus monkeys (*Macaca fascicularis*) in harems. *Laboratory Animals*, 15: 119-123.
- Tollman, S.G., 1975. An examination of the apparently "wasteful" feeding behaviour in *Cercopithecus aethiops*: a new perspective? *Journal of Behavioural Science*, 2(3): 99-114.
- Tollman, S.G., 1981. Adaptative strategies adopted by a free-ranging troop of vervets when placed in a specially designed enclosed environment. *Primate behavior and sociobiology*. A.B. Chiarelli & R.S. Corruccini (eds.). pp. 43-51. Heidelberg, Berlin: Springer-Verlag.
- Tollman, S.G., 1984. *Behaviour, biology and the social condition of Cercopithecus aethiops, the vervet monkey*. Unpublished Ph.D. of the Department of Psychology at the University of Natal (Durban).
- Tollman, S.G. & Lucas, J.W., 1979. Design and establishment of a primate troop enclosure. *South African Journal of Psychology*, 9: 138-144.
- Torres de Assumpcao, C. & Deag, J.M., 1979. Attention structure in monkeys. A search for a common trend. *Folia primatologica*, 31: 285-300.
- Trivers, R.L., 1972. Parental investment and sexual selection. *Sexual selection and the descent of Man*. B. Campdell (ed.). pp. 136-179. Chicago: Aldine.
- Troisi, A. & Schino, G., 1986. Diurnal and climatic influences on allogrooming behaviour in a captive group of Jave monkeys. *Animal Behavior*, 34: 1420-1426.
- Tsukahara, T., 1990. Initiation and solicitation in male-female grooming in a wild Japanese macaque troop on Yakushima Island. *Primates*, 31(2): 147-156.
- Underwood, R., 1982. Vigilance behaviour in grazing african antelopes. *Behaviour*, 79: 81-107.
- de Waal, F.B.M., 1982. *Chimpanzee politics*. London: Allen & Unwin.
- de Waal, F.B.M., 1991. Rank distance as a central feature of rhesus monkey social organization: A sociometric analysis. *Animal Behaviour*, 41: 383-395.
- Waites, G.M.H., 1970. Temperature regulation and the testis. *The Testis*. (Vol.I). A.D. Johnson, W.R. Gomes & N.L. Vandemark (eds.). pp. 241-279. New York: Academic Press.
- Walker, M.L., Wilson, M.E. & Gordon, T.P., 1983. Female rhesus monkey aggression during the menstrual cycle. *Animal Behaviour*, 31: 1047-1054.
- Wallis, J., 1981. Sexual behaviour in captive female chimpanzees (*Pan troglodytes*): Frequency and success rate in relation to various levels of tumescence and reproductive status. *American Journal of Primatology*, 11: 335 (Abstracts).
- Wasser, S.K., 1983. Reproductive competition and copulation among female yellow baboons. *Social behavior of female vertebrates*. S.K. Wasser (ed.). New York: Academic Press.

- Watson, L.H., 1985. *The feeding ecology of chacma baboons and vervet monkeys in the Hluhluwe-Umfolozi reserve*. Master of Science Thesis. Department of Zoology. University of Natal. Pietermaritzburg. South Africa.
- Wheatley, B.P., 1980. Feeding and ranging of east Bornean *Macaca fascicularis*. *The macaques: Studies in ecology, behavior and evolution*. Primate behavior and development series. D.G. Lindburg (ed.). pp.215-246. New York: Van Nostrand Reinhold Company.
- Whiten, A., Byrne, R.W. & Henzi, S.P., 1987. The behavioural ecology of mountain baboons. *International Journal of Primatology*, 8: 367-388.
- Wickler, W., 1967. Socio-sexual signals. *Primate ethology*. D. Morris (ed.). London: Weidenfeld & Nicholson.
- Wilson, E.O., 1975. *Sociobiology: The new synthesis*. Cambridge: Belknap Press of Harvard University Press.
- Wilson, M.E., 1980. Serum testosterone and social context influences on behavior of adult male rhesus monkeys. *Biology of Reproduction*, 22 (Suppl. 1): 137A.
- Wilson, M.E., Gordon, T.P. & Bernstein, I.S., 1978. Timing of births and reproductive success in rhesus monkeys social groups. *Journal of Medical Primatology*, 7: 202-212.
- Witt, R., Schimdt, C. & Schimtt, J., 1981. Social rank and Darwinian fitness in a multimale group of barbary macaques (*Macaca sylvana*, Linnaeus, 1758). *Folia primatologica*, 36: 201-211.
- Wrangham, R.W., 1979. On the evolution of ape social systems. *Social Science Information*, 18: 335-368.
- Wrangham, R.W., 1980. An ecological model of female-bonded groups. *Behaviour*, 75: 362-300.
- Wrangham, R.W., 1981. Drinking competition in vervet monkeys. *Animal Behaviour* 29: 904-910.
- Wrangham, R.W., 1986. Ecology and social relationships in two species of chimpanzee. *Ecological aspects of vertebrate social evolution: Birds and mammals*. D.I. Rubenstein & R.W. Wrangham (eds.). pp. 352-378. Princeton, New Jersey: Princeton University Press.
- Wrangham, R.W., 1987. Evolution of social structure. *Primate societies*. B.B. Smuts, D.L. Cheney, R.W. Wrangham, & T.T. Struhsaker (eds.). pp. 282-296. Chicago: University of Chicago Press.
- Young, O.P., 1981. Chasing behaviour between males within a howler monkey troop. *Primates*, 22: 424-426.
- Young, O.P., 1983. An example of 'apparent' dominance-submission behaviour between adult male howler monkeys (*Alouatta palliata*). *Primates*, 24: 283-287.
- Zar, J.H., 1974. *Biostatistical Analysis*. Prentice-Hall, N.J.
- Zeller, A.C., 1987. Communication by sight and smell. *Primates Societies*. B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, T. Struhsaker (eds.), pp. 433-439. Chicago: University of Chicago Press.

- Zucker, E.L., 1987. Social status and the distribution of social behavior by adult female patas monkey: A comparative perspective. *Comparative behavior of African monkeys*. Monographs in Primatology (Vol.10). E.L.Zucker (ed.). pp. 151-173. New York: Alan R. Liss. Inc.
- Zuckerman, S., 1932. *The social life of monkeys and apes*. London: Kegal Paul.
- Zumpe, D. & Michael, R.P., 1985. Effects of ovarian hormones on the behavior of captive *Macaca fascicularis*. *American Journal of Primatology*, 8: 167-181.



## Appendix A.

Direction of agonistic encounters involving adult males of the free-ranging troop (WT). They are ordered in decreasing dominance rank. Data was obtained from focal and scan sampling. The figures represent total frequency.

		R E C E P T O R				
		RO	LE	PE	CH	GR
A	RO	-	222	28	6	11
C	LE	2	-	13	8	0
T	PE	0	1	-	1	0
O	CH	0	0	0	-	0
R	GR	0	0	0	0	-

## Appendix B.

Direction of agonistic encounters involving adult females of the free-ranging troop (WT). They are ordered in decreasing dominance rank. Data was obtained from focal and scan sampling. The figures represent total frequency. Agonistic coalitions are not included.

		R E C E P T O R							
		HI	SM	MO	BE	WE	TO	VE	ET
	HI	-	10	3	3	4	2	7	2
A	SM	0	-	14	12	7	3	4	6
C	MO	0	1	-	6	11	2	6	5
T	BE	0	2	0	-	4	2	4	7
O	WE	0	0	0	2	-	5	4	4
R	TO	0	0	0	1	0	-	2	7
	VE	0	0	0	0	1	1	-	7
	ET	0	0	0	0	0	0	0	-



**Appendix C.**

Direction of agonistic encounters involving adult males of the Cage troop (CT). They are ordered in decreasing dominance rank. Data was obtained from focal and scan sampling. The figures represent total frequency.

	<b>R E C E P T O R</b>				
	<b>FT</b>	<b>GO</b>	<b>RN</b>	<b>FY</b>	<b>LU</b>
<b>FT</b>	-	11	22	19	1
<b>GO</b>	5	-	2	0	0
<b>RN</b>	8	0	-	34	3
<b>FY</b>	10	0	7	-	1
<b>LU</b>	1	0	0	1	-

**Appendix D.**

Direction of agonistic encounters involving adult females of the Cage troop (CT). Females are ordered in decreasing dominance rank. Data was obtained from all sampling methods. The figures represent total frequency. Agonistic coalitions are not included.

	<b>R E C E P T O R</b>					
	<b>XA</b>	<b>CE</b>	<b>PT</b>	<b>MC</b>	<b>MY</b>	<b>BA</b>
<b>XA</b>	-	9	9	12	8	3
<b>CE</b>	1	-	1	13	6	1
<b>PT</b>	0	0	-	7	9	9
<b>MC</b>	3	1	4	-	2	52
<b>MY</b>	2	0	3	0	-	9
<b>BA</b>	0	1	0	5	3	-