The behaviour of a social group of mandrills, *Mandrillus sphinx.*

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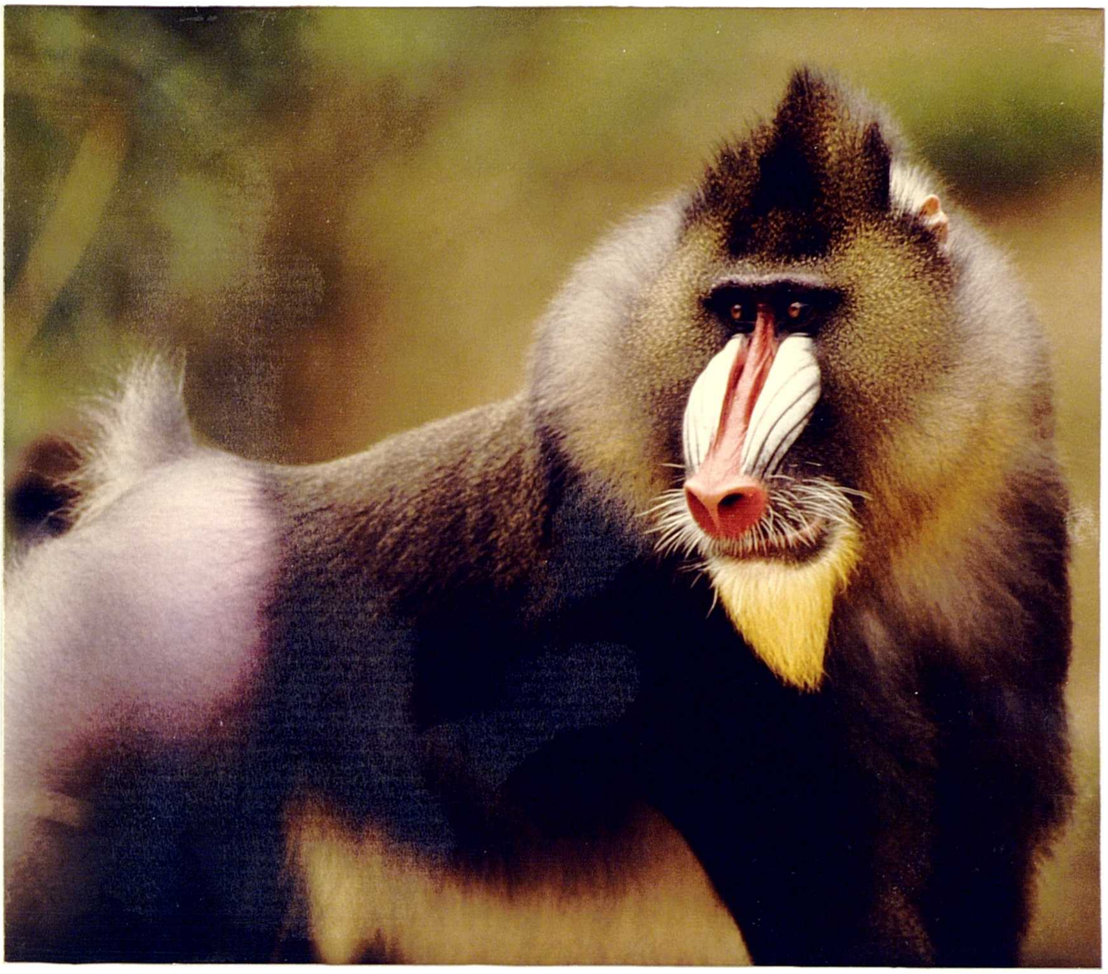

Mandrillus sphinx

The alpha male, CIRMF, Gabon

'This formidable animal, the fiercest and most powerful of its race, is a native of the Guinea Coast...Upon a nearer view however, these beauties do not compensate for its otherwise disgusting appearance.'

Jardine, 1833

These hideous and extraordinary animals live together in large companies, and are a terror to the natives...when adult, they are very savage.'

Lloyd, 1896

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ABSTRACT

A social group of 37 mandrills, with composition resembling a wild group, maintained in a 5.3 ha enclosure of natural relict gallery forest at CIRMF, Gabon was studied over 29 months. The 14 wild-caught founders (7 adult females, 2 adult and 5 subadult males) were the subjects of detailed behavioural study (15 months, 1200+ hours observation). Mandrills were captured at least annually to obtain blood samples, data on body weight, dental and reproductive status, and testicular volume.

Breeding was seasonal, with a 4-month mating season in which 92% of oestrous periods occurred. Oestrus synchrony was evident, with up to 5 females maximally swollen on any one day. Most (92%) copulations occurred at maximum swelling, with ejaculation in a single mount. 'Mate-guarding' of peri-ovulatory females by the alpha male involved sustained proximity to her and 'warning grunts' to other males. No herding behaviour was observed.

Spatial, grooming, and agonistic relationships were examined in detail. During anoestrus, males were rarely near females; three males were never recorded allogrooming. The alpha male spent significantly more time close to anoestrous females, grooming with them significantly more than the other males. Females spent time near each other, groomed with their offspring, and gave three-quarters of their grooming to and received nearly all grooming from founder females. During oestrus, male-female proximity increased, females spent more time grooming, groomed with fewer age-sex classes, groomed mostly with male founders, and received more grooming from males. Stable, linear dominance hierarchies existed within each sex.

Various aspects of mandrill biology - colouration, scent-marking, vocalisations - were interpreted as adaptations to ecological constraints of living semi-terrestrially in tropical forest. Results were used to assess models of single- and multi-male social organisation and male mating strategies. It was suggested that mandrills form one-male units, different from those of hamadryas and gelada baboons. Instead similarities with an Asian ecological analogue of the mandrill, the pig-tailed macaque, were emphasised.

CONTENTS

APPENDICES

CHAPTER I. INTRODUCTION

The aim of this introduction is to place the current study of the behaviour and social organisation of mandrills, *Mandrillus sphinx,* within a broad framework. First a brief outline of the history and taxonomy of the whole baboon group is given. Then the current distribution of the two members of the genus *Mandrillus* is described and their conservation status discussed. The state of the captive collections and the studies of zoo mandrills and drills are reviewed, followed by a brief synopsis of the data from studies of feral populations. Studying baboons is suggested as a useful means of examining the evolution and maintenance of sociality, with mandrills perhaps representing an ancestral condition. The present study of a group of semifree-ranging mandrills is introduced.

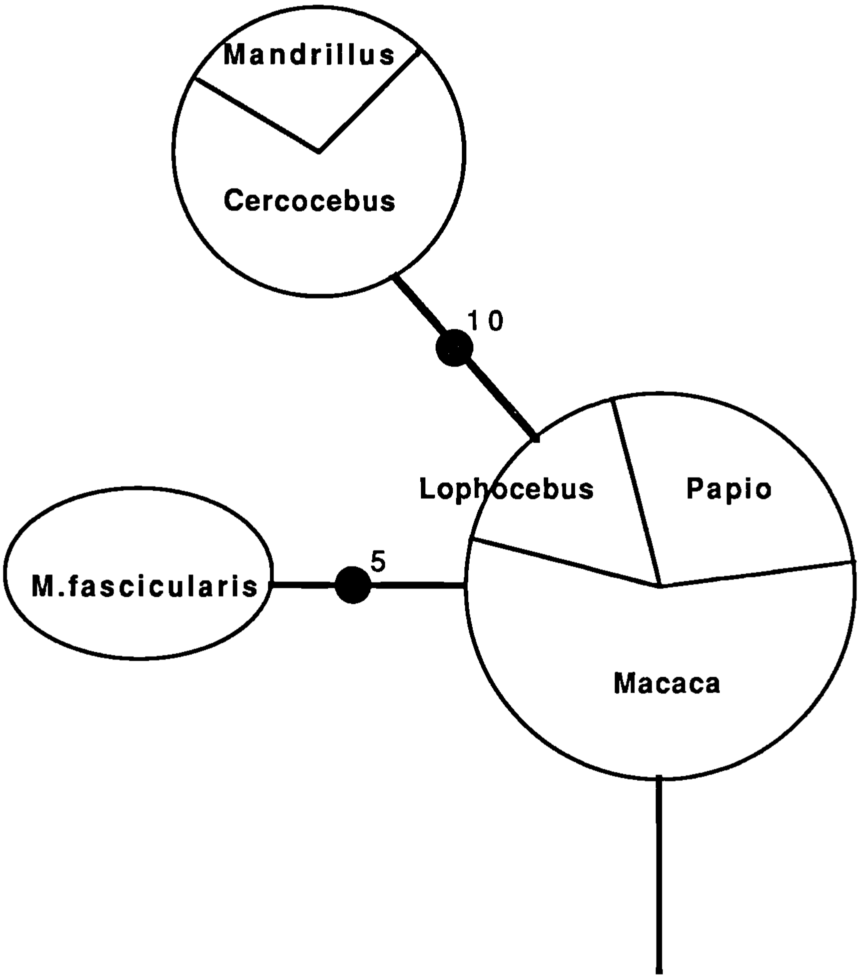
Hill (1970) gives a thorough account of the history of mandrills and drills (*Mandrillus sphinx* and *M. leucophaeus*) and the following is a summary from his description. Although at least two species of baboons (anubis and hamadryas) have been known since 4000 BC, the earliest reliable reference to a mandrill was in 1551 AD, when Gesner published a drawing of one. A male mandrill was first exhibited in captivity in Europe in the mid-17th century, at the Royal Menagerie at Copenhagen. Bartholin (1671-72) dissected the Copenhagen mandrill, drew it, and called it mammonet, an old French name coming from the medieval Latin mamonetus, which in turn was derived from the Old Persian word maimon or maimun, meaning ape (Hill, 1970). A mandrill was first brought to London in 1702. By the early 18th century there were more live mandrills in Europe and increasingly accurate descriptions, taken from living animals, were produced. For example, Alstroemer (1766) and Buffon (1766) both described live mandrills from the Paris menagerie. Previous accounts had been mostly copies from older texts, and transcriptions of verbal reports of travellers. Buffon was the first naturalist to adopt the name 'mandrill' and he claimed it was the one used by British traders along the West African coast. The first definite academic reference to a drill was in 1807 by Cuvier who described, figured, and named living individuals from the Paris menagerie.

A description of the historical taxonomy of the baboon group is also presented by Hill (1970). Although *Theropithecus* (Rüppell 1935) has long been the accepted generic name for the gelada (but see Buettner-Janusch, 1966) there has been considerable confusion over the correct generic name for the other baboons. Following Hill (1970) and Delson (1982) I will use *Papio* (Erxleben 1777) for the long-tailed savanna baboons and *Mandrillus* (Ritgen 1824) for the short-tailed forest baboons, since I think their generic separation is justified (see below). The medieval Latin name 'papio' was adapted from the Italian diminutive 'babbo'. From this root came also the modern European names, for example, German pavian, Polish pawian, Danish bavian, Spanish papion, French papion and babuin, Italian babbuino, and English baboon.

The generic splitting of *Papio* and *Mandrillus* is supported by immunological, chromosomal, and morphological data. Sarich (1970, p.206) stated that " 'baboon' albumins fall quite sharply into two groups: Drill and mandrill in one and all the others tested ... into the other" and it seems probable that the separation of the two genera is quite ancient (Cronin and Sarich, 1976). There has been limited chromosomal evolution in the Papioninae and only two alterations separate the karyotypes of the various genera. One (an inversion of chromosome 5) separates *Macaca fascicularis* (see Figure I.1). The other, a complex (3-break) rearrangement in chromosome 10, is common only to *Cercocebus* and *Mandrillus*, and thus separates them from *Papio*, *Theropithecus*, *Lophocebus*, and *Macaca* (Dutrillaux *et al.*, 1982; Muleris *et al.*, 1986). *Mandrillus* can be distinguished morphologically from *Papio* in the following ways: the nostrils are thick and distensible and surrounded by erectile tissue (not kept uniformly rigid by cartilage as in *Papio*); the upper surface of the muzzle has fusiform ridges; the hands and feet are adapted for arboreal climbing and branch walking and the hallux is long and powerful; the tail is a conical stump; the meatal cleft on the glans penis extends proximally on the dorsum almost to the corona; the catamenial swelling is between the

Figure I.1. Chromosomal evolution in the Papioninae

(redrawn from Muleris et al., 1986)



ischial callosities (not extending laterally beyond them as in *Papio*) and resembles that of mangabeys; there is a sternal glandular area with a tuft of hairs (Hill, 1970); and the premolar tooth series converge posteriorly (Napier and Napier, 1967).

Historically the specific nomenclature of the baboon group has also been muddled as the same epithet has frequently been used for a number of different species and even (for example in the Linnaean name sphinx) for different genera. There is still considerable discussion about the specific classification of the savanna baboons. Hill (1970) classifies the *Papio* baboons into five extant species (*P. anubis*, *P. cynocephalus*, *P. hamadryas*, *P. papio*, *P. ursinus*), the gelada baboon as *T. gelada*, and the forest baboons into two species, the mandrill and drill (*M. sphinx* (Linnaeus 1758) and *M. leucophaeus* (Cuvier 1807) respectively).

Electrophoresis of serum proteins suggests that the mandrill and drill are well differentiated (15 of 51 chromosome bands are different, D = 0.29, Lucotte and Jouventin, 1980; 4 out of 10 genes are different, D = 0.40, Lucotte, 1983). By contrast, all the *Papio* baboons seem very closely related (Lucotte, 1979; Lucotte and Lefebvre, 1980) - their chromosomes are identical (Dutrillaux *et al.*, 1982) - and some authors consider them phenotypic and genetic subspecies of *P. cynocephalus* (e.g., Devore and Washburn, 1963; Wiener and Moor-Jankowsky, 1969; cited in Dutrillaux *et al.*, 1982; Buettner-Janusch, 1966).

Both mandrill and drill are limited in distribution to areas of tropical forest in Central West Africa, but their exact distribution is unknown to the extent that it is still unclear whether they are allopatric (Grubb, 1973), or sympatric as implied originally by Zukowsky (1922, 1926), Jeannin (1936), Malbrant and Maclatchy (1949), and Dobroruka (1966), subsequently by Jolly (1970) and Hill (1970), and more recently by E.A. Williamson (pers. comm.), Nicoll and Langrand (1986), and Tutin and Fernandez (1987). The drill is the more northern of the two and has the more limited distribution, ranging from the Cross River in Nigeria to the Sanaga River in Cameroon (Grubb, 1973). It also exists offshore on Bioko (Fernando Po) (Grubb, 1973; Gartlan, 1975).

However, the drill is close to extinction in Nigeria and is restricted to an area of 300 by 250 km in Cameroon (IUCN, 1988). The mandrill ranges south from the River Sanaga throughout Rio Muni, Equatorial Guinea (Sabater Pi and Jones, 1967), although it seems to have been largely hunted out north of the Rio Mbini (M.P.T. Alers and A. Blom, pers. comm.). Further south, in Gabon, the distribution seems to be considerably more restricted than previously assumed (Malbrant and Maclatchy, 1949; Grubb, 1973; Harrison, 1988). The Ivindo and Ogooué Rivers form the eastern limits of distribution (Harrison, 1988; M.P.T. Alers and A. Blom, pers. comm.). The mandrill is absent from the coastal region west of the River Ngounié between the Rivers Ogooué and Nyanga, although it does occur south of the Nyanga (M.P.T. Alers and A. Blom, pers. comm.) and has been reported in parts of Congo (Grubb, 1973) and as far south as the mouth of the Zaire River (Malbrant and Maclatchy, 1949). The available data support allopatry with the Sanaga River dividing the two species. A critical examination of museum records (Grubb, 1973) showed that specimens indicative of sympatry had been misidentified or their localities confused. Observation of drills within the range of the mandrill has yet to be confirmed by a good photograph or a captured animal.

The relatively limited distribution of these two species, their restriction to areas of tropical forest, and the rapidity with which forest is being felled, means that both these forest baboons are vulnerable to extinction and their conservation status is of concern. They are at risk both through habitat destruction and from hunting.

Humans are the major predators of mandrills and drills throughout their range. Mandrills come under heavy hunting pressure in Cameroon (Wolfheim, 1983) and Equatorial Guinea (Sabater Pi, 1972). In Equatorial Guinea an enquiry into the diet of the Fang people revealed that 20% (from 100 reliable responses) of individuals classified mandrills as their most preferred meat, although only 4% stated it was the meat they consumed most frequently (Sabater Pi and Groves, 1972). Smoked and dried mandrill meat was often found in native markets (Sabater Pi, 1972). In Gabon, mandrill meat is also prized (pers. obs.). Mandrills and drills are caught in snares set for forest antelope and also are hunted with dogs, who drive the monkeys into the trees where they are easy targets for hunters with guns (Sabater Pi, 1972; Gartlan, 1975; Jouventin, 1975a; Harrison, 1988), and where twenty or more animals can be shot in a single encounter (M. Kabinga, pers. comm. for mandrills; Gartlan, 1975 for drills).

Both species are on Appendix I of CITES (1973) and are classified as endangered by the U.S. Endangered Species Act (1977). The mandrill is vulnerable to and the drill is in danger of extinction according to IUCN Red Data Book (1988) classification. The mandrill is found in five reserves (Dipikar and Campo, Cameroon; Wonga-Wongue and Lopé-Okanda, Gabon; Niari Valley, Congo) and the drill in three (South Bakundu and Korup, Cameroon; Oban, Nigeria) (Wolfheim, 1983). Korup and Oban are contiguous and both have national park status and so may protect a substantial part of the remaining drill population. However, in no reserve are either mandrills or drills completely protected, for example, logging continues and forestry permits have not been revoked in the Lopé Reserve, Gabon (Harrison, 1988) and hunting levels in Korup, Cameroon have not changed since the park's inception in 1986 (Gadsby, unpubl.).

Mandrills are popular zoo exhibits and nearly 50 zoos worldwide hold mandrills in their collections (ISIS, Dec. 1988). However, they are thinly distributed in zoos and average group size is four. Thirty-one percent of zoos have only a solitary or a pair of mandrills (ISIS, *op.cit.*). Although there are sufficient numbers (250 individuals) in captivity, the current situation is not conducive to successful captive breeding and adequate socialisation. Suggestions for improvement in the captive management of mandrills are made in Feistner and Cooper (in press). The captive population is not internationally managed and no studbook for mandrills has yet been compiled. The captive situation for drills is worse. There are fewer (approximately 60) drills in captivity (Böer, 1987a) and there has been only one zoo birth (the infant died within 30 days) since at least Dec. 1985 (ISIS, Dec. 1986, Dec. 1987, Jun. 1988, Dec. 1988).

This poor breeding record is perhaps partly explained by the fact that 75% of drills are not in the breeding population and most are kept as pairs or solitary individuals (Böer, 1985). However, it is hoped that this situation will improve as their captive propagation is now being coordinated. An international stud book has been compiled (Böer, 1987a), as well as a regional one for the United States. Propagation Groups have been set up by the seven North American zoos holding drills (C. Cox, pers. comm.). However, a large percentage of the current captive population is not yet sexually mature or is younger than ten years of age (Böer, 1987b).

With the exception of its congener the drill, the mandrill is the most poorly known in the wild of any member of the baboon family. The tropical forest environment, with its thick vegetation and poor, visibility, coupled with the wide-ranging and largely terrestrial habits of forest baboons has made them particularly difficult to study. There have been but five published field studies on mandrills (in Cameroon, Equatorial Guinea, and Gabon) totalling only 73 months and just one on drills (from Cameroon). This contrasts greatly with the extensively studied gelada, hamadryas, and savanna baboons. Information from the available literature on both forest species is reviewed and the socioecology of the genus *Mandrillus* is described in detail in a later chapter so the following is but a brief synopsis.

Mandrills and drills are usually found in groups of 20 to 40 individuals, but solitary individuals and large groups of a few hundred animals also have been observed. Adult males, due to their large size, bright colouring, and distinctive vocalisations, are the most noticeable individuals in the field, and it is clear that mandrills and drills form both one-male and multi-male groups. Small groups of less than 20 individuals contain only one adult male and larger groups contain more. From four to eight adult males are present in the largest groups. It seems that mandrills and drills may be polygynous, living in one-male groups which sometimes coalesce to form large congregations. Solitary individuals are invariably males but no all-male bands have been reported. The coalescing of one-male units into large groups has a seasonal basis in mandrills and is probably a consequence of food availability. Mandrills and drills are largely terrestrial, especially the adult males, although juveniles and adult females also use the higher strata of the forest. Both species climb high in the trees at night to sleep.

Mandrills are omnivorous, with fruit being the major constituent of the diet. Other plant parts and a wide variety of invertebrates make up most of the rest of the diet. Fungi, small vertebrates, and even young ungulates are occasionally taken. It is highly probable that the diet of drills is very similar to that of mandrills and so both are eclectic and catholic feeders, as are most baboons. Mandrills and drills are preyed on by leopards and crowned hawk eagles, although humans are probably their major predators.

The considerable size, impressive canines, and exuberant colouring of male mandrills makes them a popular exhibit in zoos, but they have been studied little in captivity. At the San Diego Zoo, California, Emory (1975a, 1975b, 1976) studied a group of five mandrills and compared their behaviour with a similarly-sized and identically-housed group of gelada baboons. At Washington Park Zoo, Oregon, Mellen *et al.* (1981) observed a group of six mandrills. These mandrills were also involved in studies of behavioural engineering (Yanofsky and Markowitz, 1978; Markowitz *et al.*, 1981). Kawata (1980) reported on 15 hours of observation of six mandrills at Tulsa Zoo, Oklahoma, and Chamove *et al.* (1988) on the effects of visitors on mandrills in the Vienna Zoo. There are even fewer published studies of zoo drills (Cox, 1987; Böer, 1987c; Hearn *et al.*, 1988). All have concentrated on social and reproductive behaviour with a view to improving captive breeding, both through environmental change (Hearn *et al.*, 1988) and behaviour modification (Cox, 1987; Desmond *et al.*, unpubl.; Desmond, 1988).

Of the Cercopithecidae the baboons exhibit perhaps the greatest variety of social groupings, both in terms of size, which may range from one to several hundred animals, and in terms of composition, with individuals grouped in all-male bands, one-male-units, or in multi-male troops. This range of social organisation indicates that study of baboons may be an interesting and useful way to explore the evolution of sociality in primates.

There are basically two sorts of pressures which influence the evolution and maintenance of sociality: (1) ecological pressures (of which the principal two are the distribution of food (Wrangham, 1980) and predation (Bertram, 1978)), and (2) social pressures (the behaviour of conspecifics in the individual's social milieu). The combined effects of these pressures are complex, partly because the nature of social pressure depends on ecological pressure (Wrangham, 1987).

In general, female behaviour seems closely adapted to ecological pressures as female reproductive success is directly affected by ecological constraints such as access to resources, especially food. By contrast, male fitness seems to vary as a function of access to females and mating success, and this depends on the distribution and behaviour of females (Emlen and Oring, 1977; Wrangham, 1979, 1980). Simplified, social organisation can be summarised as a result of the relationships of females to their environment and to each other, and the relationship of males to females and to other potentially competing males. However, it has also been argued that ecological pressure can act directly on males and influence male mating competition (Popp, 1983).

Various types of baboons are found over about two-thirds of the African continent, in habitats ranging from tropical forest to semi-desert, and in conditions of high to low predation risk, i.e., under a variety of ecological conditions and pressures. Baboons are behaviourally complicated animals and form groups containing individuals of different ages, sexes, dominance ranks, and kinship. In addition baboons also form temporary alliances, sub-groups, and long-term associations. This results in a complex network of interactions with numerous alternative strategies for survival and reproduction, and in social groups in which individuals are likely to pursue a number of different strategies during their lifetimes (Cheney *et al.*, 1987, p.3). In other words baboons also live under a variety of social conditions and pressures. So in relation to ecological and social constraints baboons again provide an instructive means by which to examine the evolution of social organisation.

In general the baboons are an extremely well-known group of monkeys, having been more widely and intensively studied in the wild than any other primate group (Richard, 1985); large amounts of data have accumulated on all but *P. papio* and the forest species - mandrills and drills. These last two forms, which live in the most complex habitat in terms of both floral and faunal communities, may represent the ancestral baboon condition (Szalay and Delson, 1979). If this is so, their social structure may be the 'basic' baboon organisation from which other species' social organisations evolved under the influence of various ecological and social pressures. The limited information available from field studies of mandrills and drills gives clues to some of the ecological pressures faced by a large-bodied, semi-terrestrial, frugivorous, tropical forest-dwelling primate and indicates that their basic social grouping may be a one-male-unit. However, virtually nothing is known about their social behaviour or the interactions and relationships between individuals which characterise and maintain their social organisation.

My aim then was to make a contribution to filling this gap by unravelling the nature of mandrill society using a study of social behaviour. In order to do this it was necessary to find a suitable study population.

As mentioned above, captive groups of mandrills in zoos generally contain very few individuals and so do not provide a suitable basis for studies of social behaviour. In addition abnormal behaviours and stereotypies are common (P. Schätzel, pers. comm., Chamove *et al.*, for mandrills; Hearn *et al.*, 1986 for drills) and several zoos contain drill x mandrill hybrids. Field study of wild mandrills is notoriously difficult and to date habituation and sustained observation has not been accomplished (there are no published field reports of social behaviour).

An excellent and unique compromise between these two alternatives was provided at the International Medical Research Centre of Franceville (CIRMF) in

Gabon, which had developed and maintained a semifree-ranging group of mandrills since 1979. A nine-month study of diet and feeding behaviour was carried out in 1982 and 1983 following the release of an initial 12 mandrills into a 1.4 ha enclosure (Norris, 1988). Since then the mandrills had formed a cohesive, reproducing group, and had been left undisturbed in their enclosure, except for limited daily provisioning at a peripheral feeding site. At the time of the current study the mandrills lived in a 5.3 ha enclosure of natural relict gallery forest and the group had grown in number from the original 15 individuals to 37. The relatively large size of the enclosure, the natural environment it provided, the mix of animals (all age- and sex-classes were represented), the presence of two generations and the beginning of matrilines, and the fact that Gabon is a habitat country for mandrills allows expression of a broad range of behaviour and the adoption of a reproductive pattern which may reflect that of wild mandrills. Thus in many respects the CIRMF mandrill facility provided ideal conditions for the close observation and study of social behaviour. The mandrills were the subjects of my behavioural study from 1986 to 1988.

The following chapter describes the establishment and history of the study group and the methodology used to describe and quantify various aspects of mandrill behaviour. The biology of the CIRMF mandrills, including information on their growth and reproduction, is described in Chapter III. Descriptions of mandrill behaviour and a review of the field studies on mandrills and drills are presented in Chapter IV. Chapters V and VI present data on social behaviour (particularly in terms of proximity, grooming, and agonistic relationships) of the group. Chapter V contains information on interactions and relationships during periods when females were anoestrous and in Chapter VI sexual relationships and the effect of oestrus on relationships are described.

In Chapter VII an attempt is made to provide a more complete understanding of mandrills by integrating the biological and behavioural data on mandrills resulting from this study and ecological information from studies of wild mandrills. Various aspects of mandrill biology and behaviour are discussed in the context of their ecology as a large-bodied, frugivorous, semi-terrestrial, tropical-forest dwelling primate. Diet and inter-specific competition for food are considered. Features of mandrills such as colouration, scent-marking, and vocalisations are interpreted as adaptations to the ecological constraints of tropical forest. The lack of consensus as to mandrill social organisation, i.e., whether the basic social grouping of mandrills is a single- or multi-male group is discussed and data from this thesis are applied to Dunbar's (1988) model relating to this. Spatial, grooming, and agonistic relationships of mandrills are discussed and briefly compared with those of hamadryas and gelada baboons. Popp's (1983) predictions relating to ecological determinism in baboons are assessed using the data on mandrills. Similarities of mandrills to a possible Asian ecological analogue, the pig-tailed macaque, are explored.

CHAPTER II.

MATERIALS AND METHODS

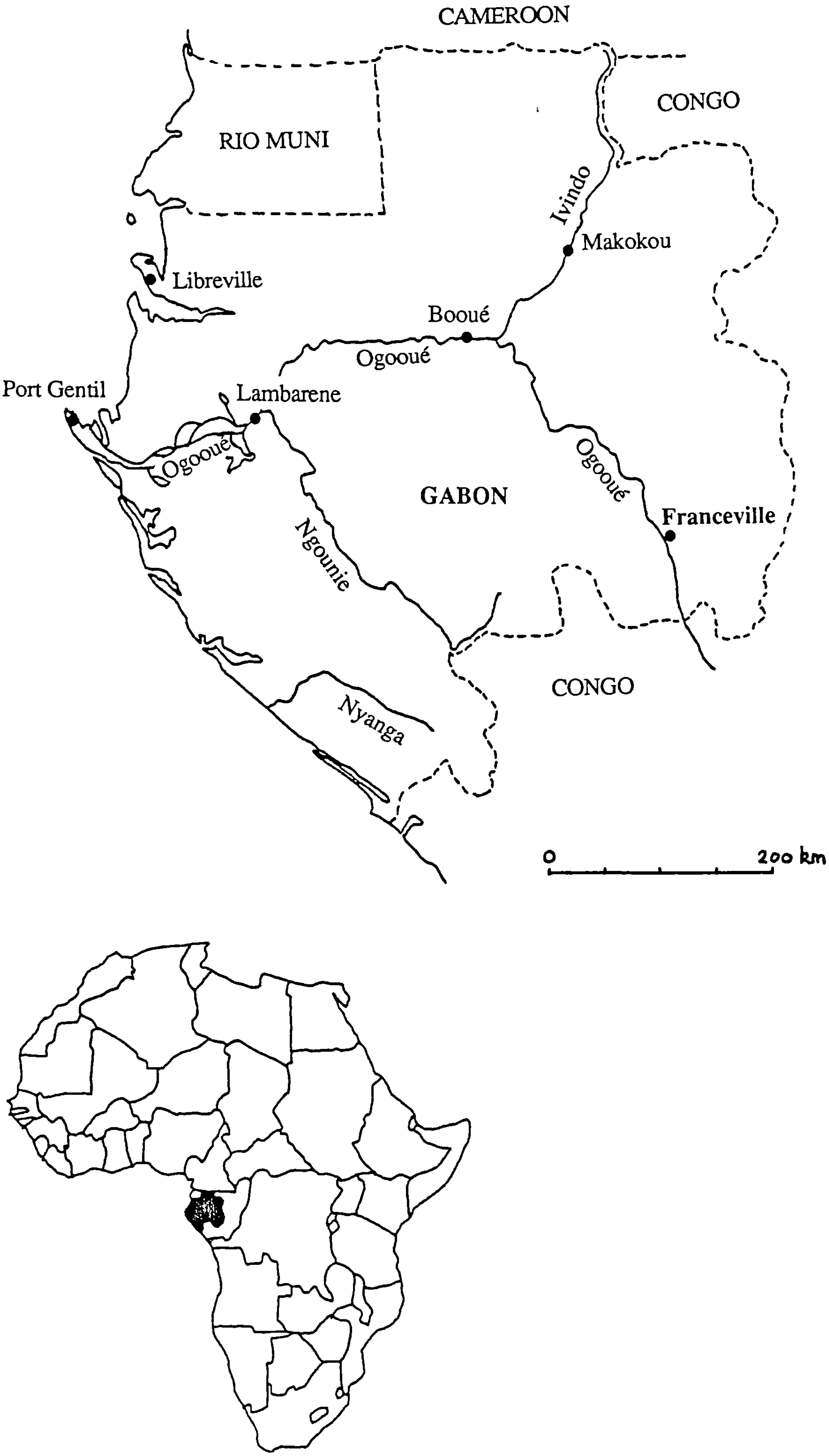
In this chapter the study site and the establishment and history of the mandrill group are described. The mandrills were trapped periodically and capture procedures involving anaesthesia and examination are reported. A brief description is given of the feasibility study, and of the preparatory work, including habituation and identification of the mandrills. Sampling and recording techniques are described and discussed. The main study is divided into two parts, and the behavioural observations made in each are described. Definitions of behaviour are given later, in Chapter IV. Some examples of individual checksheets are included in the appendices. Finally, some practical problems, particularly in relation to poor visibility of the mandrills and aggression directed at the observer, are discussed.

Study Site

The International Medical Research Centre (Centre International de Recherches Médicales de Franceville, CIRMF) is situated in Franceville (15 5' S, 13 40' E), the capital of the Haut Ogooué Province, in the south-east of Gabon - a region of savanna and gallery forest mosaic. The town of Franceville is just outside the natural range of the mandrill, being on the east side of the Ogooué River (Figure II.1). However, mandrills can be found wild only 30 to 50 km away to the west and south-west. The Primatology Centre (Centre de Primatologie, CDP) at CIRMF managed captive groups of chimpanzees, gorillas, guenons, and macaques, as well as the mandrills who were the subjects of this study.

Mandrill enclosures: An upper tributary of the Ogooué River, the M'Passa River, marks the northern boundary of the CIRMF campus, and much of its bank is

Figure II.1. Map of Gabon



lined by a narrow gallery forest. An extension of this relict forest exists southward along a small stream at CIRMF in terrain too steep near its double origins and along most of its 500 m course, and too swampy near its terminus, to have been cleared in the past for plantations. It was here, during the construction of CIRMF in the late 1970's, that nearly seven hectares of forest were fenced and divided to provide two adjacent enclosures as naturalistic settings for the study of Gabonese primates. The area is surrounded and partitioned by a low (0.60 m) cement block wall which supports a chain link fence 1.86 m tall, on top of which five pairs of alternating electrified and ground wires are angled inwards. On the perimeter and connected to both enclosures is a small service structure with an enclosed cage 5.95 x 2.90 x 1.80 m for animal introductions or treatment, and adjacent feeding yards 11.85 x 5.50 m in which animals can also be captured or held.

Immediately inside the perimeter fence is a 2 m ring of bare or sparsely vegetated earth, maintained by occasional cutting. Any saplings which might overhang the fence are also cut. The cleared area outside the fence, due to the presence of a service road which encircles most of the enclosure, prevents branches hanging into the enclosure from outside. Between the peripheral clearing just inside the fence and the taller trees in the centres of the enclosures is a variable band of grass, fern, shrubs, and saplings. The most dominant tree species (with a diameter at breast height of at least 13 cm) is *Musanga cecropoides*, which grows mainly at the grass-sapling interface. The next most common species are *Pachypodanthium staudtii*, *Aucoumea klaineana*, and *Pentaclethra eetveldiana* and together they represent over 50% of the individual trees (Norris, 1988).

Establishment and history of the mandrill group

Acquisition: Between mid-1979 and mid-1981 CIRMF acquired by donation a total of 12 mandrills (six males and six females) originally orphaned by hunters as infants or, in several cases, trapped in ground snares as juveniles too small to be worth eating or selling for food. Two of the latter (Males Nos. 7 and 9) lost major portions of a limb and a few others exhibited lesser injuries, all apparently incurred during capture. With the exception of one adult female about five years old, they ranged from approximately 6 to 24 months of age upon receipt at CIRMF and were most commonly about one year old. Age estimations were based primarily on dentition (Lawrence *et al.*, 1982; Swindler, 1985), but also on body size and weight (Cooper and Feistner, unpublished observations) and, in a few cases, previous history in captivity.

Quarantine: On arrival at the CDP all mandrills had an identity number (corresponding to their order of arrival) tatooed on their chest and were quarantined. Each passed three intradermal tuberculin tests and a similar number of faecal cultures for enteric bacterial pathogens. All infestations with potentially pathogenic protozoa and helminths of the gastrointestinal tract were treated until faecal examinations were repeatedly negative. These parasitic infestations and subsequent ones are described in Chapter III. Following quarantine, each mandrill was placed in one of two 7.50 x 6.50 x 2.50 m outdoor cages in which they were segregated according to size; the oldest and largest mandrills in one, the smallest and youngest individuals in the other.

Release into the enclosure: In August 1982 the six youngest mandrills (Nos. 6, 10, 12, 13, 14, and 15) were released into the smaller (1.4 ha) of the two enclosures, followed by the next three oldest animals (Nos. 2, 3, and 5) in September and the three oldest and largest (Nos. 1, 7, and 9) in October. Once daily they were provided, at a site near the service structure, with the diet to which they were already accustomed, namely bread and a variety of wild and cultivated fruits and vegetables (aframomum, avocado, avouma, banana, cabbage, cucumber, guava, lettuce, mango, orange, papaya, pineapple, tomato), depending on the season. Despite this provisioning the mandrills spent about 67% of their time foraging elsewhere in the enclosure (Norris, 1988). Nine months after their release some vegetational damage had become obvious, particularly to young *Musanga* or parasol trees at the enclosure's edge. This was a result of the mandrills feeding heavily on petioles, emerging leaves, and apical ends of branches. In addition, the extensive undergrowth of vines and Marantaceae had been virtually cleared by mandrills feeding at ground level on leaves, shoots, stem pith, and roots (Norris, *op. cit.*). Consequently, in May 1983 the group of 12 mandrills, with some females visibly pregnant, was moved to the larger (5.3 ha) and steeper enclosure, which encompassed the middle portion of the stream and its two upper branches. Shortly thereafter a juvenile female (No. 17) was added to the group. Another female (No. 16) and a juvenile male (No. 18) joined the group in March and December 1984 respectively. All further additions to the group of 15 introduced mandrills (8 females, 7 males) occurred only by birth.

Besides continuing the once-daily provisioning of the mandrills in the large enclosure, automatic drinking valves were added at the feeding site as well as a dispenser for providing pelleted primate diet (Extralabo Croquette Singes, Pietrement, Provins, France) *ad libitum*. The mandrills continued to visit the feeding site at the elevated perimeter of the enclosure only briefly each day and to spend the rest of their time in the forest below, foraging largely in the leaf litter and to a lesser extent in the dense emergent vegetation.

Feasibility study

As no one had been in the enclosure with the mandrills for two and a half years, in October 1985 I undertook a three-week feasibility study to gauge whether or not it would be possible to do an intensive study of the mandrills. During this period I first spent some time observing the mandrills when they came to the feeding site. Then I went into the enclosure accompanied by one of the personnel of the CDP, and finally I spent many hours alone with the mandrills. As I was able to approach them closely and watch them without any adverse reaction on their part, and they seemed to show a wide range of behaviour with no obvious stereotypies, I concluded that it would be possible to carry out a longer-term study.

Captures of the mandrill group

During this brief feasibility study the entire group of mandrills was captured. The animals had not been caught and examined since October, 1983, so the group contained individuals born since that date who had no identification number. The capture gave me the opportunity to look closely at unconscious mandrills, take various measurements, and enabled the CDP records to be updated. The mandrills were trapped at the feeding site by closing the small access door remotely by pulling a rope when most or all of the group had entered. The procedures involved are described below.

Anaesthesia: The mandrills were anaesthetised with a mixture of Ketamine hydrochloride at 100mg/ml and Acepromazine at 5mg/ml on a basis of 8 to 10 mg Ketamine per kg body weight. Adult females and ventral infants were given intramuscular injections using a hand-held syringe, juveniles were caught in a net and then injected, and subadult and adult males were darted using a blow-pipe. The anaesthetised mandrills were then taken to the CDP.

Identification: All the individuals were tattooed with an identification number. To all those previously identified by chest tattoos (with the exception of those with unambiguous distinguishing marks such as a missing limb) two further tattoos were given, one on the inner thigh (right thigh for females, left for males), the other on an ischial callosity. However, this latter tattoo soon sloughed off. Previously unmarked individuals were given all three. Juveniles and infants were also given a freeze-brand on the forearm (left for females, right for males) which corresponded to their identification number. The ischial tattoo was the most easily observed of the identification marks, being visible as long as the animal did not sit down, whereas other marks were hidden by the fur. However, it was not used subsequently since it was found to provide only a temporary marking as it lasted only a few weeks before disappearing as the skin of the callosities was replaced.

Examination: The following examinations and measurements were carried out: weight (in kg to the nearest 10 g), rectal temperature (^{o}C), dental record including measurements of all permanent canine teeth (length was measured from the tip of the tooth to the gingiva using calipers), testicular measurements of all males (length and width of the left testis in mm, using calipers), and digital rectal palpation for pregnancy of adolescent and adult females.

Sampling and treatment: Blood was drawn for blood formula, routine haematology, and blood parasite screening (for microfilaria and *Plasmodium* trophozoites). Serum samples were stored at -70^{o} C. Each mandrill was tuberculin tested (Intramax poly-intravac; Rhone Merieux) using 0.1 ml intradermally for adults, and 0.05 ml I.D. for juveniles. An anti-helminth (Zentel albendazole; Smith Kline and French) was administered by gastric tube; 20 ml for adults, 10 ml for juveniles, and 5 ml for infants.

Recovery: The animals were then returned to the enclosure and placed in the shade to recover from anaesthesia. Large males were left at widely-separated locations, infants were left with their mothers, and all individuals were monitored to recovery.

The whole group was captured and 'processed' in this way every October from 1985 to 1987 inclusive. In addition, adult females were captured within a few months of giving birth to tatoo and freeze-brand their young infants, and the whole group was captured in April 1988.

In January 1986 I commenced my study.

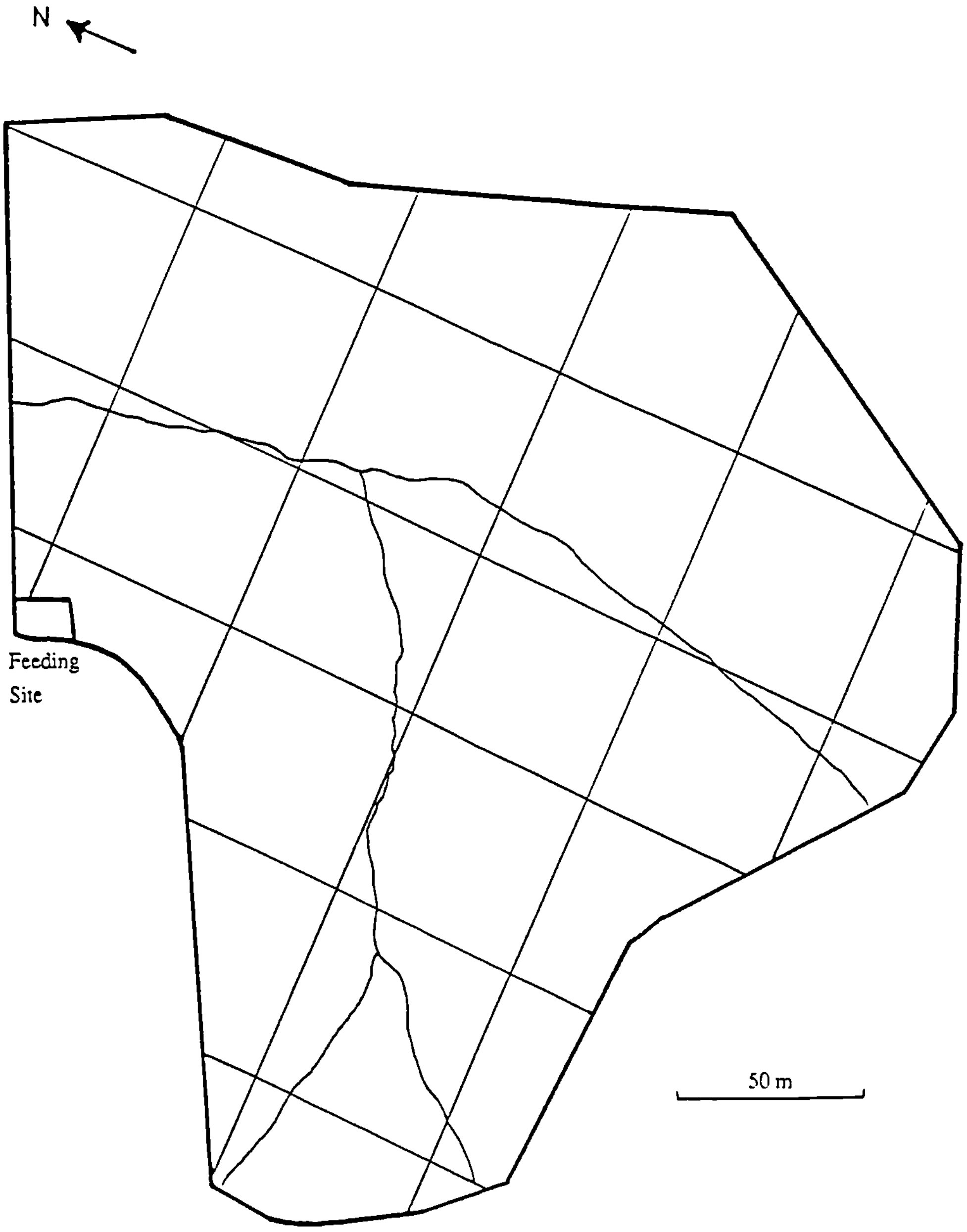
Preparation

Transects: During a preliminary two-month period two series of transects (a total of 1750 m) were cut in the enclosure. One set of five was aligned north-south, roughly following the contours of the enclosure, at 50 m intervals. Another series of five transects was cut east-west, thus dividing the enclosure into 50 x 50 m quadrats. A simple plan of the enclosure and transects is given in Figure II.2. The transects greatly increased the ease with which I could move about the enclosure. Damage to the vegetation was kept to a minimum and only a small path allowing passage of a single person was initially cleared and subsequently maintained with secateurs. In general the presence of cleared paths did not appear to affect the movement patterns of most of the mandrills, who kept to their well-worn travel routes. However, some of the larger males tended to use the paths rather than go through the thick undergrowth that the females and juveniles were traversing nearby.

Habituation: In order to study closely a group of primates it is necessary to habituate them to observation so that the presence of a human observer does not disrupt their natural behaviour. Contrary to my own experiences with wild mandrills and other mammals, and the experience of most fieldworkers, I was not faced with the problem of studying animals who fled every time I approached. Rather it was the reverse; the mandrills stopped what they were doing and approached me. Sometimes they travelled across the enclosure to find me. Initially they often behaved submissively. I avoided interacting with them, did not feed them, did not stare them straight in the eyes, and stood or sat quietly while they sniffed me. With time and repeated exposure to me these reactions of curiosity decreased, they did not approach me, and they seemed almost to ignore my presence, although they often vocalised when I left them. On the days when I did not go into the enclosure early enough to find them still at their sleeping site, it could take frustratingly long to find them; it was surprising how 30+ mandrills in a fenced enclosure could be so difficult to locate.

Individual identification: Before starting data collection I learned to identify the individual mandrills. It took me about a week to learn to recognize the subadult and adult males individually, and a little longer for the adult females, despite

Figure II.2. A simple plan of the 5.3 ha mandrill enclosure, showing the feeding site, streams, and transects.



the fact that the tatoos were not always readily visible. The mandrills' posture sometimes hid the tatoos and in addition they were placed so as not to detract from the aesthetic appearance of the animal. However there were numerous other cues for identifying individuals, such as facial and rump colour, scars, and personality. With time my familiarity with the mandrills increased and I could often recognize them simply by the way they walked. The juveniles took longer to recognise individually and the infants the longest of all. As the cumulative time that I spent with the mandrills increased I became aware of family resemblances, and within a few months all the individuals were recognizable to me.

As I familiarised myself with mandrill behaviour I constructed an ethogram to use in data collection and also experimented with check-sheet design and different methods of recording data.

Group composition: The composition of the group at the start of the study in January 1986 is shown in Table II.1. The group consisted of 25 individuals, 15 subadult and adult mandrills and 10 youngsters (sex ratio 1:1). By the end of the study, in May 1988, the group numbered 37 individuals. This size range was within the limits of group sizes of 20 to 40 individuals reported for wild mandrills (Jouventin, 1975a; Hoshino *et al.*, 1984). At the start of the study 40% of the group were juveniles or younger; by May 1988 this had risen, due to births in the group, to 64%. These ratios are comparable to those in groups of wild mandrills. Data from observation of four groups of wild mandrills in Gabon indicated that juvenile individuals may form 57% to 63% of a group (Jouventin, 1975a). Hoshino *et al.* (1984) reported that in one study troop (B group) in Cameroon, 55% of the group were juvenile individuals. Analysis of weights of five sets of faecal data from the same study gave similar proportions, with an average of 50% of the group being juvenile individuals.

Choice of focal animals: Although I was interested in the behaviour of all the mandrills in the group (as so little is known about mandrill behaviour), I chose to

Table II.1. Composition of the mandrill group at the start of the study in January 1986

Founder Identity	Sex	Offspring Identity	Sex	Date of Birth
1	F			
2	F	2A	M	01 Jul. 1983
		2B	M	29 Jan. 1985
		2C	F	02 Jan. 1986
3	M			
5	F	5A	F	12 Jul. 1983
		5B	M	14 Sep. 1985
6	F	6A	M	23 Jul. 1983
7	M			
9	M			
10	F	10A	F	06 Mar. 1984
12	F	12A	F	13 Jun. 1983
		12B	M	07 Feb. 1985
13	M			
14	M			
15	M			
16	F			
17	F	17A	F	22 Nov. 1985
18	M			

concentrate my observations on the 15 founder mandrills. Interactions between subadults and adults appear to play a greater role in structuring a group of monkeys than do those of juveniles, so concentrating on and collecting behavioural data on the former seemed an instructive means of looking at social organisation in mandrills. In addition I thought it would be difficult to get adequate sample sizes if I collected focal samples on all 25 members of the group.

Details of the 15 founders are given in Table II.2. There were two adult and five subadult founder males. All the eight founder females were parous or pregnant at the start of the study. Three adolescent female offspring (Nos. 5A, 10A, and 12A) began cycling and conceived during the study but were not added as focal subjects. On 17th March 1986 the eight female subjects were reduced to seven by the removal of Female No. 1, then the dominant female, for reasons of safety.

She was repeatedly aggressive towards me (she had a history of biting people, see Norris, 1988), which was not only somewhat dangerous but also disrupted observation in that I needed constantly to monitor her whereabouts, which hindered my ability to collect data on other mandrills. She had no offspring (see Table II.1), so her removal did not sever any kin relationships. The remaining female hierarchy did not change, the beta female (No. 2) simply taking alpha status. The focal population thus consisted of seven males and seven females.

Main study

Equipment: On 10th March 1986 I started systematic data collection using Zeiss 10 x 40 binoculars, a digital stop-watch, and a clipboard and checksheets, some examples of which are given in the Appendices. I carried secateurs to clip vegetation growing over the transects. At first I also carried a small Sony tape recorder, but I later abandoned it due to technical problems and the inefficiency of transcribing a mixture of recorded and written notes.

Table II.2. Details of the 15 founder focal mandrills

		On arrival at CIRMF				At start of study (January 1986)	
Identity No.	Sex	Date	Weight (kg)	Estimated age (months)	Estimated date of birth	Weight* (kg)	Estimated age (months)
1	F	30 Nov. 1979	11.00	61	Oct. 1974	15.87	135
2	F	30 Nov. 1979	5.64	29	Jun. 1977	10.34	103
3	M	22 Jan. 1980	4.65	17	Aug. 1978	43.45	89
5	F	30 Sep. 1980	5.01	27	Jun. 1978	12.90	91
6	F	30 Nov. 1979	1.43	5	Jun. 1979	12.41	79
7	M	07 Nov. 1979	2.82	20	Mar. 1978	25.48	94
9	M	20 Aug. 1980	3.45	13	Jul. 1979	19.43	78
10	F	20 Aug. 1980	2.90	12	Aug. 1979	14.34	77
12	F	10 Oct. 1980	3.51	15	Jul. 1979	10.47	78
13	M	06 Nov. 1980	2.32	18	May 1979	17.40	80
14	M	06 Nov. 1980	2.40	10	Jan. 1980	26.59	72
15	M	15 Aug. 1981	2.49	10	Oct. 1980	18.53	63
16	F	19 Jul. 1983	3.30	14	May 1982	7.20	44
17	F	22 Mar. 1983	6.94	33	Jun. 1980	11.63	67
18	M	04 Oct. 1984	7.37	31	Mar. 1982	12.68	46

* Weights are at October 1985, three months prior to the start of the study

Mandrills Nos. 4, 8, and 11 died soon after their arrival at CIRMF

Censusing: On every day of observation I carried out a census of the mandrills. All the individuals were checked for signs of ill-health, the presence of wounds, and the condition of previous injuries. Female reproductive condition, the colour and size of the clitoris and perineum, were also recorded. These data were written on a checksheet as was any other relevant information such as the occurrence of menstrual bleeding. The size of each female's perineum was scored on a 20-point scale of zero (flat) to ten (maximum swelling) graded by half units. Unlike Hausfater's (1975) system in which 20 represented the maximum swelling any female ever achieved (and where most females only ever reached 10 or 12), in the present study ten was the maximum size achieved by each female. In this way a score of ten indicated maximum tumescence for that female regardlesss of the actual size of the swelling, which showed considerable variation between females. Maximum swelling size appeared consistent within females. Once a week I carried out a census of infants and juveniles for developmental characters such as coat and muzzle colour (see Appendix II.).

Sampling Techniques

Data were collected using a variety of sampling techniques, namely *ad libitum* sampling, behaviour sampling, focal sampling, and scan sampling (Martin and Bateson, 1986). These techniques were used both alone and in combination. A summary of the advantages and drawbacks of each is given in Table II.3.

***Ad libitum* sampling**: With this sampling technique no systematic constraints are placed on what is recorded. *Ad lib.* sampling is a useful way of recording rare but important events, and general information. Observations may be biased towards individuals or behaviour which are relatively conspicuous. I used this method to record events of interest, for example, any unusual feeding behaviour, especially predation; the 'atmosphere' in the group; arrival and departure of subadult males; notes on the weather; progression data; and anything else of interest, such as the reaction of mandrills to various birds, snakes, an escaped guenon, etc., and small experiments such as the presentation of a model of a male mandrill. These notes were later transcribed into a log book and provided a daily record of events within the group.

Behaviour sampling: With this method each observed occurrence of a particular type of behaviour, together with details of which individuals are involved, is recorded. This technique is useful for recording rare behaviour patterns such as copulations which tend to be missed by focal or scan sampling. Observations may be biased if some individuals are more easily visible than others. I used this method to record relatively rare behaviour such as scent-marking. Further details of behaviour categories scored with this method are given in the section 'Behavioural observation' below.

Due to the nature of the vegetation, the spread of the group, and the high level of activity, especially among the juveniles and infants, it was not possible to record all behaviour by all mandrills. Some behaviour, e.g., agonistic interaction, was only recorded when one of the 14 focal subjects was involved. Other less frequent behaviour, such as regurgitation and scent-marking, was recorded whenever it occurred regardless of the identity of the mandrill involved. Further details are given in the section 'Behavioural observations' below.

Focal sampling: For focal sampling a single individual is observed at a time for a specified period of time. When recording social behaviour the identity and behaviour of individuals interacting with the focal animal is also recorded. Bias can occur e.g., if certain individuals are systematically observed at a particular time. This can be avoided by scheduling samples in a randomised or balanced design. Focal sampling is a good sampling technique for obtaining detailed records of behavioural events and states.

The order in which individual mandrills were focal subjects was determined prior to the observation sessions and was randomised. Focal sampling under the naturalistic conditions of the enclosure was not always easy as individuals were sometimes difficult to locate or could 'disappear' in the vegetation. If a mandrill could not be found, after ten minutes searching I sampled the next individual. I went back to the 'missing' individual at the next opportunity. If an individual passed behind a tree or travelled briefly through a thicket during a focal sample I noted 'not visible' (NV) on the checksheet and continued the sample. When a focal individual went into a tangle of undergrowth, did not reappear, and I could not find it within five minutes, I sampled the next individual on the list.

The order in which focal samples were done was determined prior to the observation sessions and was randomised. Animals were sampled for 15 minutes. Trial and error during the preparatory period had shown that 30-minute samples were largely impractical as it was difficult to keep an animal consistently in view for that long.

Scan sampling: This technique involves scanning a whole group of subjects and recording the behaviour of each individual at that instant. Bias is introduced if certain individuals or certain types of behaviour are more visible than others. It is not a good technique for behaviour such as complex social interactions. I used scan sampling to record only relatively few clearly defined behaviour categories.

Recording techniques

Two main types of recording rules were used, continuous recording and time sampling (Martin and Bateson, 1986). The latter was divided into one-zero sampling and instantaneous sampling. A summary of the utility and drawbacks of each technique is given in Table II.3.

Continuous recording: This technique aims to provide an exact record, in terms of frequency and duration, of behaviour and the times at which behaviour stopped and started. Although this technique gives very thorough description of the

Table II.3. Summary of sampling and recording techniques

Technique	Useful for	Drawbacks
Sampling techniques		
Ad libitum	infrequent, unpredictable behaviour; general qualitative notes	bias if some individuals and behaviour more conspicuous than others
Behaviour	rates of behaviour	bias if some individuals more conspicuous than others
Focal	detailed record of events and states of behaviour	bias if samples not scheduled in a randomised or balanced design
Scan	states of behaviour, especially long-duration behaviour, presence/absence of individuals	bias as for *ad lib.*; rare, short duration behaviour likely to be missed
Recording techniques		
Continuous	true frequency and true duration	impractical with large number of high frequency behaviour
One-zero	correlates well with frequency and duration if small sample interval used	does not give true duration or true frequency of behaviour
Instantaneous	behaviour state; proportion of behaviour if small sampling interval used	rare, short-duration behaviour likely to be missed

time of behaviour and is useful when data on the sequence of behaviour are required, continuous recording is very demanding for the observer. Initially I tried this technique but found it to be impractical for recording mandrill behaviour as there was a large number of behaviour categories, which changed frequently, and which included several generally short-duration behaviours. At a later phase of the study (see Part 2 below) continuous recording was used, but was limited to collection of social interaction data.

With time sampling methods behaviour is sampled periodically. A complete record of behaviour is not obtained but time sampling techniques are useful when many different categories of behaviour need to be recorded since they provide a means of condensing information. The majority of data on the mandrills was collected using time sampling techniques.

One-zero sampling: One-zero scores are collected by choosing a time period, e.g., 30 seconds, and then recording a frequency of one if a specified behaviour occurs at least once during that period. Zero is recorded if the behaviour does not occur. One-zero scores, especially when small sampling intervals are used, can give a good composite measure of amount of behaviour, measuring both prevalence and incidence (Kraemer, 1979) and so are 'arguably, valid scores in their own right' (Martin and Bateson, 1986, p. 62), as they are strongly correlated with both frequency and duration (Rhine and Linville, 1980). It has been suggested that one-zero scores may be a more realistic index of behaviour than either frequency or duration (Slater, 1978; Smith, 1985; both cited in Martin and Bateson, 1986) particularly since these measures do not always correlate highly with each other (Rhine and Linville, 1980). In addition, one-zero sampling is practical and reliable (Rhine and Linville, *op. cit.*). This sampling technique has been critisised (e.g., Altmann, 1974; Dunbar, 1976) mainly because one-zero scores do not provide an accurate estimate of true frequency or of true duration, unless the sample interval is very short. I used this technique, employing relatively short sampling intervals, to record the occurrence of a large number of behaviour categories (see below for details).

Instantaneous sampling: With this method the observation session is divided into short sample intervals, and on the instant of each point the observer records whether or not a particular behaviour is occurring. Instantaneous sampling can approximate continuous recording and give a good record of the proportion of time spent performing a particular behaviour if a very short sample interval is used, especially if the sample interval is short in relation to the duration of the behaviour (Dunbar, 1976; Simpson and Simpson, 1977; Rhine and Flanigon, 1978). This method is thus useful for sampling behavioural states. Instantaneous sampling is not a good method for recording discrete events of short duration (Martin and Bateson, 1986) as these and rare behaviour patterns are likely to be missed as they would seldom occur on the tone. I used instantaneous sampling to record behavioural states and obtain unbiased estimates of time spent in various behaviour.

Behavioural observations

In order to answer specific questions about mandrill behaviour, different types of data and collection methods were used. The main study can be divided into two parts, and the details of focal sampling methods differed in each part and are described below. Many aspects of data collection however were consistent throughout the whole study. These included the individuals observed, the use of focal samples of 15-minutes' duration, and behavioural observations collected by *ad lib.* and behaviour sampling techniques. Observations recorded using behaviour sampling are given below and definitions of the behaviour categories used in this study are given in Chapter IV.

The following behaviour was recorded throughout the study whenever it was observed regardless of the identity of the individual/s involved: (1) scent-marking; (2) copulation; (3) regurgitation; and (4) alarm reactions. These behaviour categories and the parameters recorded about each are shown in Table II.4. The following behaviour was also recorded throughout the study but only if one of the 14 founder subadults and adults was involved (5) agonistic: displacements, threats, and submissive behaviour; (6) grooming; (7) play; and (8) male 'loud-calls' or roars. These categories and the information recorded about each are detailed in Table II.5.

All data on scent-marking, copulation, regurgitation, agonism, and grooming were transcribed onto separate checksheets. Observations from focal samples were distinguished on the checksheets from those recorded by other methods. Agonistic interactions recorded at the feeding site were distinguished on the checksheets from those recorded elsewhere in the enclosure.

Part 1

From March to early September 1986 focal samples in which the data were collected by one-zero sampling were used. As stated above continuous recording had been tried during the preparatory study and found to be impractical. As a large number (n = 28) of different behaviour categories was recorded (see checksheet in Appendix II.), one-zero proved to be a useful way of recording and condensing information. In addition it was the only practicable way of recording intermittent behaviour. Actual frequencies were also recorded for behaviour of very short duration such as threat-bobs and yawns. Fifteen-second intervals were used as sampling intervals. At the end of March these were increased to 30-second intervals. This change was justified by the results of a Spearman Rank Order Correlation statistic on the total number of intervals (by the 15- and 30-second methods) of four behaviours (foraging, allogrooming, climb, and aggression) from five randomly-chosen focal samples from each of the 14 focal animals (i.e., n = 70 samples). The significant high correlations (Table II.6) indicated that 30-second intervals could be used without compromising 'accuracy'.

After samples containing less than 10 minutes of data were discarded, a total of

Table II.4. Behaviour categories scored by behaviour sampling throughout the study whoever performed the behaviour

Behaviour category	Parameters recorded
Scent-marking	Date, Time, Identity Height Diameter at breast height (DBH) Sniff Lip Number of rubs Other individuals at <5 m Comments e.g., atmosphere in the group
Copulations	Date, Time Identity of male Identity of female Number of thrusts Occurrence of ejaculation Comments e.g., presence of other males
Regurgitation	Date, Time, Identity Noise Heaving Chewing Presence of food in pouch Comments e.g., type of food recently eaten
Alarm	Date, Time, Identity Elicitor of alarm Response of other individuals

All behaviour except alarm was transcribed to checksheets

Table II.5. Behaviour categories scored throughout the study by behaviour sampling if one of the 14 founder mandrills was involved

Behaviour category	Parameters recorded
Agonistic	Date, Time Identity of individual A Behaviour of individual A Identity of individual B Behaviour of individual B Comments e.g., occurrence of support or alliance
Grooming	Date, Time Identity of groomer Identity of recipient Comments e.g., occurrence of solicitation
Play	Date, Time, Identity Identity of other individual/s Comments e.g., who initiated play
Loud calls	Date, Time, Identity Response of others Comments e.g., precipitating factor

Agonistic and grooming behaviour was transcribed to checksheets

Table II.6. Spearman correlations for one-zero scores at 15- and 30-second intervals

Behaviour	Rs	p
Forage	0.99	<0.01
Allogroom	1.00	<0.01
Climb	0.98	<0.01
Aggression*	1.00	<0.01

* composite of head bob, head bob+call, and threat rush; n = 14

667 15-minute focal samples was collected by the one-zero method (Table II.7). The modal number for each individual was 48 (range = 43 to 51). All these samples (detailed in Table II.7) were collected during a period when females were anoestrous, i.e., they were either pregnant or lactating. When females began to have sexual cycles I attempted to sample more frequently females those who had maximal sexual swellings. Female monkeys are mainly either pregnant or lactating, so that periods of sexual activity are relatively brief. For example, in yellow baboons (*Papio cynocephalus*) 'there are only short periods of adulthood, on the order of 4-6 mo per 2 yr, during which females are not providing either uterine or postnatal care for an offspring' (Altmann, 1983, p.70). Because of the relative rarity of oestrus, and the fact that no sexual behaviour was observed during the first six months of the study, I decided to attempt to sample females in oestrus more frequently and for 30-minute focal samples. The number of 30-minute one-zero focal samples collected on females in oestrus is given in Table II.8. In total, 177.13 hours of focal samples were accumulated by the one-zero method.

Immediately pre- and post- all one-zero focal samples, the identity, distance, height, and activity of all founder mandrills visible from the stationary observer standing near the focal animal were recorded on a checksheet in instantaneous scan samples. A total of 1376 scans was done.

Part 2

From September 1986 to May 1987 a different format of randomly sequenced 15-minute focal samples was used. This was done so as to be able to quantify inter-individual relationships in terms of proximity, social interactions etc. At the start of each sample and at 1-minute intervals throughout the sample (resulting in 16 data points) instantaneous scans of the focal animal's activity (e.g., forage, rest, travel, groom) were recorded and the identity of all subadult and adult mandrills within 5 m was recorded. Distance categories were subdivided as follows: I = <1 m, II = 1-2 m,

Table II.7. Part 1 One-zero focal samples

Mandrill Identity	Number of samples	Focal minutes
Males		
No. 7	47	705
No. 3	43	645
No. 14	47	705
No. 9	48	720
No. 13	48	720
No. 15	49	735
No. 18	48	720
Females		
No. 2	47	705
No. 5	48	720
No. 6	50	750
No. 10	47	705
No. 12	51	765
No. 17	46	690
No. 16	48	720
Total	667	10,005

Manrills are shown in order of decreasing dominance rank

Table II.8. Part 1 30-minute one-zero focal samples on oestrous females

Mandrill identity	Number of samples	Focal minutes
No. 6	2	60
No. 12	12	354
No. 17	7	209
Total	21	623

III = 2-5 m. At the start of the sample and at 5-minute intervals (resulting in four data points) I recorded the identity of all subadults and adults within 10 m (i.e., IV = 5-10 m). All individuals were recorded as either being terrestrial (on the ground or less than 1 m from the ground) or arboreal (at more than 1 m height). During the 15-minute focal sample every social interaction between the focal individual and other subadult and adult mandrills was recorded by continuous recording. These data were all collected on the same checksheet (Appendix II.). This method had been used by Smuts (1985) to collect similar data on *Papio anubis* baboons.

A total of 522 focal samples was collected on female mandrills. Samples containing less than 10 minutes of data were discarded (n = 26). Also excluded from analysis were 'cycling' samples (n = 16), collected when female sexual swellings were increasing in size, or were decreasing or flat between periods of maximum tumescence. These are shown in Table II.9. Females were categorised as pregnant, lactating, or in oestrus (restricted to the period of maximum tumescence - see Chapter III). The remaining 480 focal samples collected on females in these reproductive stages are shown in Table II.10.

In total 448 samples were done on the male mandrills, but 5% were discarded (n = 22) since they contained less than 10 minutes of data. The remaining 426 focal samples, about 60 per male, are detailed in Table II.11. Samples were divided into two categories; those collected on days on which at least one female had a maximally swollen perineal skin (i.e., in oestrus) and those collected on non-oestrous days.

Follow-up

Although the intensive study ended in May 1987 I continued to monitor the mandrills for female reproductive condition (perineal state, pregnancy, and birth) and wounds and injuries for the following 12 months to May 1988 and these data are also included. In addition, the mandrills were captured in October 1987 and April 1988.

Table II.9. Part 2 Focal samples on cycling females

Mandrill	FS	Mins
No. 2	6	90
No. 6	2	30
No. 10	8	117
Total	16	237

Table II.10. Part 2 Focal samples on females

Mandrill	Total Samples		Oestrus		Pregnant		Lactating	
Identity	FS	Mins	FS	Mins	FS	Mins	FS	Mins
No. 2	75	1133	18	288	48	713	9	132
No. 5	60	934	0	0	28	447	32	487
No. 6	73	1152	13	208	60	944	0	0
No. 10	84	1303	31	487	53	816	0	0
No. 12	61	949	0	0	29	464	32	485
No. 17	65	1009	0	0	41	642	24	367
No. 16	62	970	0	0	0	0	62	970
Total	480	7450	62	983	259	4026	159	2441

Females are shown in order of decreasing dominance rank

FS = Number of focal samples; Mins = Number of focal minutes

Table II.11. Part 2 Focal samples on males

Mandrill Identity	Total Samples FS	 Mins	Non-oestrous FS	 Mins	Oestrous FS	 Mins
No. 7	60	934	49	763	11	171
No. 3	60	952	51	809	9	143
No. 14	59	927	50	783	9	144
No. 9	64	1004	49	775	15	229
No. 13	60	939	49	764	11	175
No. 15	62	976	51	800	11	176
No. 18	61	971	49	779	12	192
Total	426	6703	348	5473	78	1230

Oestrous samples are those taken on days in which at least one female was in oestrus (n = 63 days). Non-oestrous samples were taken on days on which no female was in oestrus.

Mandrills are shown in order of decreasing dominance rank

FS = Number of focal samples; Mins = Number of focal minutes

Data collection

Observation of the mandrills can be divided into four periods, a three-week feasibility study, a preparatory period of approximately two month's duration, the 15-month main study, and a 12-month follow up. The bulk of the quantified behavioural data reported in the following chapters comes from the main study.

Observation Schedules

Hours of observation: Focal data were collected between 0700-1100 and 1400-1800 hours. The time the mandrill-day started depended on the weather. On dull days and when there had been rain in the night the mandrills woke later and then stayed longer in their sleeping trees, dozing and grooming, and sometimes did not descend until 0800 hours or even later. On bright mornings they woke before 0700 hours and were often active and foraging before 0800 hours. I usually waited until at least half of the group was active before commencing focal sampling.

The mandrills usually came up to the peripheral feeding site at 1100-1130 hours, depending on when the CDP staff provisioned them. They fed rapidly, filling their cheek pouches with fruit and vegetables, and then chow from the dispenser. They also drank from the water spouts. Frequently individuals carried bread in their hands and mouth away from the feeding site. Preliminary observations during the preparatory study had shown that on leaving the feeding site the mandrills generally sat in the shady undergrowth and gradually processed the contents of their cheek pouches. I did not collect focal samples after 1100 hours due to the effects of provisioning on their activity. The mandrills often rested during the heat of the day until the early afternoon and during this quiet period it was sometimes difficult to find them. Although I was usually with them earlier I did not resume focal sampling until 1400 hours and then continued until 1800 hours when the mandrills were nearly always in their sleeping trees and settling for the night. Darkness fell about 1830 hours.

Statistics

Analyses were carried out using SPSSx (Statistical Package for the Social Sciences, version x). A variety of tests, both parametric and nonparametric, was used. Difference tests included the independent t-test, paired t-test, and one-sample t-test. To test for association both Pearson Product Moment Correlatioons and Spearman Rank Correlations were used. All probabilities were two-tailed and alpha was set at 0.05.

Summary

The data to be presented in the following chapters taken from Parts 1 and 2 of the main study can be summarised as follows. From *Part 1* the one-zero focal samples were used to compare individuals in the proportion of time spent in particular behaviour (Chapter IV). A sample of the scans, which were done immediately before and after the focal samples, was analysed as an indication of the visibility of the mandrills (Chapter II). From *Part 2* all the focal samples were used to quantify proximity and grooming relationships. The data were analysed in relation to female reproductive state and divided into anoestrus (Chapter V) and oestrus (Chapter VI) categories. Behavioural data collected by *ad lib.* and behaviour sampling, such as copulations, agonistic interactions etc., were analysed over the whole study. Further details are provided in the appropriate chapters.

Practical problems

As mentioned in the previous chapter the CIRMF mandrill facility represented what appeared to be a good compromise between captive and feral conditions. This situation however also brings with it problems associated with both these conditions, especially poor visibility and aggression due to tameness.

Visibility: Problems akin to those faced by researchers working with wild animals are those related to the difficulty of observing one's study animals. One of the major reasons for the impressive amount of data which have accumulated on the terrestrial savanna baboons is the relative ease of observation in a short-grass savanna habitat. By contrast, most of the work on forest monkeys has been on arboreal species. Although I am not claiming that these are easily visible all the time, they are likely not as difficult to observe as terrestrial forest species. The paucity of data on terrestrial forest primates such as the *Cercocebus* mangabeys, De Brazza monkeys, and lowland gorillas, and the lack of behavioural observation in the mandrill field studies in particular, attest to this. As mentioned above, the CIRMF mandrills lived in a naturalistic habitat; the enclosure had never been cleared or burnt and it contained tangles of lianas and vines, and thickets of razor grass. All these were ideal places into which mandrills, especially focal individuals, could and did disappear at whim. About 5% of focal samples were abandoned due to the focal subject disappearing from view.

The poor visibility in the enclosure also affected data collection methods. Visibility varied according to the type of vegetation (e.g., mandrills were less visible in razor-grass thickets than in the grassy verges of the enclosure), the nature of the terrain (e.g., they were more easily visible on steep banks of streams than on flatter swampy stream margins), and whether the mandrills were arboreal or terrestrial (e.g., they were generally more visible in the trees than on the ground, although this depended on leaf cover which also varied with season). Considerable variability in visibility was also reported by Norris while he had been observing the same mandrills after their initial release into the adjacent 1.4 ha enclosure in 1982-83; they were observable from 2m to 25m (Norris, 1988, p.451). Field workers reported visibility in the forest as being frequently less than 20 metres (Hoshino *et al.*, 1984; Lahm, 1986). However, there are no reports of detailed behaviour in wild mandrills. This is presumably due to the lack of close observation. Being able to identify mandrill presence and to locate a mandrill and being able to record its behaviour accurately and in detail are different and the last requires good visibility. In many parts of the enclosure individual mandrills could only clearly and reliably be observed at distances less than 10 metres. Good visibility was particularly important in Part 2 of the study when, as well as the focal animal, the position of other individuals in relation to the focal animal needed accurately to be recorded.

Initially I had intended to do regular group scans as a means of quantifying group composition. However, the poor visibility meant that it was easy to miss individuals. An accurate 'group count' would have entailed considerable time spent searching. Although some workers have done this (e.g., Harrison (1982, p.3-7) 'allowed a 5 minute period ... in which to walk around and maximise the number of monkeys that were recorded in each scan'), I found this to be impractical and it meant that scans were no longer instantaneous. Instead, as indicated above, scans were done from a stationary point near the focal animal. This gave an indication of the number and identity of individuals in clear view from the position of the focal mandrill.

A sample of the scans (total = 1376) done immediately pre- and post- the one-zero focal samples was analysed. At first, ten scans were chosen at random from each focal individual. For each scan the identity of other founder mandrills was recorded. However, as the confidence interval was relatively large, the number of scans per focal was subsequently increased to 25, by analysis of a further 15 randomly-chosen scans per focal individual. The 95% confidence interval associated with this increased number of scans was smaller, so the measure of visibility reported below is based on 25 scans for each focal individual, i.e., a total of 350 scans.

For each individual, the total number of times it was recorded in a scan was divided by the number of scans (No. of scans = No. scans per individual x No. of individuals = 25 x 13 = 325) and converted to a percentage. The percentage visibility of each founder mandrill is shown in Table II.12. The most striking feature was the low visibility of the mandrills. On average a mandrill (excluding Male No. 3) was visible on only 21% of scans (mean = 21.3, range 11 to 33). The alpha male (No. 7) had the

Table II.12. Percentage visibility of the founder mandrills

Identity	Percentage visibility
Males	
No. 7	32.9
No. 3	3.7
No. 14	10.5
No. 9	15.7
No. 13	10.8
No. 15	24.9
No. 18	11.4
Mean*	17.8
Females	
No. 2	28.0
No. 5	26.1
No. 6	22.8
No. 10	20.6
No. 12	24.6
No. 17	28.3
No. 16	19.7
Mean	24.4

Mandrills are shown in order of decreasing dominance rank

*The solitary male (No. 3) was excluded from calculation of the mean highest visibility, appearing in 33% of scans and the second ranking male (No. 3) had the lowest, being recorded in only 4% of scans. There was no significant difference between the 18% visibility of males (excluding No. 3) and 24% of females (t = 1.784, df = 11, N.S.). The means are shown in Table II.12 and indicate that females were 7% more visible than males. These low scores also indicated that the group was not very compact, given that so few individuals could be seen from the position of a mandrill in the group.

The transects were cut with the intention of walking them regularly in order to plot the location of individuals and measure cohesion in the group. However, it soon became clear that walking the transects was not a useful thing to do, for two reasons. Firstly, walking 1750 m of transects at regular intervals was unacceptably time-consuming. I felt that the time was better spent in concentrating on focal samples. Secondly, walking transects was not a useful method of locating individual mandrills. As the transects were at 50 m intervals and visibility was reliably only 10 m, there remained 30 m in which a mandrill could be present but not visible.

Observations during the feasibility and preparatory studies had shown that all females and their offspring were always together and the alpha male, No. 7, was always associated with them and these individuals thus constituted 'the group'. Thus the practical solution was simply to record in the *ad lib.* notes who was not with the group. I was unable to specify where subadult or adult males who were absent from the group were, simply that they were not associated with the group. The only individual who was consistently absent from the group was Male No. 3 and he was referred to as the solitary male.

Male 3's absence from the group meant that it was not always possible to sample his behaviour according to the randomised schedule, since I rarely saw him and was unable to locate him even if I left the group to look for him. Often I was behind with data collection from him. If I found him by chance I did consecutive samples on him, to a maximum of four. I waited at least 15 mins between samples. Since I had no reason to believe that his behaviour when alone and while I was watching him was any different from that when he was not with the group and I was watching them, I assumed that his samples represented an unbiased sample of behaviour. The same assumption was made about the data collected on the other mandrills. This compromise of strict random sampling of Male 3 seemed the best solution given the difficulties. I was able to monitor his condition regularly since he often came to the feeding site before the group and I could usually find him once he had climbed up into a sleeping tree in the evening. This also provided me with a means to locate him early the following morning.

Notably missing from the literature are reports of wild primates interacting with human observers during (and even after) the period of habituation (but see Caldecott, 1986a). I think this may be an example of biased reporting as I find it hard to believe that animals as curious and as intelligent as primates are, having lost their fear of people, would not attempt to interact with them in some way.

Aggression: In common with some captive groups, the CIRMF founder mandrills had had relatively close contact with people from an early age. Although they generally seemed to consider themselves as subordinate to me, they were not as intimidated by people as they might have been had they been trapped as older individuals. One female (No. 16) who had been raised by people for at least a year initially tried to interact with me by grooming me. Later she tried to involve me in agonistic interactions by approaching me and hiding behind me when threatened, and later still when she was threatened (as she often was, being the most subordinate female in the group) she redirected the aggression and started threatening me. As she was so used to people she seemed to lack the reticence which normally inhibited the mandrills from actually attacking in most cases, and she sometimes escalated from threats to action and bit me. Primates are aware of the sex of their observer (perhaps from olfactory cues) and it was interesting to note that, mirroring the mandrill pattern of relatively high frequency female-female agonism, all but one of the 'attacks' on me were by female mandrills. Being the target of aggression from one's study animals poses a number of problems.

What does one do in the face of threats? I did not want to carry any kind of weapon such as a blank-firing pistol, cattle-prod, or stick with me. Firstly I already had my hands full with binoculars, stopwatch, and clipboard, and secondly I did not want to appear threatening. However when I was threatened I also wanted to maintain some kind of psychological presence and to appear to be not intimidated. In fact my response and that of the mandrills depended on who was threatening me. If it was the dominant female she was often immediately supported by other females and their combined threats would often attract the alpha male. When I was attacked by the most subordinate female (No. 16) she was often ignored by the others and I had little reticence about threatening her in return. The risk of serious injury is from the males due to their large and sharp canine teeth, so I did not want to provoke the alpha male into attacking me. In fact I dealt with each (rare) case individually, sometimes quietly withdrawing and sometimes holding my ground but looking away and seeming as detached from the situation as possible. Occasionally the alpha male placed himself between me and threatening females. In the majority of these cases he faced them, thus protecting me and simultaneously showing submission and appeasement towards me by presenting his rear. An extract from my field notes illustrates this.

> 2 October 1986
> 1541: Adolescent female 5A is foraging 8 m from me (I am sitting on a grassy bank). She gradually forages closer until she is only 2 m from me.
> 1542: Then she threatens me with 'head-bobs' and 'threat grunts', and then 'scream incites' at male No. 7 (the alpha male), who comes

> over immediately, puts himself between us, facing 5A, and presents to me.

His behaviour perhaps indicated that he was aware of my gender, treated me as one of 'his' females and protected me from threat as he did other females. Once or twice he faced me, but his presence always inhibited the females from approaching me.

From the above description it could be argued that the mandrills were not completely habituated to a human observer, and that my presence in the enclosure altered their behaviour considerably as they interacted with me, and perhaps regarded me as an 'honorary' member of the group. However the agonistic problems were <u>rare</u> and in general I was ignored by the mandrills.

The mandrill group at CIRMF was a resource for the centre and not for my exclusive use. Data collection was sometimes interrupted by the requirements of others. For example, for three weeks in August 1986 I acted as a consultant to a Japanese film crew who wanted to film the mandrills. I was also involved in coordinating captures of individual mandrills for other studies (e.g., Cooper *et al.*, in press).

Weather: During the rainy seasons observations were hampered by heavy storms, particularly in the afternoon. During light drizzle the mandrills continued their usual activities and I was able to follow my observation schedule as normal. However, at the start of a downpour the mandrills climbed into the trees and remained there hunched over and motionless for the duration of the storm. During the main study at least 12% of observation days were curtailed by heavy rain.

CHAPTER III. REPRODUCTIVE BIOLOGY OF CIRMF MANDRILLS

In this chapter the reproductive biology of the CIRMF mandrills is reported. In addition, some information on body weight and dental status is also included. Pathological findings are also presented. Data from other captive mandrills and drills are included for comparison and some reference is made to wild savanna baboons.

FEMALES

The body weight profiles and parturitional history for each of the eight introduced females and their reproducing daughters, from their arrival at CIRMF up to April 1988, are shown in Figure III.1. The end of the plot for Female No. 1 indicates her removal from the group in March 1986. By March 1988 a total of 33 infants was produced in the mandrill group, with the first birth in June 1983. Nine of these infants died perinatally and one of the remaining 24 disappeared at 14 months of age and was presumed dead. The sex ratio of animals surviving to at least a year old was exactly 1:1. The dates of all births and concurrent maternal dental eruption status are presented in Table III.1.

The female mandrills reproduced before attaining full body growth. This is illustrated in Figure III.1 by the continued weight gain after first (and in some cases subsequent) birth. This resembled the pattern reported for wild savanna baboons, who generally attain full growth at about six to seven years old (Altmann *et al.*, 1977, 1981; Rowell, 1972). Reproduction was precocious in the CIRMF mandrill group. Excluding a female received as an adult (No. 1) and another (No. 2) who was also reproductively mature well before the oldest male (No. 7), the mean estimated age at first known

Figure III.1. Body weight and parturitional history in female mandrills

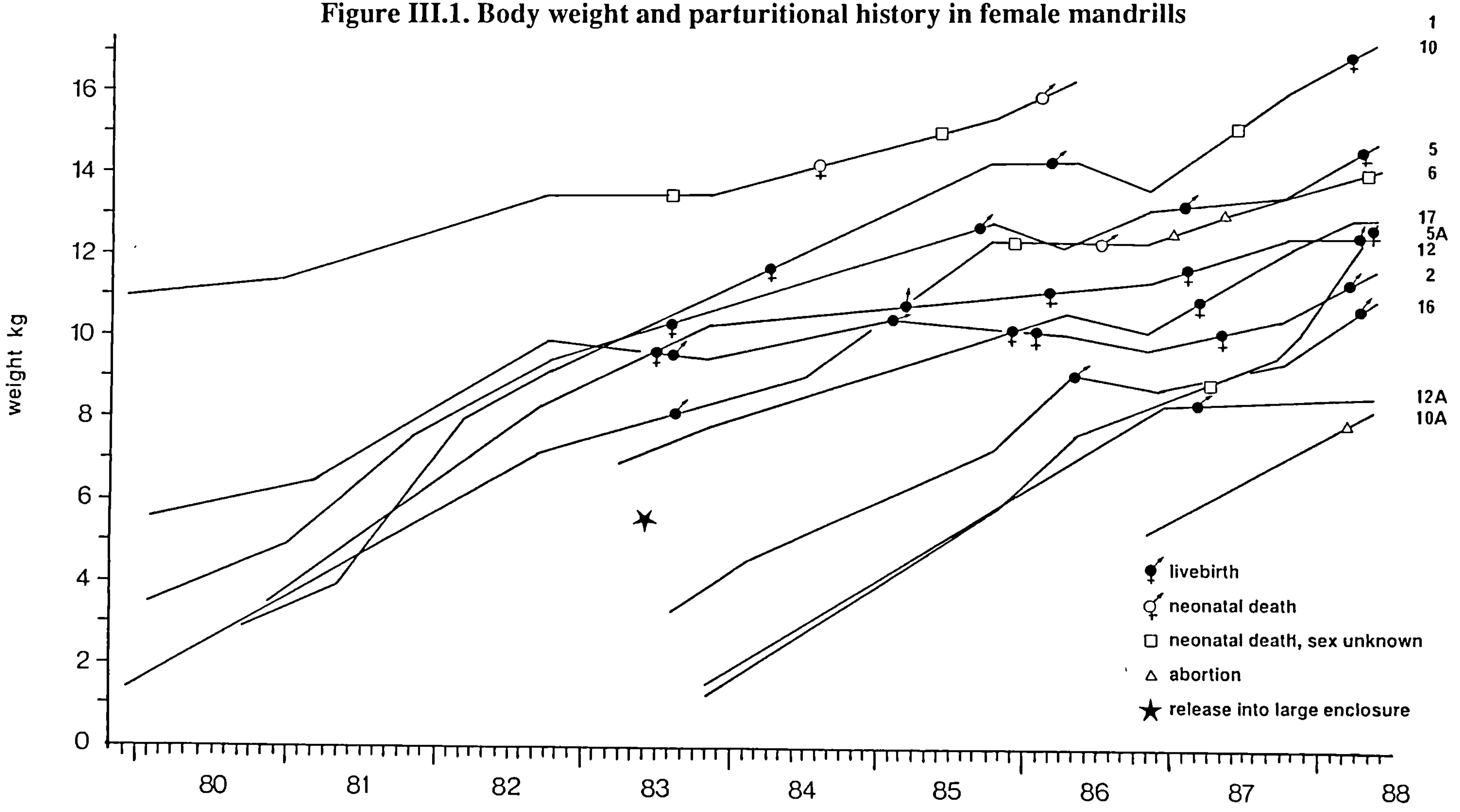


Table III.1. Reproduction in the mandrill group at CIRMF: Date of birth, survival and sex of offspring, estimated age at first conception and maternal dental eruption status at time of parturition.

Maternal identity	Offspring identity	sex	date of birth	Inter-birth interval (months)	No. of permanent teeth	No. of unerupted teeth	Estimated age at conception (months)
1	101*	?	Jul 1983		32	0	98
	1@	?	Dec 1983	5			
	102*	F	Jul 1984	7	32	0	
	103*	?	May 1985	10	32	0	
	104*	M	Jan 1986	8	32	0	
2	2A	M	Jul 1983		28	4	67
	2B	M	Jan 1985	18	32	0	
	2C	F	Jan 1986	12	32	0	
	2D	F	Apr 1987	15	32	0	
	2E	M	Feb 1988	10	32	0	
5	5A	F	Jul 1983		28	4	54
	5B	M	Sep 1985	25	32	0	
	5C	M	Jan 1987	16	32	0	
	5D	F	Mar 1988	14	32	0	
5A	5A01*	?	Mar 1987		16	16	38
	5A1		Mar 1988	12	25	7	
6	6A	M	Jul 1983		22	10	43
	601*	?	Nov 1985	28	28	4	
	602*	M	Jun 1986	7	30	2	
	6@		Dec 1986	6	30	2	
	6@		Apr 1987	4	32	0	
	603*	?	Feb 1988	10	32	0	
10	10A	F	Mar 1984		28	4	49
	10B	M	Feb 1986	23	32	0	
	1001*	?	May 1987	15	32	0	
	10C	F	Feb 1988	9	32	0	
10A	10A@		Feb 1988		22	10	43
12	12A	F	Jun 1983		21	11	41
	12B+	M	Feb 1985	20	28	4	
	12C	F	Feb 1986	12	30	2	
	12D	F	Jan 1987	11	32	0	
	12E	M	Mar 1988	14	32	0	
12A	12A1	M	Feb 1987		13	19	38
16	16A	M	Apr 1986		16	16	41
	16B	M	Mar 1988	23	28	4	
17	17A	F	Nov 1985		28	4	51
	17B	F	Feb 1987	15	30	2	

@ Abortion * Stillborn or died within a few days of birth
+ Died at age 14 months

conception was approximately 47 months (range 41 to 54). At the birth of their first infant these six wild-born founder females still possessed a mean of four deciduous teeth (range 0 to 9) and lacked a mean of eight and a half adult teeth (range 4 to 15) (data in Table III.1).

Puberty

Similar female reproductive precocity appeared in the first generation of captive-born mandrills at CIRMF, and was in fact even more pronounced. The three adolescent females who reached puberty during the study had their first full sexual swellings and started copulating with subadult and adult males at a median of 39.5 months of age (range 37 to 42). This was considerably earlier than the mean age of 53 months (range 48 to 57) reported for wild adolescent olive baboons (*P. anubis*) from Gilgil, Kenya (Scott, 1984), and a median of 59 months (range 54 to 67) from Gombe, Tanzania (Packer, 1979). Yellow baboons (*P. cynocephalus*) at Amboseli, Kenya commenced cycling at 48 to 66 months (Altmann *et al*, 1977, 1981). However, wild hamadryas baboons (*P. hamadryas*) have sexual swellings and copulate with males at only two years of age (Kummer, 1968a).

Menstrual Cycles

Menstruation usually was not obvious in the CIRMF mandrills. This was in contrast to captive mandrills and drills in whom it is clearly noticeable (C. Cox, pers. comm.). It may be that in the large group of mandrills at CIRMF menstruating females were regularly cleaned by grooming from their daughters or other females. Instead of using menses, the onset of deturgescence of the sexual swelling was used as a point of reference. This day was labelled D-day, the days before as D-1, D-2 etc., following Hausfater (1975). Cycle length was given by the number of days between consecutive D-days (i.e., inter-deturgescence interval). Calculation of cycle length was further hampered by the rapidity with which the mandrills conceived (see below) and data were available only for seven pairs of cycles from four females (Nos. 2, 5A, 10, and 12). The mean length of cycle was 32.6 days (range 25 to 43). This was very similar to published cycle lengths of captive mandrills and drills (see Table III.2) and of *Papio* baboons. Savanna baboon cycles are 31.5 days long on average (n = 53 cycles) in captive olive and yellow baboons (Shaikh *et al.*, 1982) and 32.5 (range 26 to 52, n = 34) in wild yellow baboons (Hausfater, 1975).

Oestrus

Oestrus was defined as the period of maximum tumescence of the sexual swelling (i.e., a score of 10 on the swelling scale, see Chapter II). Table III.3 shows the duration in days of maximum swelling for all reproductive females. The modal duration was 14 days (range 2 to 23). [The mode was used as representing the most frequent duration rather than a calculation of mean length.] There was considerable variation between females in length of oestrus, although duration was relatively consistent within females. For example, both Females 2 and 12 had periods of maximum swelling which consistently lasted from two to eight days (Table III.3). In contrast, maximum swelling in Female 5 lasted over twice as long as in Female 2. There was no difference in the duration of oestrus between cycles in which conception occurred (mean = 12.3 days) and those in which it did not (mean = 11.2 days) (t = 0.501, df = 26, NS). Böer reported a 'plateau phase' of maximum swelling of five to seven days in captive drills (1987c, p.271).

Conception

Females were assumed to have conceived if they did not undergo another period of swelling of the sexual skin. The founder mandrills conceived rapidly. The mean number of oestrous periods up to and including the conception cycle (n = 7 females, n = 13 pregnancies) was 1.54 (range 1 to 3). This was a quarter of the mean

Table III.2. Cycle length in *Mandrillus*

Cycle length		Range	No. cycles	No. females	Source
Mandrills					
32.5	mean	25 - 44	7	4	This study
33	mean	22 - 35	9	1	Hill, 1970
33.5	median	32 - 35	46	2	Hadidian and Bernstein, 1979
Drills					
32.6	mean	29 - 36	18	?	Zuckerman and Parker, 1939 in Hill, 1970
35	median	30 - 46.5	88	3	Hadidian and Bernstein, 1979
?		25 - 42	12	3	Böer, 1987c

Table III.3. Duration in days of maximum swelling (n = 28 cycles)

Female	Duration (days) of maximum swelling				
No. 2	5	2	6*	7*	
No. 5	15*	20*			
No. 5A@	9	9*	19*		
No. 6	21	10*	14*	14	10*
No. 10	16	5	14	14*	17*
No. 10A@	14	6*			
No. 12	5*	8	4*		
No. 12A@	15*				
No. 16	15*				
No. 17	15	23*			

* periods of oestrus in which conception occurred - 61% of cycles

@ captive born adolescent females

of six cycles (range 1 to 15) to conception reported for olive baboons at Gilgil (Smuts, 1985). The relatively long periods of adolescent sterility, lasting one to two years, reported in wild savanna and hamadryas baboons (Altmann *et al.*, 1977; Kummer, 1968b) were not seen in the three young adolescent mandrills; they all conceived by their second cycle and at an average age of 40 months (about six months earlier than their mothers), when their only fully erupted adult teeth were incisors and first molars. Early conception (at 40 months) has also been reported in captive drills (Böer, 1987c). Scott (1984) observed that wild adolescent female olive baboons conceived after an average of 10.8 cycles (range 8 to 13, n = 6 females); significantly later than did adult females. In the CIRMF mandrills adult and adolescent females conceived equally rapidly (t = 0.095, df = 15, NS). Conception within two cycles (n = 4 pregnancies) was reported in a female mandrill at the London Zoo (Carman, 1979).

Gestation length

Approximate gestation length was estimated from the period of first to last day of maximum swelling (the period of oestrus) to the day of birth, giving the 'confidence interval' or range of gestation length. This is shown in Table III.4 in column A. Preceding the day of detumescence, labelled D-day, the days were designated D-1, D-2 etc., as described above. Experiments on captive baboons (yellow and guinea (*P. papio*) baboons) have indicated that ovulation occurs on days D-2 or D-3 (Hendrickx and Kraemer, 1969; Wildt *et al.*, 1977; Shaikh *et al.*, 1982). Three days were subtracted from D-day of the conception cycle to give the day of probable conception as D-3. Gestation was calculated as the interval in days between D-3 and birth, and is shown in Table III.4 in column B. The mean gestation length of live births of subsequently surviving offspring from eight females was 175.7 days (range = 172 to 182, n = 11 pregnancies). Near-term births were defined as those occurring at greater than 90% of average gestation. The mean gestation of 175.7 days was comparable to the mean of 174.6 (range 172 to 176, n = 5 pregnancies) from a single female mandrill

Table III.4. Conception cycles and gestation lengths of infants born at and near term*

Female	Infant	Oestrus of conception cycle	Date of Birth	Gestation (days) A	Gestation (days) B
2	2D	6-11 Oct 1986	1 Apr 1987	176-171	173
2	2E	30 Aug - 5 Sep 1987	29 Feb 1988	182-176	178
5	5C	14-28 Jul 1986	19 Jan 1987	188-174	176
5	5D	29 Aug - 17 Sep 1987	6 Mar 1988	189-170	172
5A	5A01†	30 Sep - 8 Oct 1986	20 Mar 1987	170-162	164
5A	5A1	26 Aug - 13 Sep 1987	5 Mar 1988	191-173	175
6	603†	19-28 Aug 1987	3 Feb 1988	167-158	160
10	1001†	7-20 Nov 1986	17 May 1987	190-177	179
10	10C	22 Jul - 7 Aug 1987	4 Feb 1988	196-180	182
12	12D	5-9 Aug 1986	29 Jan 1987	176-172	174
12	12E	30 Sep - 3 Oct 1987	29 Mar 1988	180-177	179
12A	12A1	1-15 Aug 1986	3 Feb 1987	185-171	173
16	16B	26 Aug - 9 Sep 1987	1 Mar 1988	187-173	175
17	17B	8-30 Aug 1986	21 Feb 1987	196-174	176

† stillborn or neonatal death

A Gestation as estimated from first to last day of maximum swelling to birth

B Gestation calculated from day D-3 to birth

* near-term was defined as births which occurred at > 90% mean gestation

Table III.5. Appearance of pregnancy sign in mandrills in days after conception

Pregnancy sign*	Mean	S.D.	Range
Red and wrinkled perineum	49.9	17.7	27 to 75
Small perineal swelling	74.1	30.0	30 to 125

* Data from 12 pregnancies of founder mandrills (n = 7)

at the London Zoo (Carman, 1979) and a median of 175 days (range 164 to 213, n = 4 pregnancies) from a female mandrill at the Yerkes Regional Primate Center (Hadidian and Bernstein, 1979). Drills at the Hannover Zoo had gestation lengths of 179, 182, and 183 days, as measured from the last observed copulation (Böer, 1987c).

Several investigators of captive baboons noted a slight transient decrease in swelling size on day D-2 or D-3 and this was also observed in wild baboons (Hausfater, 1975). This phenomenon also was seen in the mandrills, but often occurred well before D-3 and it thus seems doubtful that it was indicative of ovulation.

Pregnancy

As stated above, females were assumed to have conceived if they did not undergo another period of swelling of the sexual skin. In addition, there were other changes indicative of pregnancy. The occurrence of perineal changes, in days after estimated conception, from 12 pregnancies of the 7 founder females are shown in Table III.5. About 50 days after conception a female's perineum developed a dark red colour and the skin became very wrinkled. About 75 days after conception females developed a pregnancy swelling. In 10 of the 12 pregnancies reddening and wrinkling of the perineum preceded an increase in swelling size. The pregnancy swelling was usually small, reaching one to two on the scale, and was maintained throughout pregnancy. At about four months gestation females looked pregnant, as their abdomens started to become more rounded. In late pregnancy they seemed more laboured in their movements. As my familiarity with mandrills increased I was able to predict imminent parturition. Usually there was a slight decrease in swelling size, a parting of the labia, and sometimes a slight discharge.

Birth

All births occurred during the night (between 1900 and 0700 hours) so none was witnessed. When infants were first seen they usually had been cleaned by their mother and were dry and fluffy. Frequently part of the umbilical cord was still attached, but usually was removed by the following or subsequent one or two days. In one case (Infant 5D) the placenta was still attached to the 45 to 55 cm long umbilical cord when the mother-infant pair were first seen. By the following day only 1 to 1.5 cm of cord remained.

On the day following (nocturnal) birth (referred to as the day of birth) neonates' faces, ears, hands, and feet were flushed with red. This was a reliable characteristic indicating recency of birth. The redness faded by the second day. Neonates had characteristic pelage. The fur was white or grey and fluffy over the whole body with a dark grey dorsal stripe. The crown of the head was black. The skin was blue over large parts of the torso and limbs and was pink on the face.

Adolescent and adult females were very interested in neonates and frequently approached the mother to look at and handle the newborn, but were not allowed by the mother to remove it from her ventrum. The neonates genitals were frequently inspected.

Mortality

There have been ten deaths in the mandrill group. All but one involved neonates, and no subadult or adult mandrills died. A young male (12B) died of unknown causes at 14 months of age. A précied description of his decline in health over two weeks is given in Appendix III.1. The nine remaining deaths were of infants and occurred in the perinatal period.

Stillbirth and neonatal death

Of the 33 infants produced in the group, nine (born to Females 1, 5A, 6, and 10) were stillborn or died within a few days of birth.

Female 1 gave birth to live infants four times before she was removed from the group (see Chapter II), but in each case the baby died within a few days of birth. The last of these infants (104) was observed from the day of birth to its death. It appeared that death was by starvation due to maternal incompetence involving faulty positioning of the baby, which restricted its access to milk. A description taken from my *ad lib.* field notes is given in Appendix III.2.

Female 6, although giving birth to and then successfully rearing her first infant, Male 6A, never subsequently reared a baby. Her next baby (601) died neonatally; the third (602) was stillborn; then she aborted twice, both times at 98 days gestation. Her last pregnancy during the study (603) ended in a miscarriage at 160 days gestation.

Although Female 6 conceived readily she had difficulty retaining a foetus, as evidenced by repeated abortions, and carrying viable foetuses to term, as indicated by births which were somewhat premature. Her first and only surviving infant No. 6A was small and thin for his age; 601 may have been premature as 603 was; and 602 may also have been premature as he was of very low birthweight. This is shown below by a comparison with another infant, also a male.

	602	16B
Weight on day of birth (g)	473	740
Weight of mother (kg)	12.4	11.4

602 had bruising round the skull which may be indicative of trauma during birth which might have resulted in his death during labour. Autopsy indicated that he was stillborn. It is possible that mid-gestation is a vulnerable period; both abortions occurred about 100 days (56%) gestation. A mandrill at the London Zoo aborted at a similar (94 days) time (Carman, 1979).

Female 10 lost her third infant (1001) having successfully raised two previous ones. A corpse was never seen but she was observed with blood on her vulva and a noticeably much smaller and flaccid belly. She was at full term (179 days), within the normal gestation length. The following year she gave birth to and successfully raised a healthy daughter (10C).

Two of the three adolescent females (5A, 10A, 12A) who conceived during the study lost their first baby. The exception, Female 12A, gave birth at 44 months of age and successfully reared her son 12A1.

Female 5A was seen carrying a rotting corpse (5A01). Gestation was calculated at 164 days, i.e., birth appeared to have been perhaps a little premature, at 94% of full gestation. She was 44 months of age. Female 10A was never observed with a corpse, but behavioural cues (see Chapter IV) followed by observation of blood on her vulva and an obvious decrease in the size of her belly indicated that her pregnancy had terminated. She was at 154 days (87.5%) of gestation and 48 months old.

Female 5A conceived again in the following breeding season and gave birth (to 5A1) at 57 months and after a full gestation of 175 days. However, it was immediately noticeable that the infant was not normal. When standing, 5A supported the baby against her ventrum and she walked tripedally. While this was frequently observed on the day of birth, thereafter an infant usually supported itself by clinging. Other observations showed that 5A1 was retarded. Further details are given in Appendix III.3, where 5A1 is compared to another infant of the same age and sex (the fourth infant (5D) of 5A's mother, Female 5). At 48 days of age 5A1 was only 50% the weight of a normal infant, had only a third of the teeth, and was still showing neonatal pelage. Additionally her hands and feet were severely malformed.

Infants of young primiparous primate mothers experience lower survival than those of multipares (Altmann, 1986). However, as the founder mandrill females, who were all nulliparous on arrival at CIRMF, did not have an equally high rate of pregnancy failure at first known parturition as the adolescent females (founder females: 23% failure; first generation females: 67% failure) lack of experience in mothering does not adequately explain the low survival reported above. In fact the adolescent females had greater experience with infants than their wild-caught mothers, because all the captive-bred females had experience with younger siblings, whereas the wild-caught females were only a year old on average on arrival at CIRMF (see Chapter II). The extreme youth and immaturity of the first generation females may be a factor in the poor survival of their foetuses. It is also possible to attribute the poor survival of second generation infants to deleterious effects of inbreeding (Ralls and Ballou, 1982). In the breeding season preceding 5A's first pregnancy, her father (Male 7, the alpha male) mated with her in 73% of her observed copulations. The following year he was observed mate-guarding her (see Chapters IV, VI, and VII for definition and discussion), almost certainly copulated with her, and probably impregnated her too (see Chapter VI). The capacity for precocial adolescence in these female mandrills and the apparent lack of incest avoidance has implications for the management of captive mandrills; these are discussed elsewhere (Feistner and Cooper, in press). Studies identifying paternity in the CIRMF-born mandrills are currently in progress (Dixson *et al.*, in prep.).

Lactational Anoestrus

Lactational anoestrus was calculated as the interval in days between the day of birth and the subsequent first day of maximum swelling of the perineal skin. In parous mandrills lactational anoestrus subsequent to surviving offspring (n = 8 intervals) averaged 7.14 months (range 151 to 303 days) (from data in Table III.6). This was remarkably similar to the median lactational amenorrheae of 7.26 months (n = 5 intervals) reported by Hadidian and Bernstein (1979) for three captive mandrills, and was much shorter than that reported for feral savanna baboons. Olive baboons at Gilgil resumed cycling 5 to 21 months (mean = 14 months) after giving birth (Nicolson, 1982 cited in Smuts, 1985). The mean for parous female yellow baboons (n = 7) calculated from data in Altmann (1980, p.11) was 13 months (range 10 to 17). Primiparous mandrill mothers (n = 2 intervals) had significantly longer lactational anoestrus, which averaged 12.6 months, than multiparous females ($t = 2.881$, $df = 8$, $p < 0.05$). Resumption of cycling was significantly more rapid after abortion and stillbirth (although this also was influenced by seasonality - see below) than after birth of a

Table III.6. Length in days of lactational anoestrus

Infant	Date of Birth	Ist day maximum swelling	n days
2C	2 Jan 1986	28 Jul 1986	208
2D	1 Apr 1987	30 Aug 1987	151
5B	14 Sep 1985	14 Jul 1986	303
5C	19 Jan 1987	29 Aug 1987	222
5A01*	20 Mar 1987	26 Aug 1987	159
602*	12 Jun 1986	16 Jul 1986	33
6**	18 Dec 1986	27 Dec 1986	8
6**	15 Apr 1987	25 Jul 1987	100
10B	19 Feb 1986	11 Sep 1986	204
1001*	17 May 1987	22 Jul 1987	66
12C	3 Feb 1986	6 Aug 1986	184
12D	29 Jan 1987	2 Sep1987	216
16A	14 Apr 1986	26 Aug 1987	499
17A	22 Nov 1985	8 Aug 1986	259
17B	20 Feb 1987	3 Oct 1987	225

* stillborn or neonatal death

** abortion at approximately 100 days gestation surviving infant (t = 3.631, df = 13, p < 0.01). The mean interval from foetal death to maximum swelling in three female mandrills (n = 5 intervals) was 2.4 months (Table III.6). A similar pattern was observed in a captive mandrill (Carman, 1979): mean lactational anoestrus after livebirth (n = 3 intervals) was 10.2 months (range 274 to 332 days); after abortion and infant death (n = 2 intervals) it was only 1.6 months (range 36 to 58 days).

Inter-birth interval

Relatively short lactational anoestrus followed by rapid conception (in one to three cycles) led to inter-birth intervals (presented in Table III.7) that were short in comparison to those of feral savanna baboons, which range from 18 to 24 months in yellow baboons (Altmann, 1980) and average 26.5 months in olive baboons (Nicolson, 1982, cited in Smuts, 1985).

A decrease in the length of inter-birth intervals (IBI) with successive surviving offspring was observed in all four qualifying female mandrills (Nos. 2, 5, 10, 12; Table III.7). When all such inter-birth intervals are plotted against the number of maternal unerupted permanent teeth (at the first of each qualifying pair of successive births), longer inter-birth intervals were clearly associated with less mature maternal dentition (Figure III.2). This relationship held both between and within individuals. To adjust for the decrease in IBI with parity, the data cited above (e.g., for cycles to conception and lactational anoestrus) are for parous individuals unless stated otherwise.

Overall, the mean IBI subsequent to surviving offspring was 17.3 months (n = 16 intervals, range 334 to 838 days). The corresponding mean interval in a captive mandrill was similar, 17.6 months (n = 3 intervals, range 257 to 541 days) (Carman, 1979). If only parous individuals are considered (i.e., the interval between first and second offspring are omitted, marked with an asterisk in Table III.7), since IBI was longer after first birth, average inter-birth interval of these females was 13.5 months (n = 9 intervals, range 334 to 543 days). Inter-birth interval was significantly shorter after

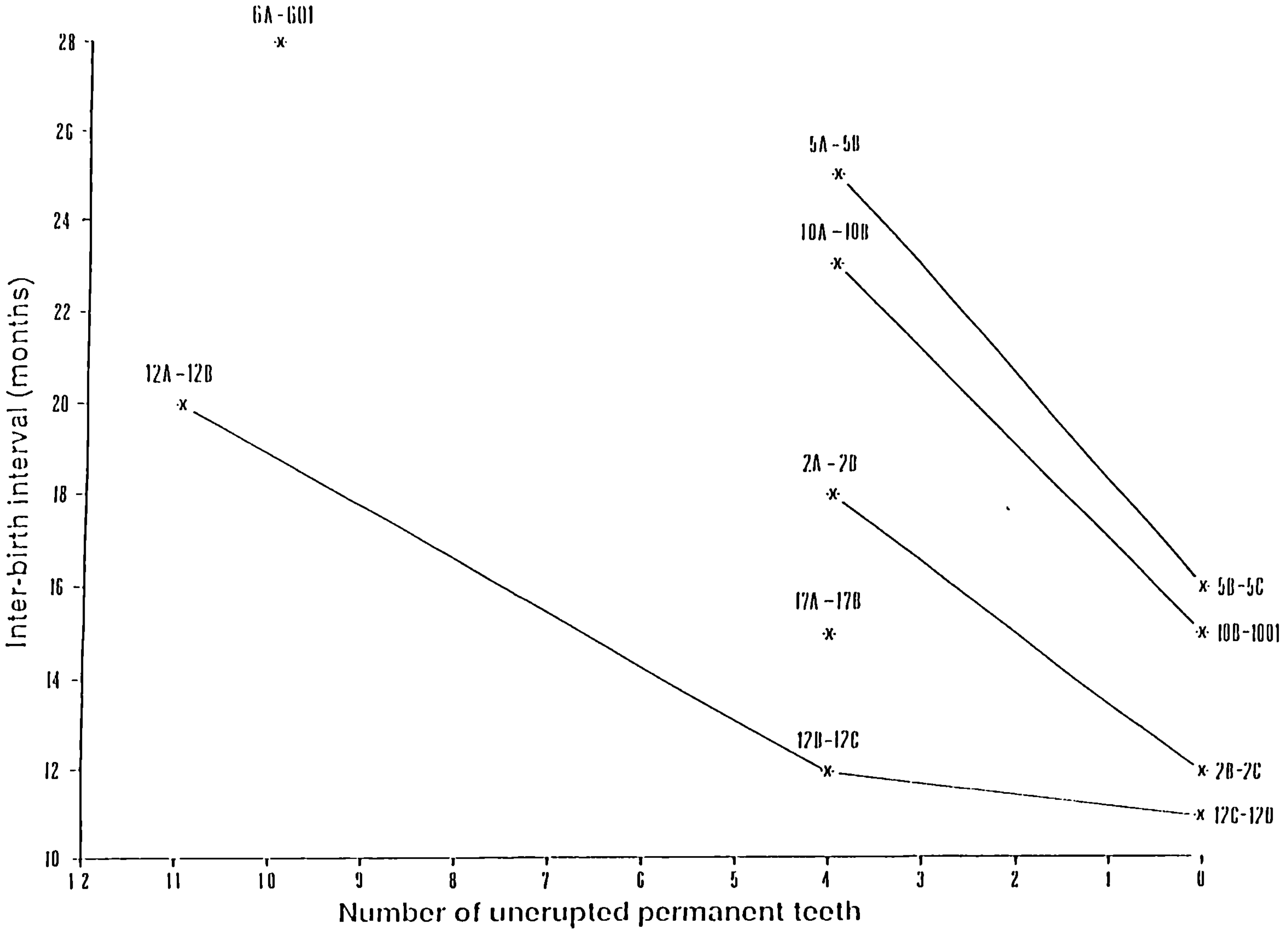
Table III.7. Inter-birth intervals in the CIRMF mandrills

Infant pair	Dates of birth	Inter-birth interval (days)
2A - 2B	01/07/83 - 29/01/85	577 *
2B - 2C	29/01/85 - 02/01/86	338
2C - 2D	02/01/86 - 01/04/87	454
2D - 2E	01/04/87 - 29/02/88	334
5A - 5B	12/07/83 - 14/08/85	763 *
5B - 5C	14/08/85 - 19/01/87	523
5C - 5D	19/01/87 - 06/03/88	412
5A01 - 5A1	20/03/87 - 05/03/88	351 †
6A - 601	23/07/83 - 08/11/85	838
601 - 602	08/11/85 - 12/06/86	216 †
602 - @	12/06/86 - 27/12/86	198 † Δ
@ - @	27/12/86 - 15/04/87	109 † Δ
@ - 603	15/04/87 - 03/02/88	294 †
10A - 10B	06/03/84 - 19/02/86	715 *
10B - 1001	19/02/86 - 17/05/87	452
1001 - 10C	17/05/87 - 04/02/88	263 †
12A - 12B	13/06/83 - 07/02/85	604 *
12B - 12C	07/02/85 - 03/02/86	361
12C - 12D	03/02/86 - 29/01/87	360
12D - 12E	29/01/87 - 29/03/88	425
16A - 16B	14/04/86 - 01/03/88	687 *
17A - 17B	22/11/85 - 20/02/87	456 *

@ abortion * primipares Δ excluded from analysis

† first infant of pair a non-survivor

Figure III.2. Inter-birth interval relative to maternal dental status



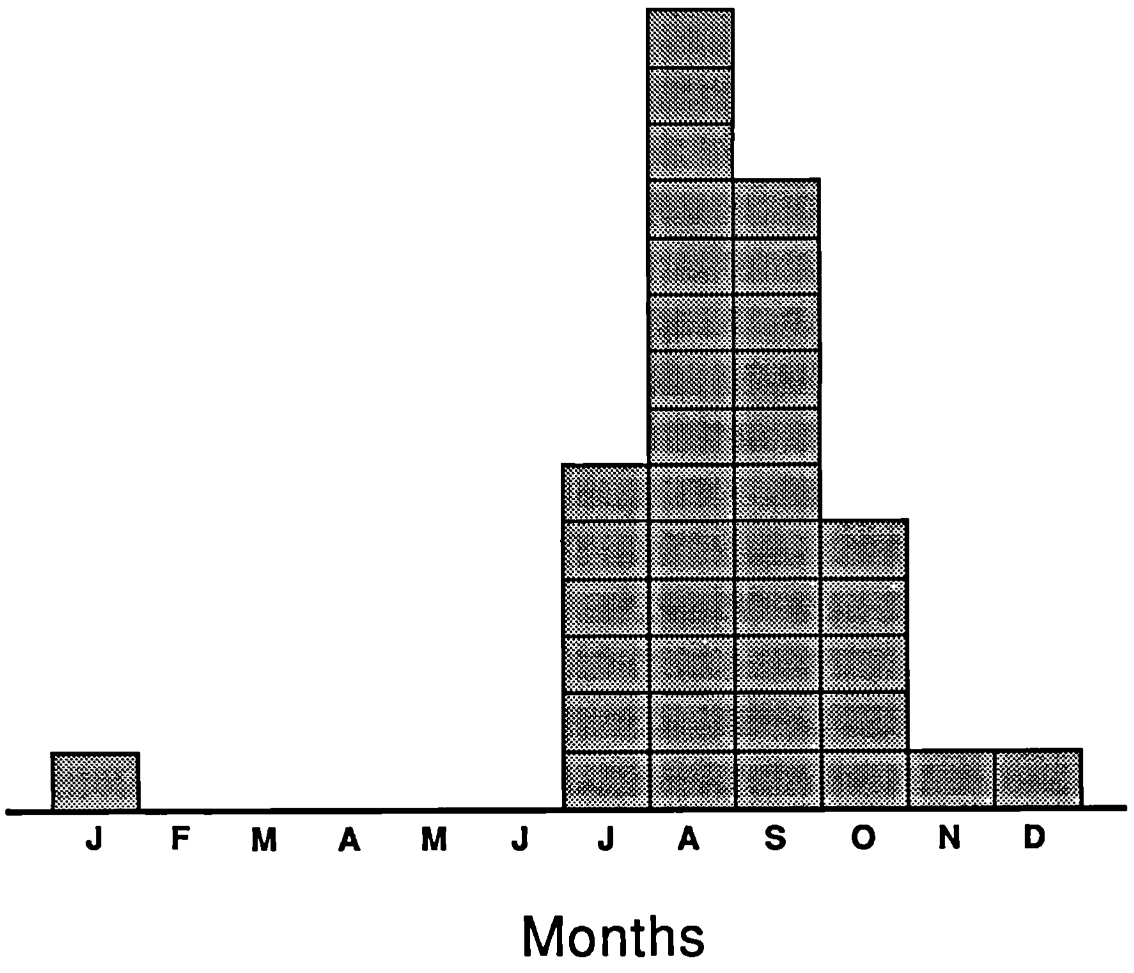
abortion, stillbirth, or death of the infant ($t = 2.893$, $df = 18$, $p < 0.02$) than after birth of a survivor. In both the CIRMF mandrills and the captive zoo female mean IBI after a non-surviving infant was 9.4 months (CIRMF: $n = 4$ intervals, range 216 to 351; zoo female: $n = 2$ intervals, range 257 to 354 days; Carman, *op. cit.*). In drills the intervals were 21 months ($n = 12$ intervals, range 409 to 1165) after survivors and 9.5 months ($n = 3$ intervals, range 228 to 319) after non-survivors (Böer, 1987c).

Mating season

The CIRMF mandrills were found to be seasonal breeders and evidence illustrating this is depicted in Figures III.3 to III.10. For each of the 39 months from January 1986 to June 1988 the occurrence of a maximum sexual swelling was noted for each female ($n = 10$) and these 'oestrous months' (i.e., a month in which any one female was observed in oestrus) are illustrated in Figure III.3. The periods of oestrus recorded in December and January were from female No. 6 who recommenced cycling after aborting in mid-December (1986). Excluding these two records, 97% of oestrous periods occurred in only four months of the year. It is shown below that copulations by subadult and adult males were confined to periods of maximum swelling and therefore it can be concluded that the CIRMF mandrills exhibited a mating season in that there was 'a distinct period of the year to which fertile copulations are confined' (Lancaster and Lee, 1965, p.488). The mating season when females showed cyclical sexual swellings and copulation occurred comprised the months of July to October. In Gabon this period corresponds largely to the long dry season (June to September; IPN, 1983).

Not only did female sexual cycles occur in a period limited to four months of the year, but within the four months there was considerable overlap between females such that they were in oestrus in synchrony. Figures III.4 and III.5 show the mating season in 1986 and 1987 respectively. The mating season was defined as the period from the day a maximum sexual swelling was first seen to the last day a female was seen with a maximum swelling. The December and January cycles of Female 6 were

Figure III.3. Months in which oestrus occurred 1986 to 1988



excluded as they occurred post-abortion, were outwith the four month period during which other females were cycling and thus could not contribute to an analysis of synchrony. In 1986 the season lasted 130 days, from the 14th July to 20th November. The days on which females (n = 8) had maximum swellings (n = 15 cycles) are shown in Figure III.4. In 1986 up to four females were in oestrus on any day. At the beginning of the season at least two females in the group had maximum swellings for 46 consecutive days. Within this block, at least three females were simultaneously in oestrus for 11 consecutive days. Figure III.5 illustrates the days on which females (n = 9) were in oestrus (n = 12 cycles) in 1987. The 1987 mating season lasted 88 days, from 22nd July to 17th October. Figure III.5 shows that up to five females were in oestrus on any one day, and that there was a concentration of females in oestrus in the middle of the season with at least two females maximally swollen simultaneously for 26 consecutive days. Within this block at least three females were in oestrus on 16 consecutive days. Thus in the mating seasons of both years there was a substantial number of days on which several females were in oestrus simultaneously. This considerable degree of synchrony among females (both adolescents and adults) has important implications for male behaviour, reproductive strategies, and social organisation. These are further discussed in Chapters VI and VII.

The proportion of days of the 1986 season on which from zero to four females were synchronously in oestrus is shown in Figure III.6. On 79% of days in the season a female was in oestrus and on 40% of days more than one female was in oestrus, as shown in the right-hand column (>1) in Figure III.6. Data for the 1987 season are shown in Figure III.7. Similar to 1986, on 74% of days in the season a female was in oestrus. More than one female had a maximum swelling on 47% of days, as shown in the right-hand column in Figure III.7.

The first period of oestrus of each of the eight females who cycled in the 1986 season is shown in Figure III.8. The first oestrus started on the 14th July, the last on the 11th September - a period of 60 days. There was considerable synchrony in onset

Figure III.4. Number of females in oestrus on each day of the 1986 mating season

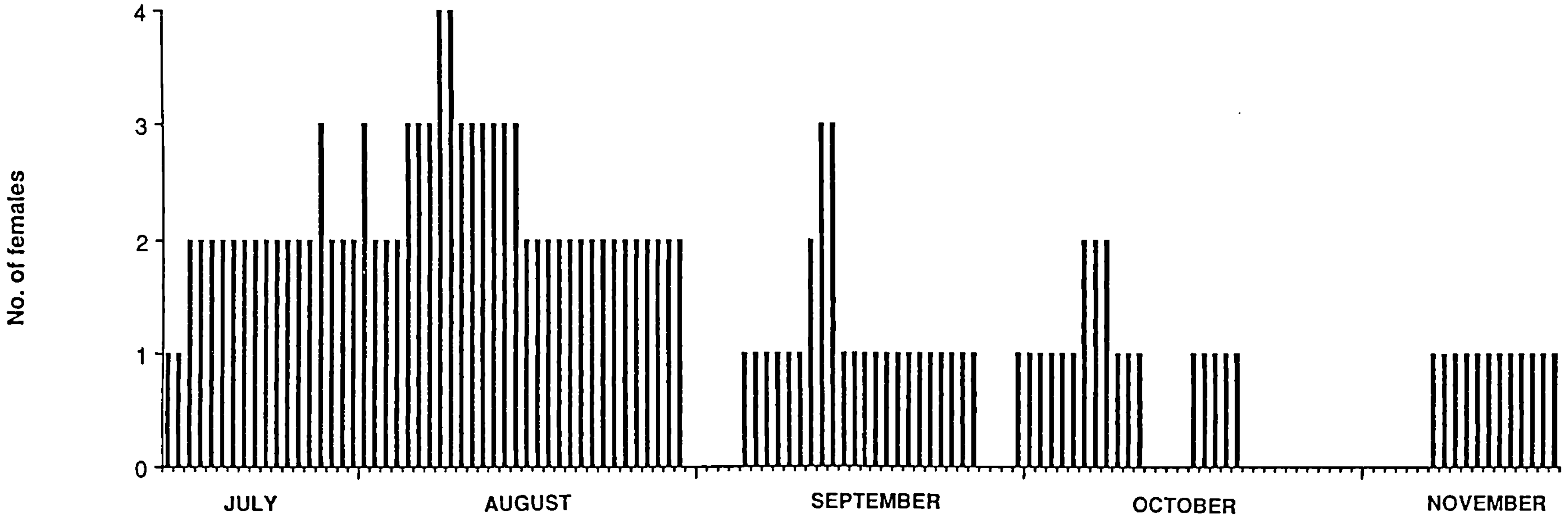


Figure III.5. Number of females in oestrus on each day of the 1987 mating season

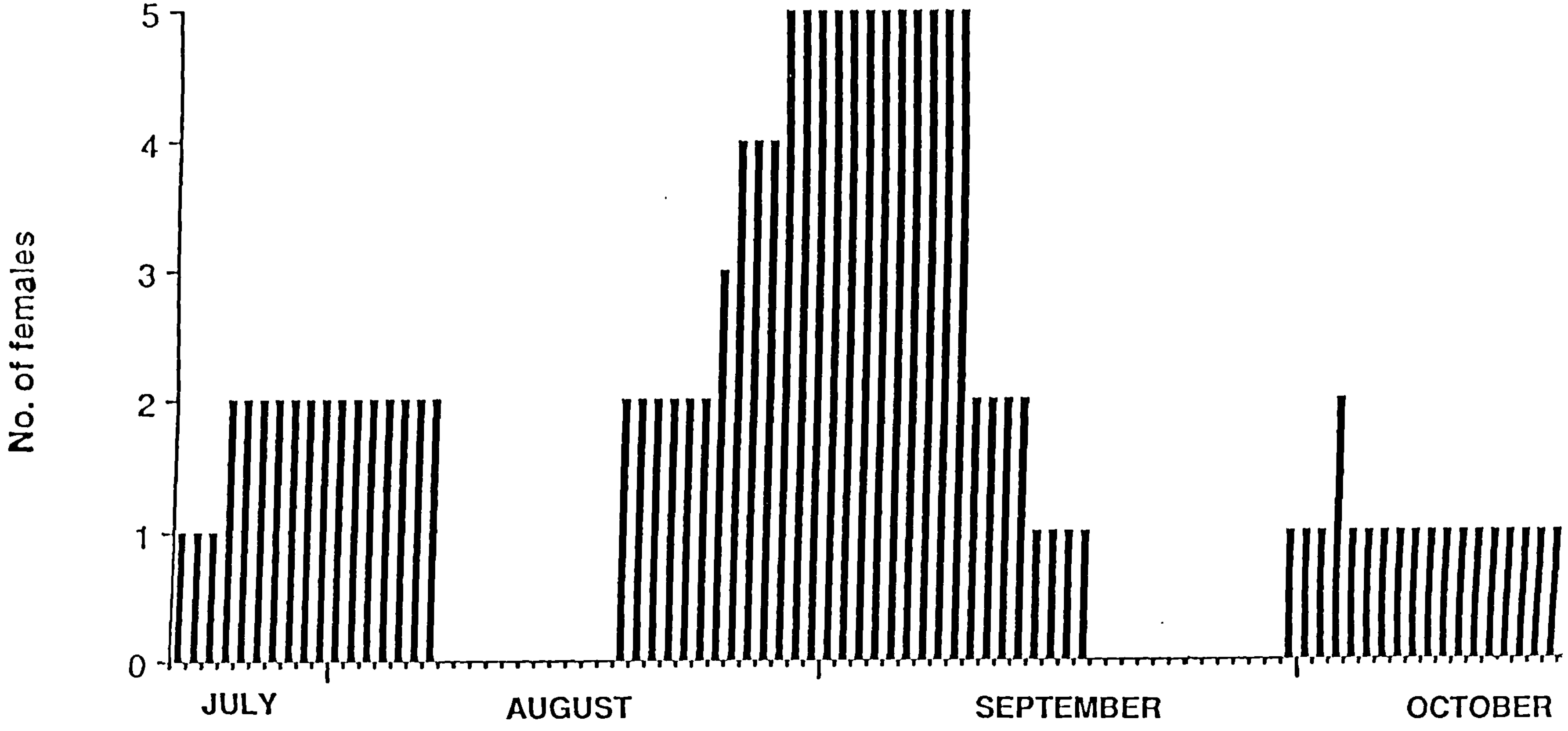


Figure III.6. Proportion of days on which females were in oestrus simultaneously (1986)

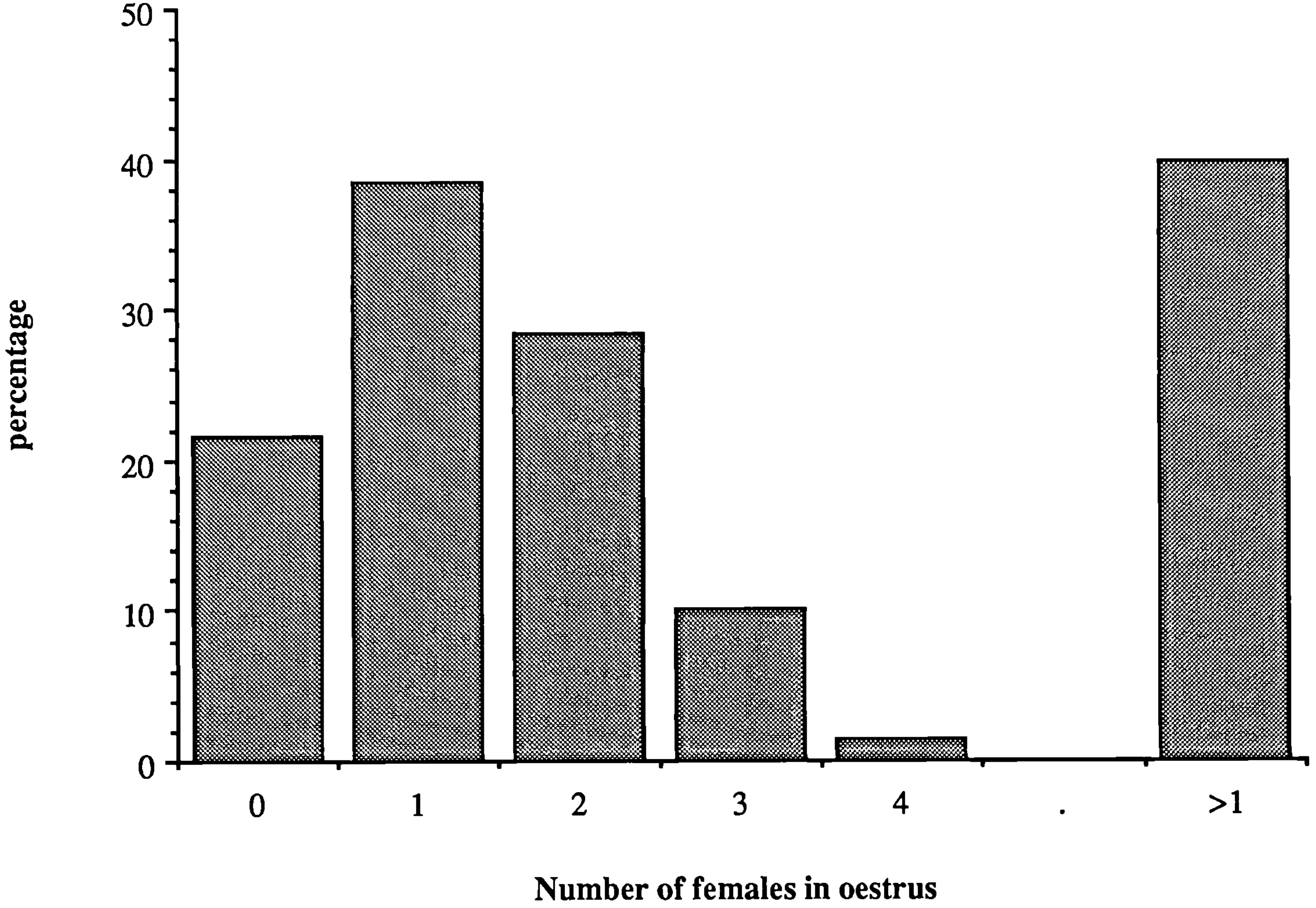


Figure III.7. Proportion of days on which females were in oestrus simultaneously (1987)

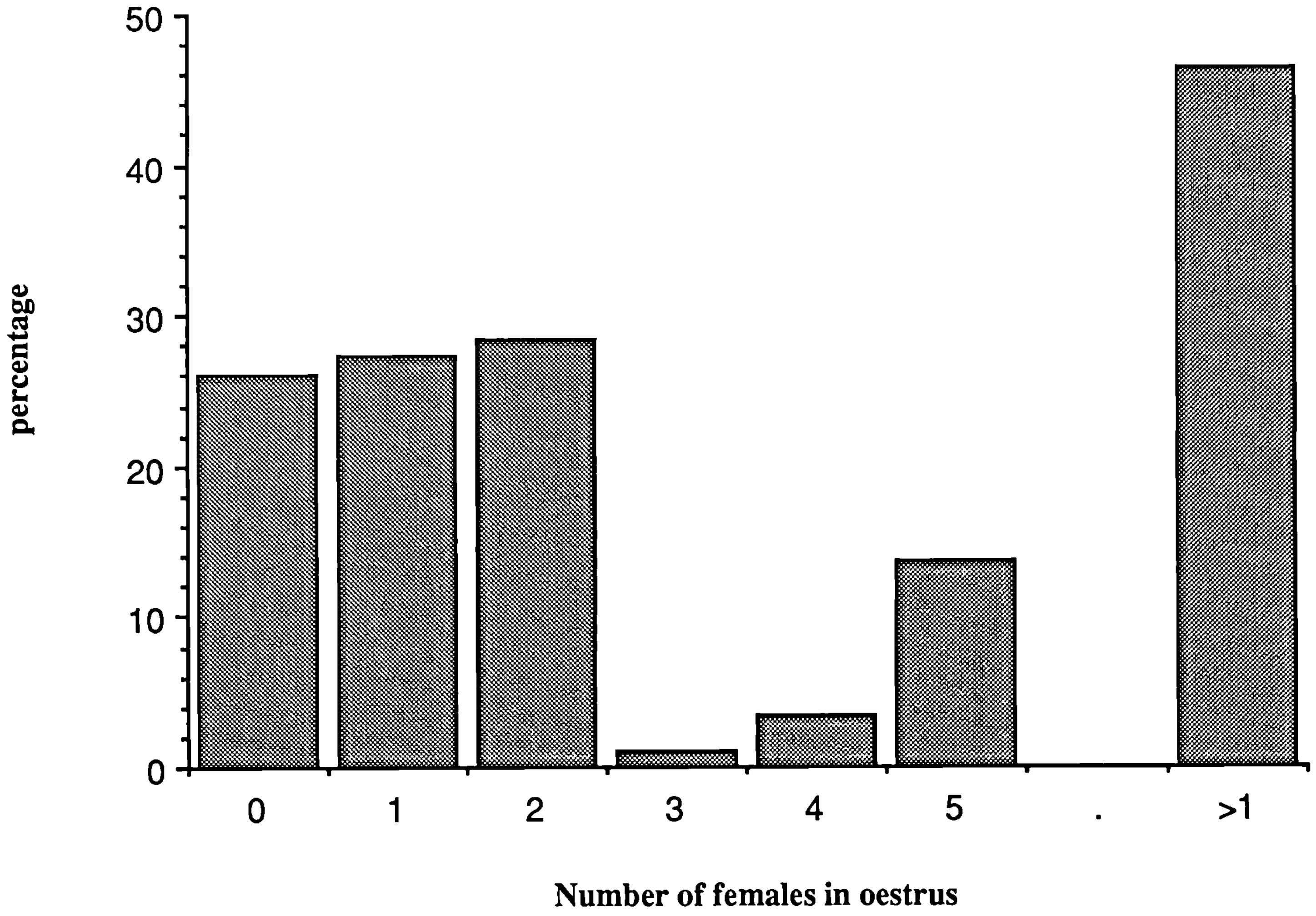
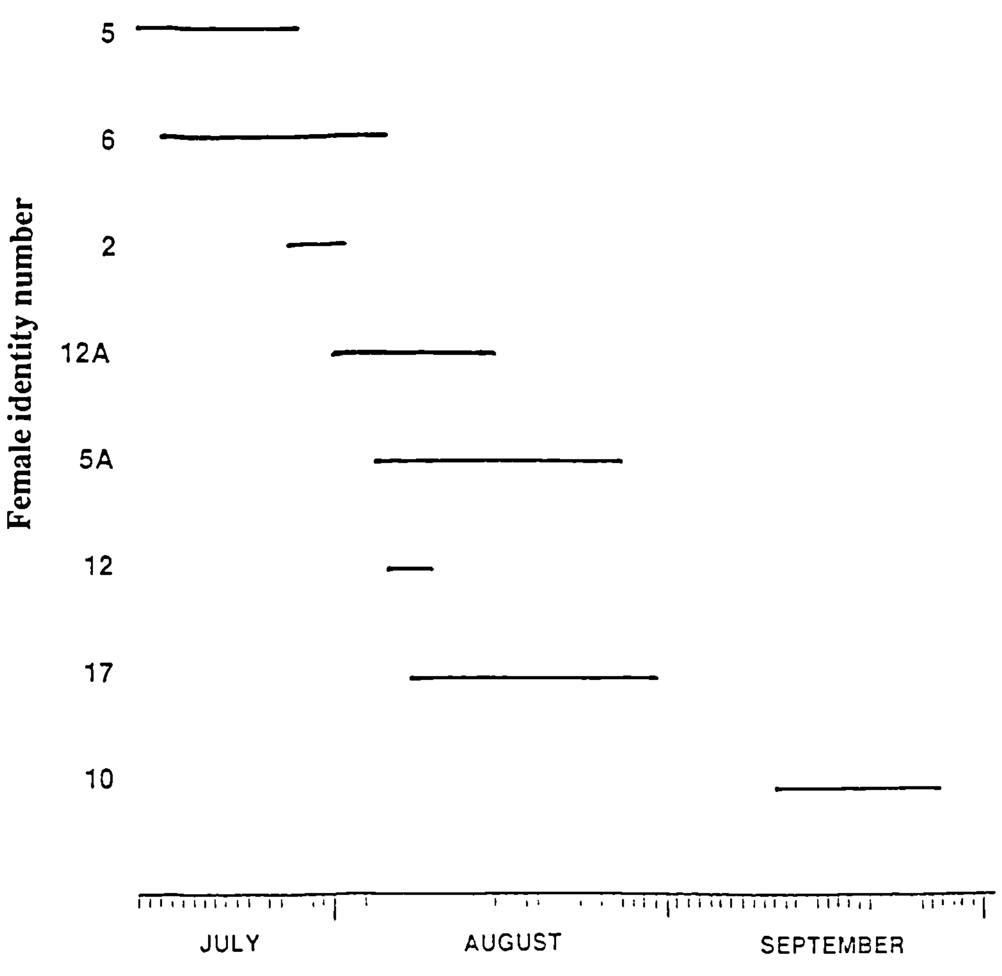


Figure III.8. First oestrus of females in 1986 mating season



of oestrus, with five of the females (63%) commencing their first oestrus in a 12-day period (i.e., in only 20% of the 60 days). There was a similar degree of synchrony in 1987. The first period of oestrus of each of the nine females who cycled in the 1987 season is shown in Figure III.9. The first oestrus started on the 22nd July (approximately the same time as in the previous year) and the last female to have her first oestrus was maximally swollen on 3rd October - a period of 74 days. As in 1986 there was considerable synchrony in onset of oestrus, with six females (67%) commencing in a 13-day period (i.e., in only 18% of days).

Birth season

A temporally restricted oestrus naturally leads to a temporally restricted birth season approximately six months later. The months of all near- and full-term births (n = 33) from June 1983 to June 1988 are depicted in Figure III.10. Although the distribution of births was greater than that of the oestrous months in Figure III.3, with births occurring over the first seven months of the year, this may have been affected by the following factors. The timing of the first births in the group (in June and July, 1983) can be attributed to the onset of viable sperm production in the oldest male (No. 7). As demonstrated by Female 6 above, mandrills could continue to cycle through to December and January if they failed to conceive, and so it is likely that the founder females cycled through the 1982 dry season and into early 1983. Counting back from the dates of birth in 1983 the females must have conceived between mid-December and the end of January. The beginning of this period thus apparently pinpoints the achievement of reproductive competence in Male No. 7. If these 1983 births (n = 5) are excluded and also those in which the infant was stillborn or died neonatally (n = 9) [on the grounds that non-survival may be influenced by timing] a much tighter grouping is seen in the remaining livebirths (as shown in Figure III.11), with 90% of births occurring in four months, January to April. If the births which occurred during the study (1986 to

Figure III.9. First oestrus of females in 1987 mating season

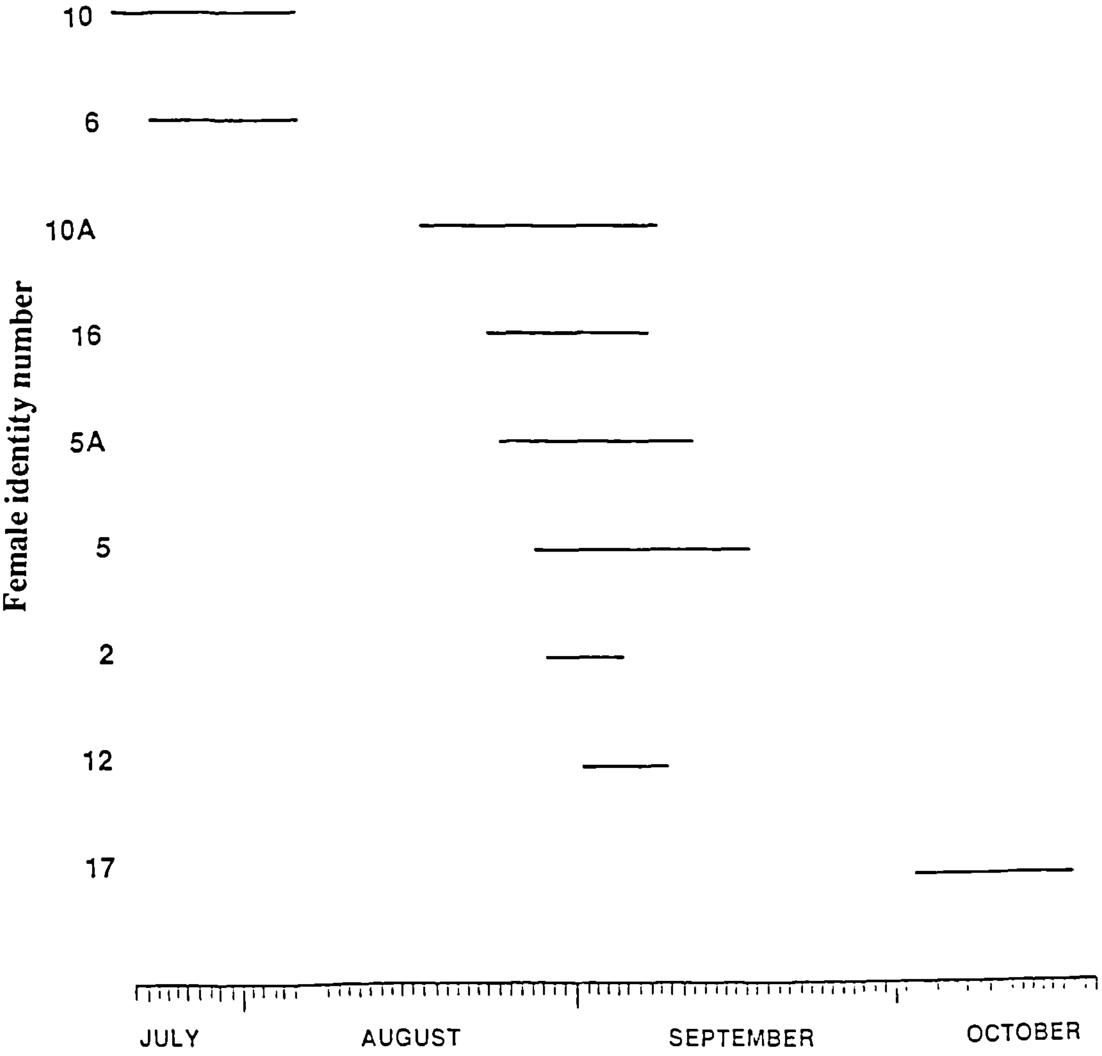


Figure III.10. Months of near and full term births (n = 33) 1983 to 1988

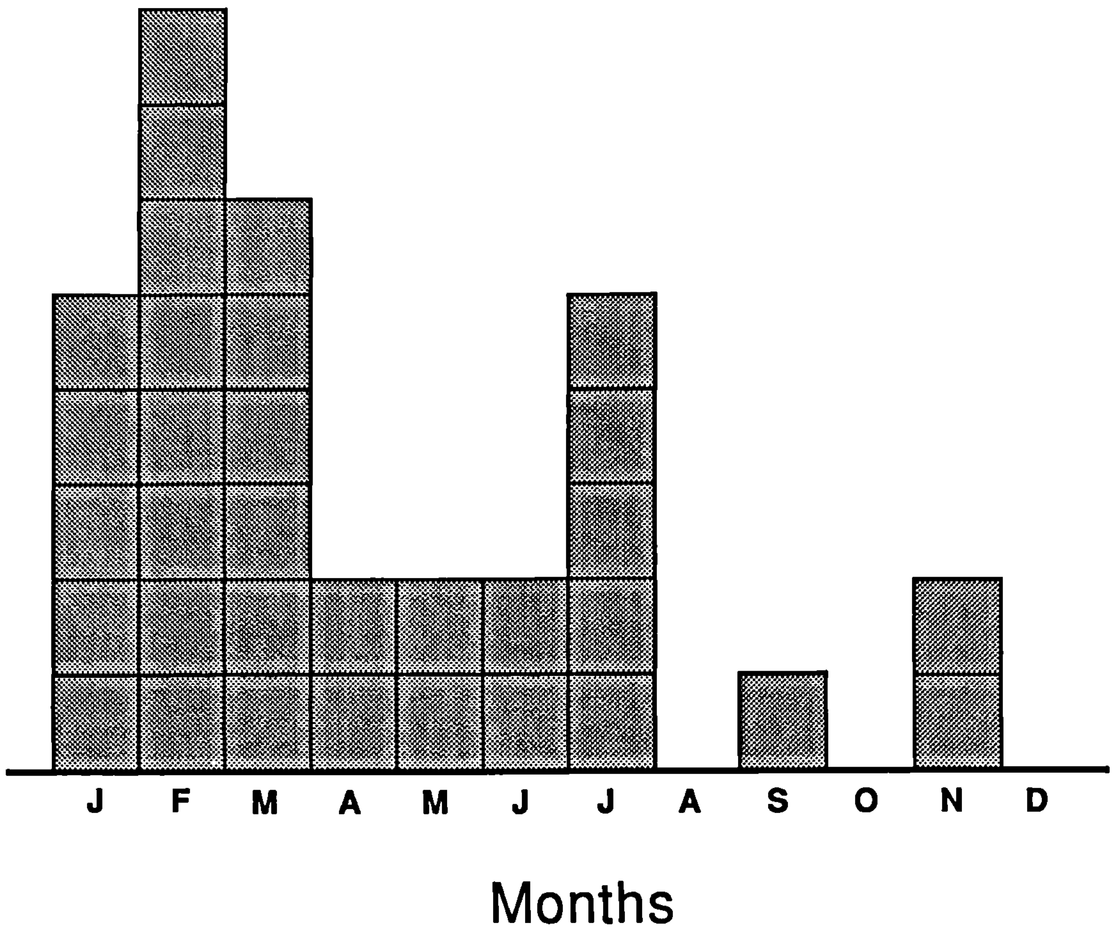
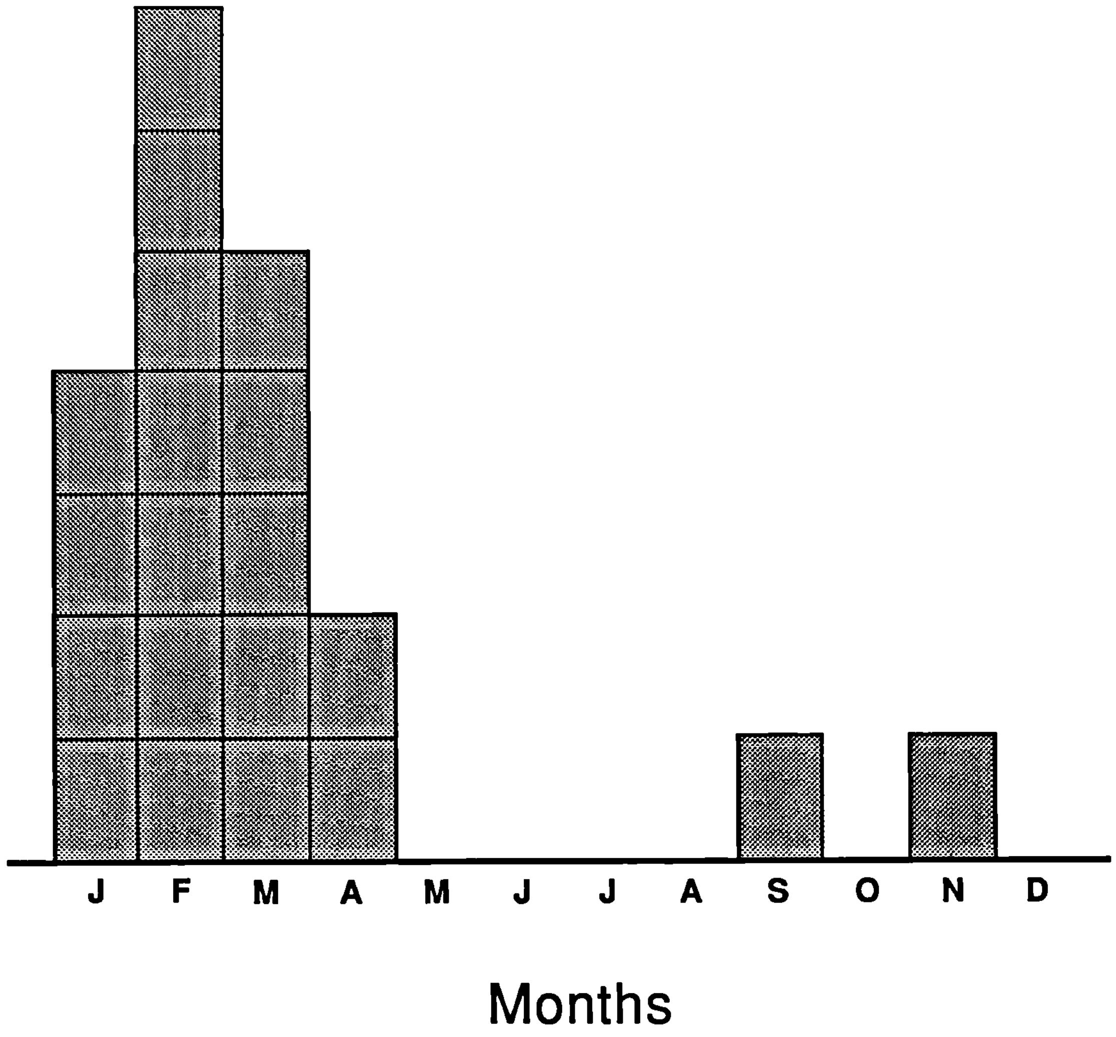


Figure III.11. Months of all full term births of surviving infants (n = 20) 1984 to 1988



1988, which thus includes the period over which the oestrous months occurred) are plotted by year (Figure III.12) it can be seen that within any year there was a tendency for births to be concentrated in two months, and that over the three years a slight trend for increased synchrony emerged.

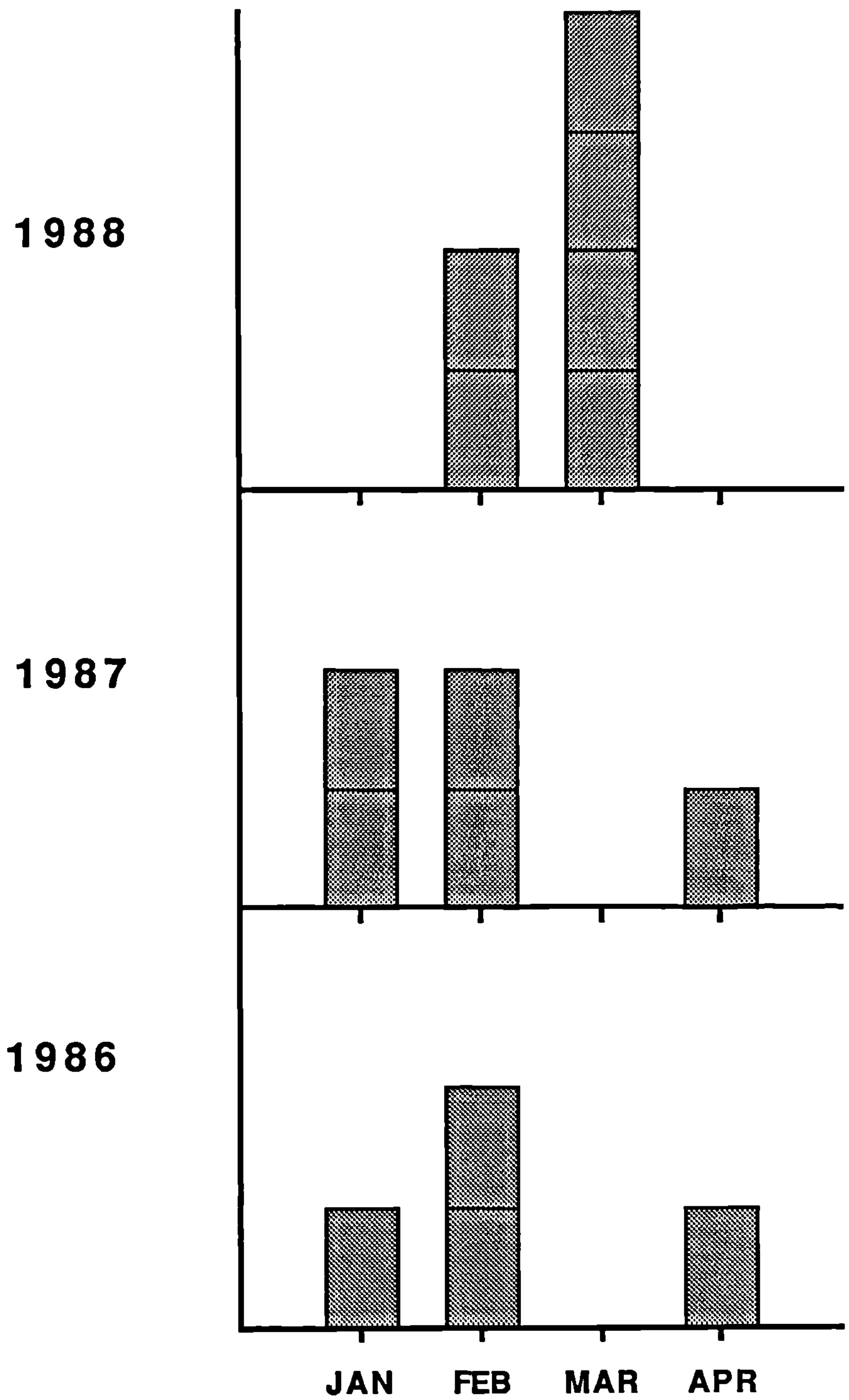
Data on cycle resumption after foetal or neonatal death further confirmed the existence of a temporal pattern in CIRMF mandrill reproduction. Those females who failed to conceive or who aborted during the mating season continued to cycle until January. Those who lost a foetus between February and May did not resume cycling until the onset of the next mating season (i.e., July). Seasonality is not evident in the reproductive behaviour of other captive groups of mandrills (Int. Zoo Yrbk., 1961; Hill, 1970) or drills (Böer, 1987c; C. Cox, pers. comm.)

The above data allow the conclusion that the CIRMF mandrills showed a birth season (sensu Lancaster and Lee, 1965) in that there was 'a discrete period of the year to which all births are confined'. The anecdotal reports from the mandrill field studies (reviewed in Chapter IV) imply a birth peak, i.e., that there is a 'period of the year in which a high proportion of births but not all births are concentrated' (Lancaster and Lee, *op. cit.*, p.488).

Birth peaks are common in the *Papio* baboons but a birth season has not been reported (Lindberg, 1987). However, olive baboons in a forested habitat showed significantly more births between February and July than at other times of the year (Rowell, 1966). Hamadryas and gelada baboons also appear to have birth peaks (Kummer, 1968b; Dunbar and Dunbar, 1975).

The seasonality of reproduction in the CIRMF mandrills matched that found in several other monkey species in Gabon. A birth season from December to February is found in *Cercopithecus cephus*, *C. nictitans*, and *C. pogonias* (Gautier-Hion, 1980). The birth season ranges from November to April in *C. neglectus* (Gautier-Hion and Gautier, 1978) and *C. (Miopithecus) talapoin*, but seasons are of about two month's duration in any given talapoin troop (Gautier-Hion, 1971). Reproductive seasonality in

Figure III.12. Months of full term births of surviving infants (n = 15) during the study (1986 to 1988)



primates has recently been reviewed by Lindburg (1987) and the tropical forest cercopithecines *C. mitis*, *C. lhoesti*, *C. mona*, and *C. ascanius* also appear to breed seasonally (references in Lindburg, 1987). *Lophocebus albigena* and *Cercocebus galeritus* are reported to be seasonal in some areas, for example in Gabon (Haltenorth and Diller, 1980) and the Tana River area (Waser, 1984), but not in others, e.g., Cameroon (Rowell, 1977). Data for *L. aterrimus*, and *C. torquatus* are absent or equivocal.

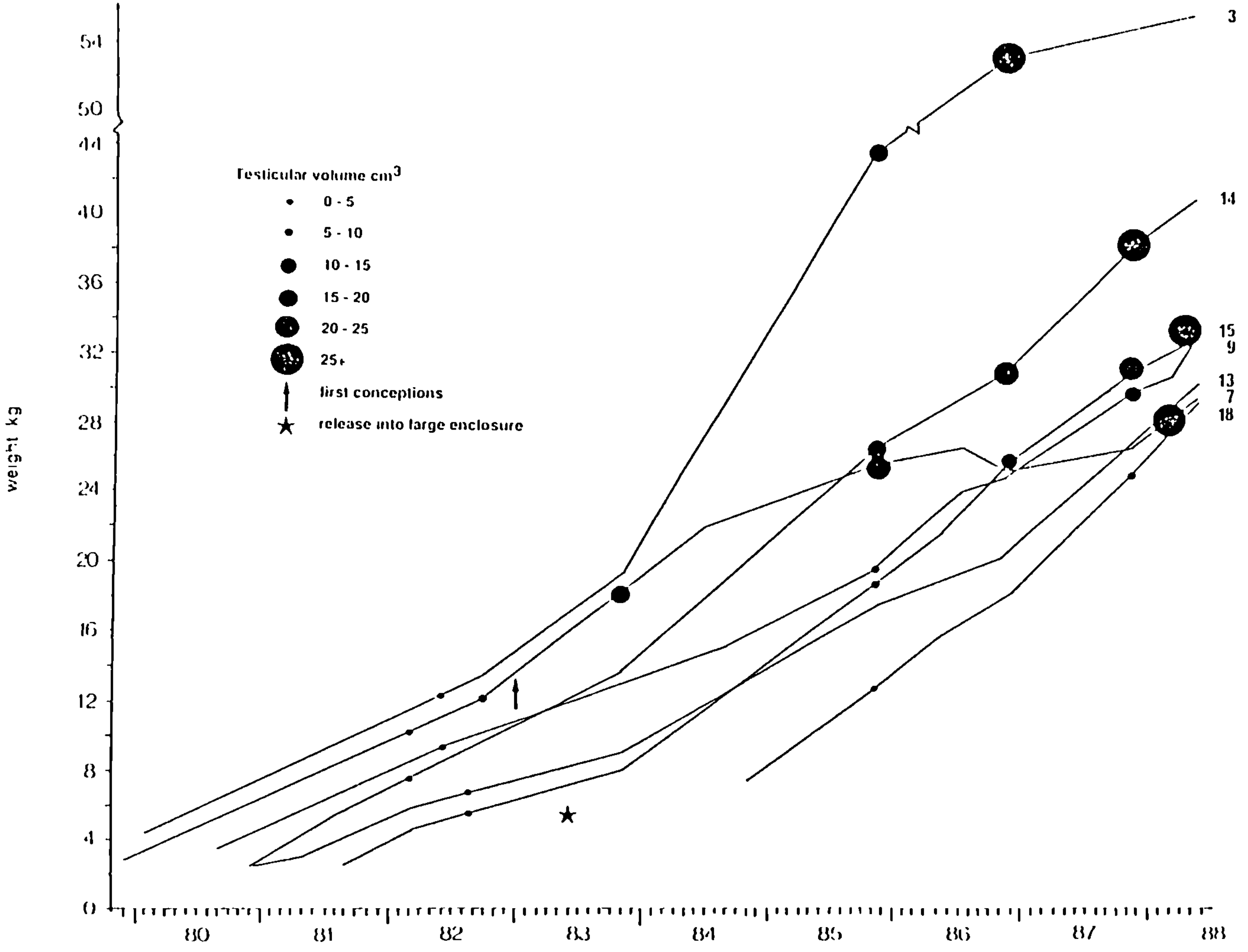
MALES

The body weight profiles and (left) testicular volumes for each of the seven introduced males from their arrival at CIRMF to April 1988 are shown in Figure III.13. Testicular volumes were calculated using the formula for the volume of an oblate spheroid, namely: volume = pi x 1/6 width^2 x length (Dixson *et al.*, 1980). All measurements were taken on anaesthetised animals.

Although the group contained seven founder males, only two (No. 7 and No. 3) could be classified as truly adult, i.e., their weight and canine tooth length had stabilised (see below). Of these two males, one (No. 7) was the alpha male, the "leader" (Jouventin, 1975a) of the group, and the other (No. 3) was solitary. This is discussed further in Chapters VI and VII. As can be seen in Figure III.13 all the other five males appeared still to be gaining weight at April 1988.

The first conceptions in the mandrill group are indicated by the arrow in Figure III.13. At this time only Male 7 could have sired these infants. He had the largest testicular volume; the next biggest volume (Male 14) was only 25% that of Male 7 and on average the other males testes were less than 1 cm^3. Reproduction in Male No. 7 was precocious as it was in the female mandrills (see above). At the time of the conceptions he was only five years old at most, weighed only 14 kg (56% of his adult weight), had deciduous upper canines and lower first premolars, and no third molars

Figure III.13. Body weight and testicular volume increase in male mandrills



(i.e., he was eight teeth short of complete adult dentition). Although he was sexually and otherwise behaviourally dominant (R.W. Cooper, J. Norris, pers. comm.), his testicular volume determined two months prior to these conceptions (6.0 cm^3) was only 30% of the adult volume achieved sometime between 20 months (15.2 cm^3) and 36 months (20.9 cm^3) later. It is likely that the restricted period (June and July, 1983) in which the first five births in the group occurred reflected the achievement of reproductive competence of Male 7 about six months previously. The earliest of the dates of conception (in mid-December 1982) apparently pinpoints his 'sudden' production of viable sperm.

The data reported below were collected when the whole group was captured (see Chapter II) in October 1985, 1986, 1987, and April 1988. In order to examine associations between various parameters, such as testicular volume and dominance, Pearson Product Moment correlations were done; body weight was controlled for using a partial correlation.

Blood samples taken in October 1985 and 1986 were assayed for testosterone (for the method see Marson *et al.*, 1988). The results for the males are shown in Figure III.14 plotted against dominance status (high (1) to low (7) rank). Blood testosterone level correlated highly and significantly with dominance rank both in 1985 and 1986 (mean $r = +0.87$) and this relationship was not altered when body weight was controlled for using a partial correlation (Table III.8). Mandrills of high dominance status had high blood levels of testosterone. The 1985 data illustrate the special position held by the most dominant male (Figure III.14). The difference between him and the next animal was much greater than that between any of the others, and his testosterone level was three times that of the beta male. This paralleled behavioural data (reported in Chapter IV) showing the alpha male to be significantly different from other males. Behavioural events in November 1986 (discussed in Chapter VI) indicated that the alpha male's relatively low testosterone levels in October 1986 may have had behavioural consequences.

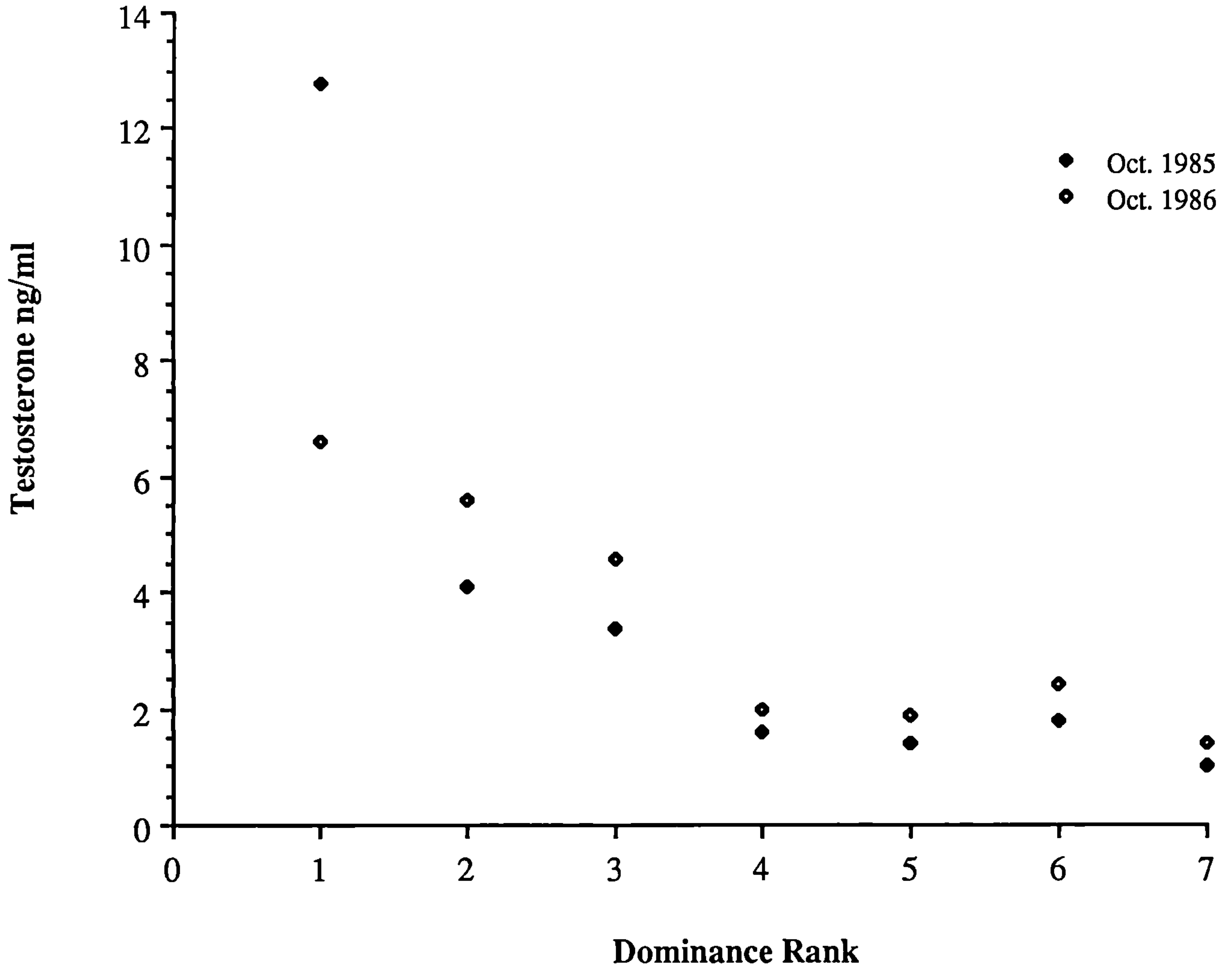
Table III.8. Pearson Correlations of testicular volume, testosterone level, dominance rank, and body weight in male mandrills

Testosterone and Dominance Rank		
1985	+0.78*	+0.84*@
1986	+0.92**	+0.88*@
Testicular volume and Testosterone		
1985	+0.79*	+0.80 @
1986	+0.81*	+0.70 @
Testicular Volume and Dominance Rank		
1985	+0.93**	+0.86*@
1986	+0.82*	+0.77 @
1987	+0.70	+0.61 @
1988	+0.70	+0.59 @
Testicular Volume and Body Weight		
1985	+0.69	
1986	+0.64	
1987	+0.79*	
1988	+0.67	

* $p<0.05$, ** $p<0.01$ (df = 5)

@ Body weight controlled for using a Partial Correlation (df = 4)

Figure III.14. Testosterone level and dominance rank (Oct. 1985 and 1986)



Testicular volume and testosterone level were significantly and strongly positively correlated (mean r = +0.80). This relationship persisted when body weight was controlled for, but was no longer significant (Table III.8). The data for 1986 are illustrated in Figure III.15.

Testicular volume and body weight were consistently positively correlated (Table III.8) over the two and a half years (mean r = +0.70). As an example the 1987 data are shown in Figure III.16.

Testicular volume and dominance were also strongly correlated (mean r = +0.81), although the strength of the relationship was slightly reduced when the effect of body weight was partialled out (Table III.8). In addition the correlation became weaker over time (i.e., from 1985 to 1988) decreasing from r = +0.93 to +0.70. The data are shown in Figure III.17 which also illustrates the annual (1985 to 1987) increase in testicular volume in each male.

MALES AND FEMALES

Reproductive biology

From January 1986 to June 1988 data on copulations were recorded whenever they were seen by behaviour sampling. Social aspects of mating are reported in Chapters IV and VI. Aspects such as timing of mating in relation to female sexual cycle and number of thrusts to ejaculation are reported below.

Temporal patterning of copulation

A total of 123 intromitted mounts was observed. Ejaculation was indicated by occurrence of an ejaculatory pause and the appearance of coagulating semen in the female's vulva and/or on her perineum. Of the 114 intromitted mounts where the occurrence or not of ejaculation was readily distinguishable, 88.6% occurred with females who were at the maximally swollen phase of their cycle (Figure III.18). Of the intromitted mounts which culminated in ejaculation (n = 96), 91.7% occurred at

Figure III.15 Testicular volume and testosterone level (Oct. 1986)

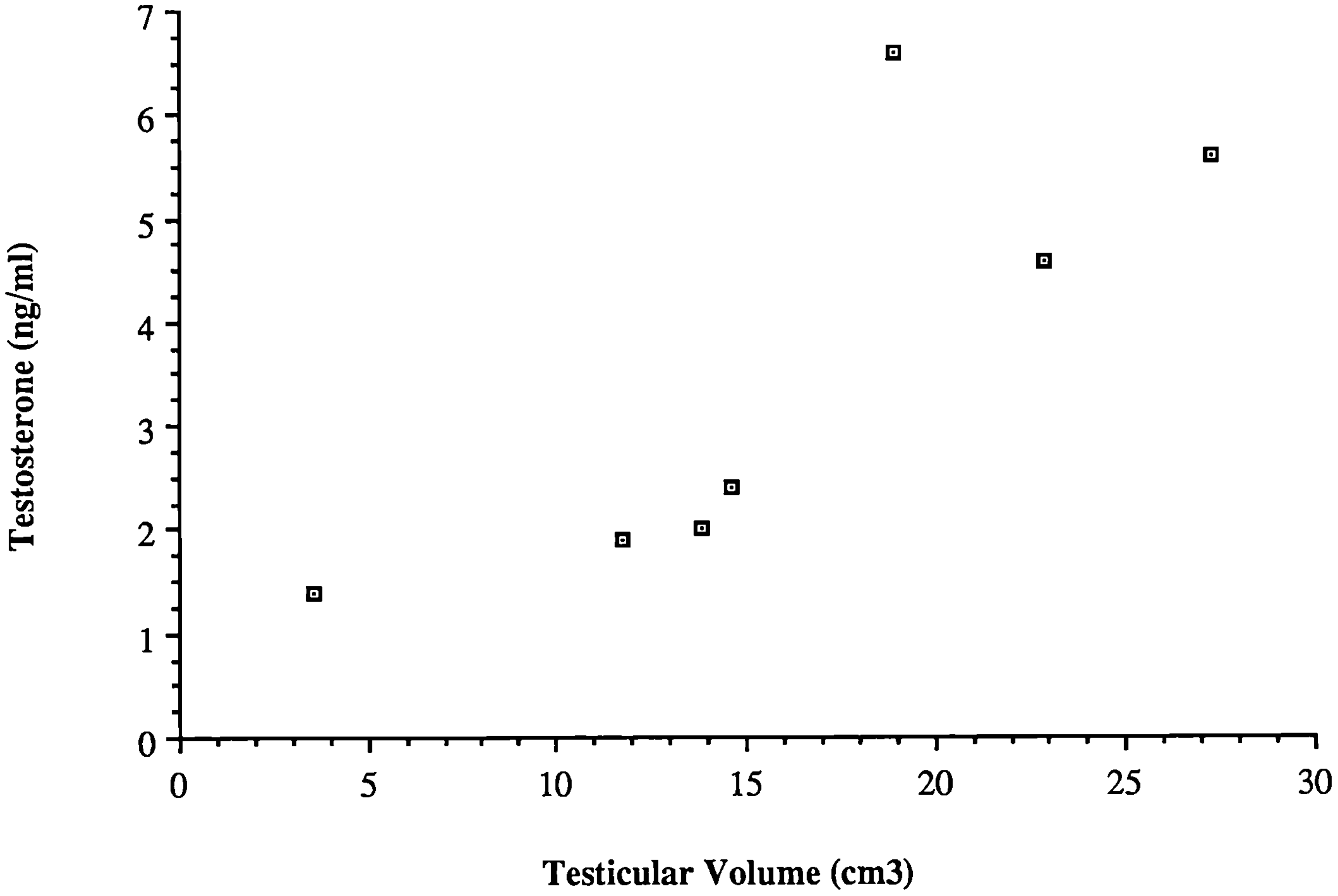


Figure III.16. Body weight and testicular volume (Oct. 1987)

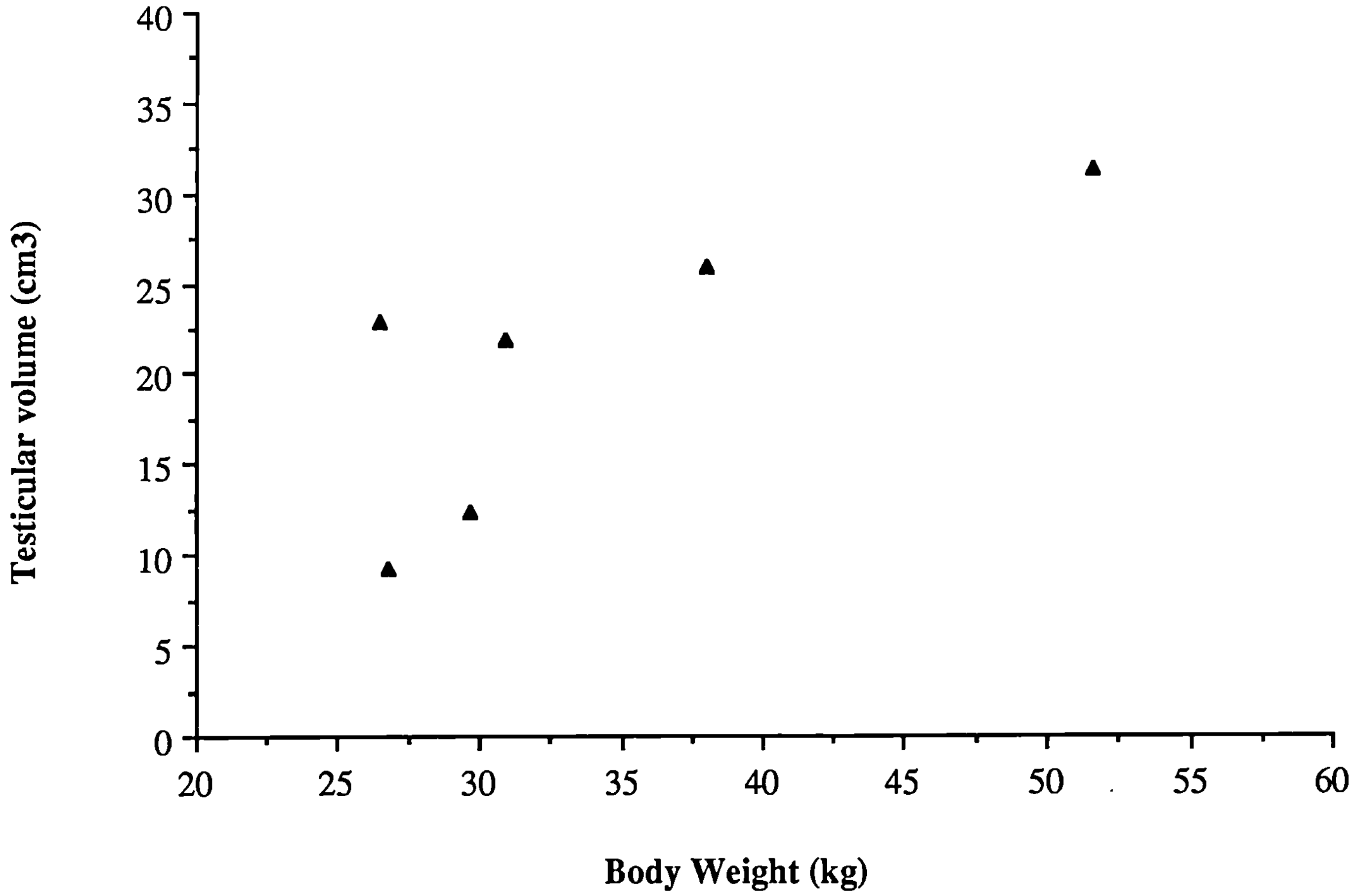


Figure III.17. Testicular volume and dominance rank

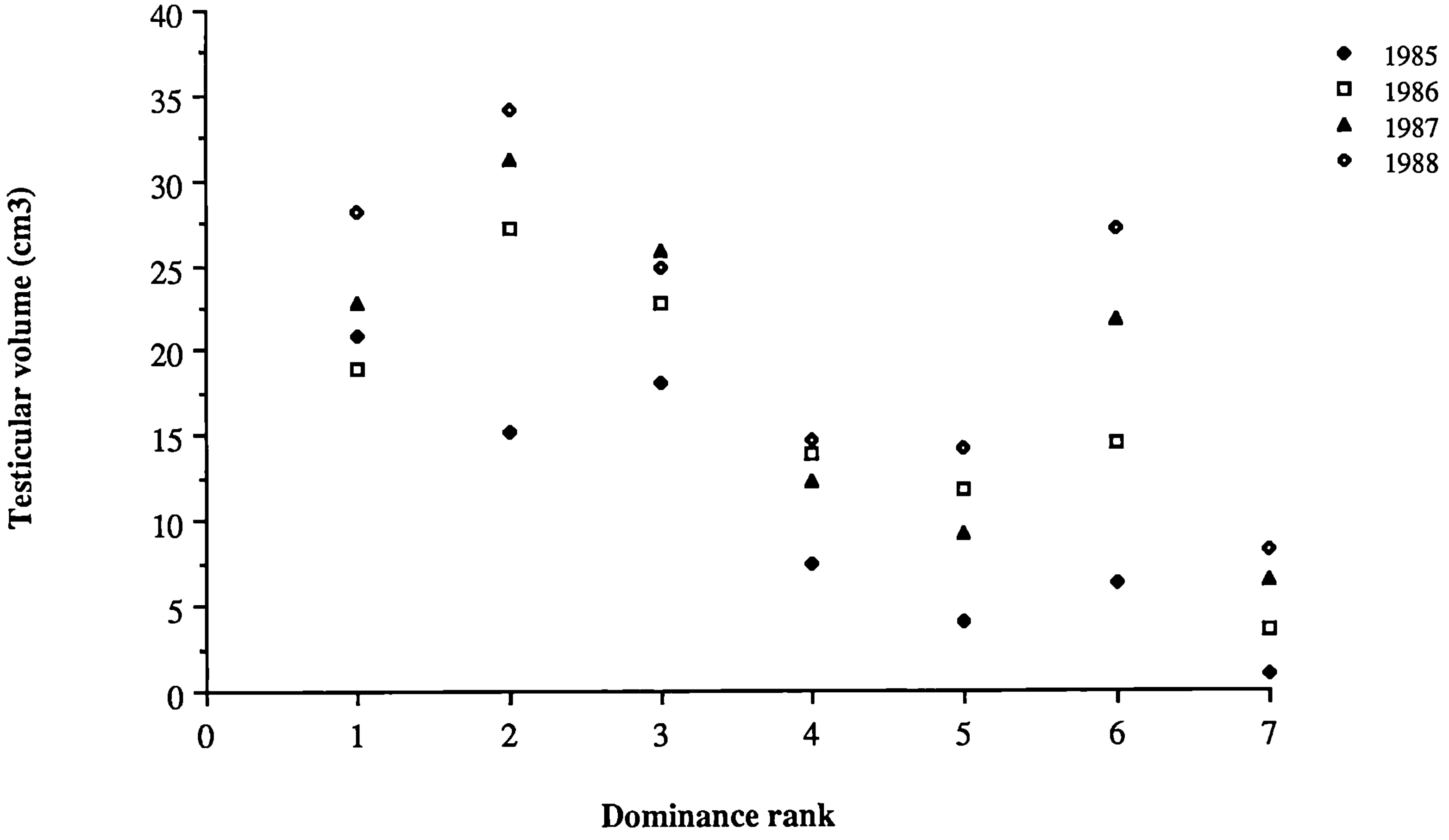
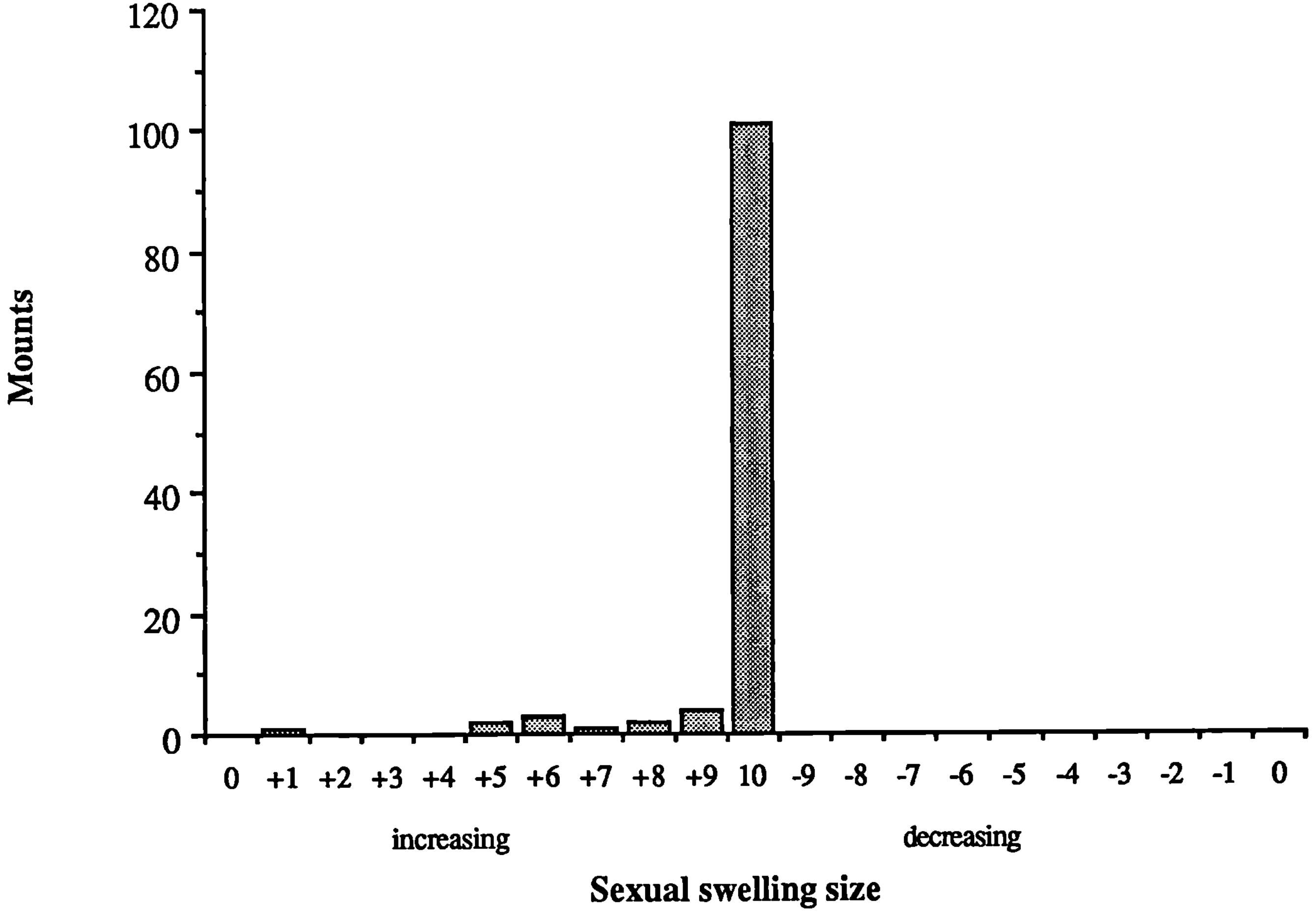


Figure III.18. Intromitted mounts (n = 114) in relation to female sexual swelling



maximum swelling, i.e., during oestrus (Figure III.19). Figure III.19 also clearly illustrates that all intromitted mounts at swelling sizes which were less than maximal were during the follicular phase of the cycle.

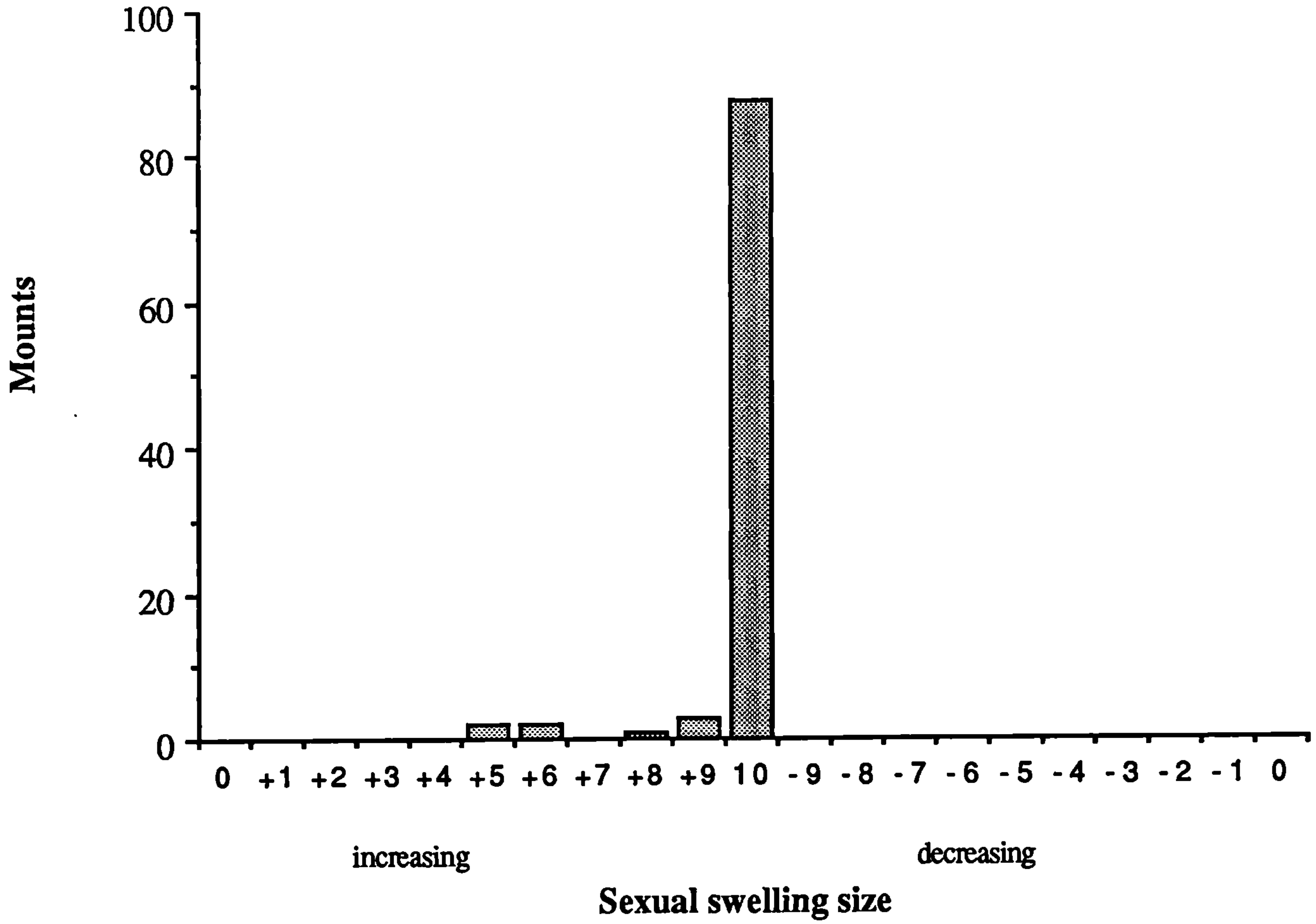
Copulation

In the CIRMF mandrills, after mounting and intromitting the male gave about 18 thrusts (mean ± sem, 17.7 ± 4.2, range 7 to 29, n = 81 copulations) before cessation of thrusting and body tremor signalled the occurrence of ejaculation. In captive groups rapid shallow thrusts may occur (5.0 ± 2.0, range 3 to 7, n = 6) as the male develops an erection (Feistner and Dixson, in prep.) but this was not observed in the CIRMF mandrills. During the first few thrusts old ejaculate was frequently 'hooked' out of the female's reproductive tract/vulva and fell to the ground. Ejaculate could be seen immediately the male dismounted and it coagulated rapidly on the female's perineum. Ejaculation occurred during a single mount in all cases. There was no evidence of female orgasm. Immediately the male dismounted the female left, withdrawing to a distance of two to five metres.

Sexual Dimorphism

Social organisation and mating system in primates, as well as other features such as habitat preference and body size, have been correlated with the presence or degree of sexual dimorphism (e.g., Clutton-Brock *et al.*, 1977; Clutton-Brock and Harvey, 1978; Leutenegger and Kelly, 1977; Leutenegger, 1978). The paucity of published information on mandrills means that these analyses have frequently used very small sample sizes which may also have been unrepresentative. Data for mandrills for two indices of dimorphism - body weight and canine tooth length - are presented below. The contributions of these data to interpretations of social organisation and mating system are discussed in Chapter VII.

Figure III.19. Ejaculatory mounts (n = 96) in relation to female sexual swelling



Body Weight

Body weights for the 14 subadult and adult mandrills are presented in Table III.9. The last three weight measurements, separated by more than two months, were used. If there was an increase in weight over the three measurements individuals were assumed still to be growing so only the last (heaviest) weight is reported in the table. If there were no consecutive increments in weight the last three weights were averaged to give a mean weight. All the females came into the latter category and their weights in Table III.9 are all means. Only Males 7 and 3 had relatively stable weights, which were averaged; the other males were still gaining weight (as illustrated in Figure III.11) and so only their last weight is cited.

Considering the two males whose weight was stable, mean (standard deviation) male body weight (in kg) was 40.41 (13.01). However, these two males were extremes in the group; the alpha male, No. 7, was surprisingly the lightest male (his 'real' weight would probably be one to two kilos heavier since he lacked his left leg from just above the knee), whereas No. 3 was the heaviest. The average of all the males was 35.19 (8.43), although this represents an underestimate of their projected stable adult weight. There are relatively few published weights for mandrills. Jouventin (1975a) stated that males could weigh more than 30 kg, and Malbrant and Maclatchy (1949, p.54) reported weights of wild-shot mandrills from which a mean of 28.2 (5.6) kg for adult males (n = 6) can be calculated. Secondary sources cite weight ranges of over 100 lbs (Tappen, 1960, p.103), 20 to 30 kg (Haltenorth and Diller, 1980, p.266), up to 40 kg (Dorst and Dandelot, 1976, p.51), over 50 kg (Fiedler, 1972, p.424), and up to 54 kg (Walker, 1983, p.422). Male mandrills are thus 'the largest of all monkeys' (Walker, *op. cit.*, p.422).

Mean (S.D.) body weight (in kg) over all seven CIRMF founder females was 13.22 (1.89) (see Table III.9). Jouventin (1975a) stated that females weighed three times less than males, and Malbrant and Maclatchy (1949) gave weights for three wild-shot females of 11 and 12 kg. A range of 10 to 15 kg was reported in Haltenorth

Table III.9. Body weight (in kg) of male and female mandrills

Males		Females	
ID	Weight (kg)	ID	Weight (kg)
7	27.40	2	10.97
3	53.43	5	14.03
9	32.80*	6	13.90
13	30.10*	10	17.07
14	40.70*	12	12.60
15	32.80*	16	11.40
18	29.10*	17	12.57
mean (S.D.)	35.19 (8.43)	mean (S.D.)	13.22 (1.89)

Values are means of last 3 weighings separated by more than 2 months, except
* last weight (April 1988)

and Diller (1980).

A comparison of overall mean body weight of all the male (n = 7) and female (n = 7) mandrills at CIRMF indicated that female weight was 38% that of males. If the mean of the two full-grown males was used for comparison, the ratio was 33%. These data corroborate Popp's (1983) suggestion that mandrills are the most sexually dimorphic in body weight of the baboons. This is further discussed in Chapter VII.

Canine tooth length

Data on length (in cm) of upper and lower canines for all 14 subadult and adult mandrills are presented in Appendix III.4. Where there were no fluctuations greater than 0.1 mm in canine tooth length over the six months up to April 1988, the two last measurements were averaged. If there were increases of over 0.1 mm the canine teeth were assumed still to be growing and so only the last (April 1988) data were given. Canine tooth length was stable in all seven females but only in Males 7 and 3 was canine eruption shown to be complete. In the remaining five males canine length was increasing.

The mean upper and lower canine tooth lengths of Males 7 and 3, and all seven females are presented in Table III.10. Jouventin (1975a, p.527) presented upper canine tooth lengths for eight wild-shot male mandrills. Four of these individuals had worn and broken teeth, but an average of 4.93 cm (range = 4.6 to 5.4) can be calculated from the remaining four males. This was half a cm longer than the 4.4 average of the CIRMF mandrills. Mean upper canine length for nine wild-shot females (Jouventin, *op. cit.*) averaged 1.3 cm (range = 1.2 to 1.5), somewhat longer than the average 1.0 cm in the CIRMF animals. Jouventin did not state how these lengths were measured. Figure III.20 shows the skull of a wild-shot adult male mandrill and in Figure III.21 the upper and lower jaws are illustrated. The large upper canines and the lower first premolars on which the canines are honed are clearly visible.

There were considerable differences in the length of both upper and lower

Table III.10. Canine tooth length (in cm) of male and female mandrills

Standard Deviation	Mean	Upper Right Lower Right	Upper Left Lower Left	Mean	Standard Deviation
Mean of Males 7 and 3					
0.25	4.5	UR	UL	4.3	0.25
0.15	2.5	LR	LL	2.6	0.10
Mean of all females					
0.14	1.0	UR	UL	1.0	0.15
0.12	0.9	LR	LL	0.9	0.12

Table III.11. Male canine tooth length as a percentage of female canine tooth length

Upper Right	450	430	Upper Left
Lower Right	278	289	Lower Left

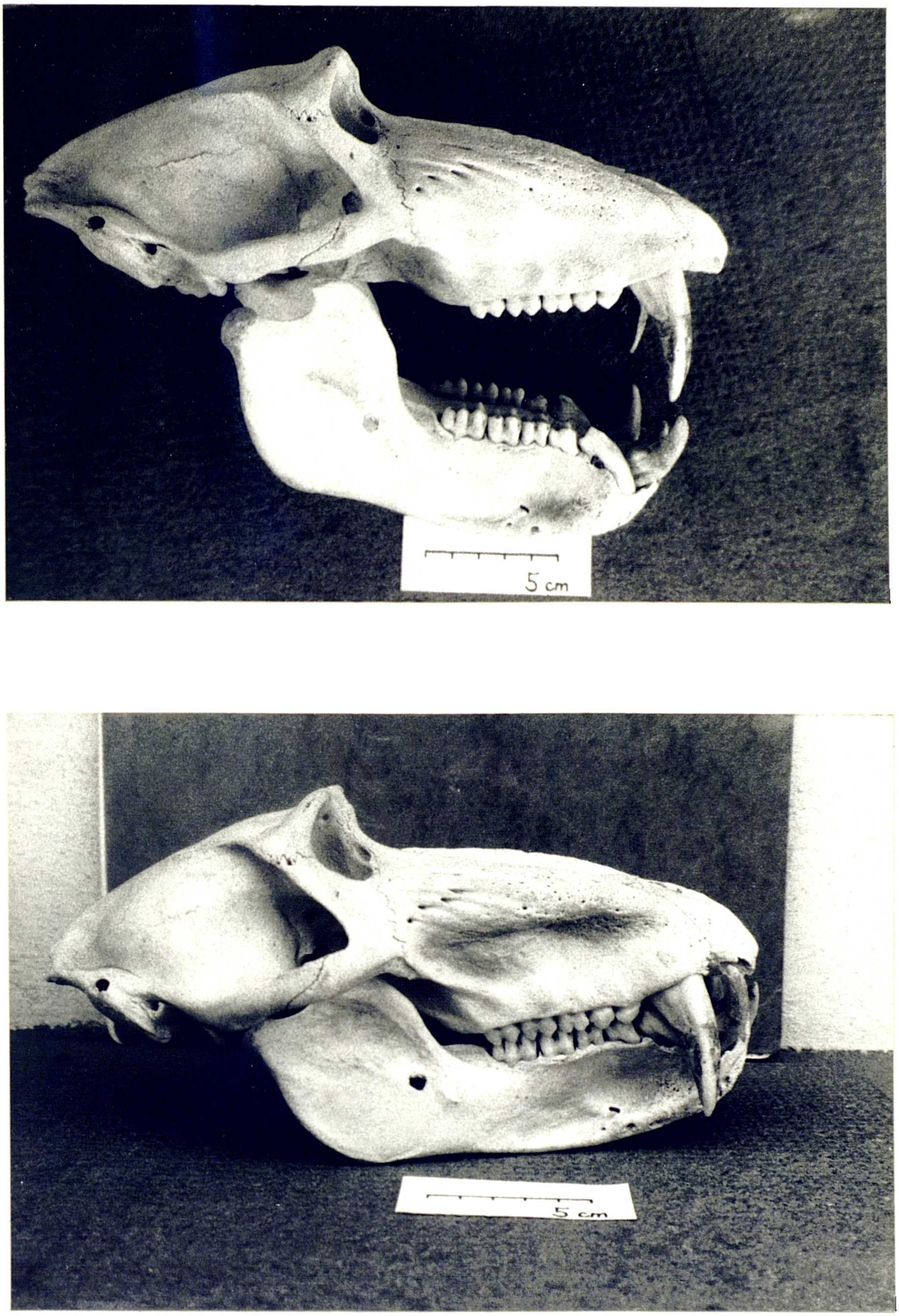


Figure III.20. Skull of wild-shot adult male mandrill

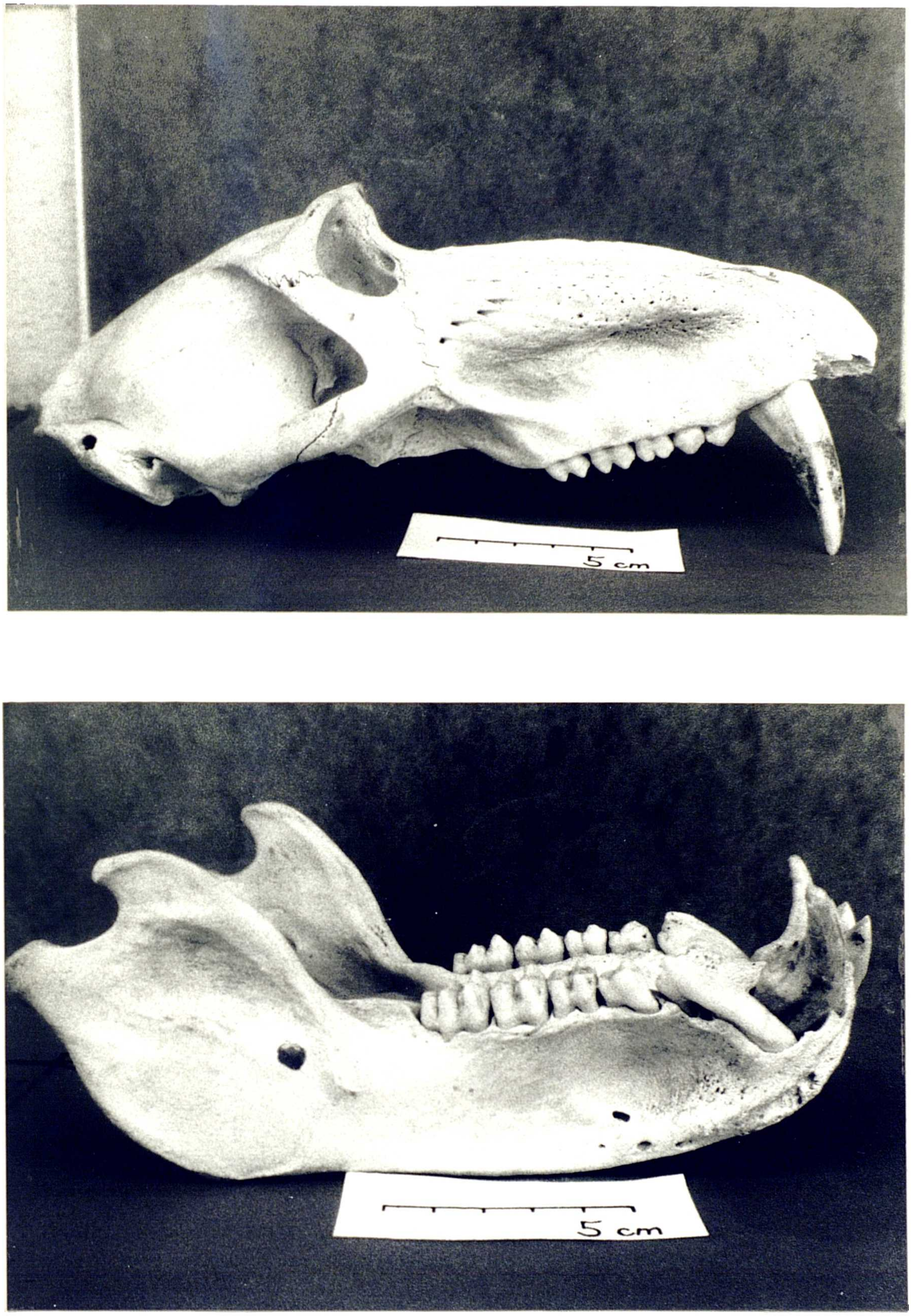


Figure III.21. Upper and lower jaws of wild-shot adult male mandrill; Note the large upper canines and lower first premolars canines between males and females. Mean male tooth length expressed as a percentage of mean female tooth length is given in Table III.11. Differences were much greater in upper canines than lower ones. On average female upper canines were only a fifth the size of males', and lower canines about a third. Female canines were about the same length as incisors of both adult males and females. Implications of tooth size for diet and ecology are discussed briefly in Chapter VII.

A comparison of the limited data on body weight from wild mandrills with those presented above for the CIRMF animals shows that the latter were heavier. Wild females (n = 3) were 85.6% the weight of the CIRMF females (n = 7), and wild males (n = 6) 80.1% of the semifree-ranging males (n = 7). If only the two fully adult CIRMF males are used, the ratio is 69.8%. The opposite trend was found for canine teeth, with male canine length in the two fully adult CIRMF males being 89.2% that of wild males (n = 4) and CIRMF females (n = 7) 76.9% that of wild females (n = 9). Increased body weight under conditions of good nutrition in captivity is a widespread phenomenon and is discussed below.

EFFECTS OF CAPTIVITY

The data collated from five years of mandrill records and two and a half of more detailed observations indicated considerable precocity in reproduction in the CIRMF mandrills in comparison to wild savanna baboons. The mandrill data (with the exception of seasonality which has not been reported in captivity) are consistent with those reported from laboratory and zoo mandrills (Hadidian and Bernstein, 1979; Carman, 1979). There are no comparable data from wild populations. This consensus may reflect either the influence of enhanced food intake in captivity or a characteristic of mandrills *per se*. The effects of enhanced food intake are discussed below. Relatively precocious reproduction in relation to other baboons as a characteristic of mandrills is discussed in Chapter VII.

Effects of enhanced food intake

It is clear from published work on captive and free-ranging but provisioned groups of monkeys, that availability of food affects reproductive output. In general enhanced food intake and an increase in quality and quantity of diet has the effect of increasing rates of reproduction (e.g., Mori, 1979; Sugiyama and Ohsawa, 1982; Lee, 1987). This acceleration in reproductive rate is correlated with and is commonly attributed to the increase in body weight which results from a better diet. The reported effects of enhanced food intake on reproductive parameters are summarised in Table III.12. It seems likely that the early onset and relatively high rate of reproduction in the CIRMF mandrills may be related to the superior quality and quantity of diet which they received, and their relative freedom from parasites.

The ecology and behaviour of primates with enhanced food intake have been thoroughly described in a recent volume (Fa and Southwick, 1988). In particular, the effects of supplementary feeding on maturation and fertility in primate groups has recently been reviewed by Loy (1988). Although a broad trend for increased reproductive output with enhanced food intake exists, few firm conclusions can be drawn due to lack of adequate data (Loy, *op. cit.*). Loy concludes (p.163) 'provisioning effects can be documented presently for only one measure of fertility, birth rate' and only in the Japanese macaque. He also points out that ' . . variation between species, even congeners, can equal or exceed the apparent effects of provisioning' (1988, p.163). A second example of this is the observation that not all primates reproduce so precociously in captivity, e.g., gorillas do and chimpanzees do not, although both probably reproduce earlier than in nature (R.W. Cooper, pers. comm.). An alternative explanation for precocious breeding in mandrills is presented in Chapter VII.

Table III.12. Effects of increased food-intake on reproductive parameters*

Parameter	Change	Species	Source
Birth rate	increase	*M. fuscata*	Mori, 1979; Sugiyama and Ohsawa, 1982
	increase	*M. mulatta*	Loy, 1988
Infant mortality	decrease	*M. fuscata*	Mori, 1979
Age at menarche	decrease	*C. aethiops*	Lee, 1987
		P. cynocephalus	Altmann, 1986; Altmann and Alberts, 1987; Altmann *et al.*, 1988
Age at first birth	decrease	*P. anubis*	Strum and Western, 1982
Inter-birth interval	decrease	*C. aethiops*	Lee, 1987
		P. anubis	Strum and Western, 1982

* Adapted from Feistner, in press

PATHOLOGY

Table III.13 lists the parasites recorded in faecal samples from the CIRMF mandrills. All parasites were found at initial screening of the wild-born mandrills upon their receipt at CIRMF, with the exception of *Giardia, Necator-* and *Strongyloides*-type parasites which were found in later screenings, including those of faecal samples which I collected periodically during my study. Mandrills harbouring parasites that were potentially pathogenic were treated although none of the animals showed any symptoms of illness.

Protozoans: Wild primates are commonly host to a number of protozoans, some of which have been associated with pathology in captivity. Parasitic protozoa from all four phyla (Sarcodina, Mastigophora, Ciliophora, and Sporozoa) were recorded from the CIRMF mandrills. With the exception of a malarial parasite, all were parasites of the digestive tract whose presence was diagnosed from faecal examination. The majority were harmless commensals (Table III.13). *Balantidium coli* (a bowel parasite found in pigs) is an important ciliate parasite of captive primates (Fiennes, 1967) and has previously been recorded from a mandrill (Joyeux, 1911, cited in Brumpt, 1949). All the CIRMF mandrills were screened at least annually for the presence of blood parasites. One individual (male No. 9) frequently tested positive for *Plasmodium* sp. but was asymptomatic.

Flatworms: Platyhelminth parasires were found very rarely in the CIRMF mandrills, although trematode ova were recorded. The drill is a natural host of the African lung fluke (*Paragonimus africanus*) in Cameroon (Sachs and Voelker, 1975). Captive mandrills can act as hosts for cestodes such as *Cysticercus tenuicollis* (Stiles and Hassal, 1929, cited in Fiennes, 1967), and hydatid disease due to *Echinococcus* has been reported in captive mandrills and drills (Boever and Britt, 1975).

Aschelminthes: The *Ancylostoma-*, *Necator-*, and *Trichostrongylus*-type nematode ova reported in the CIRMF mandrills were more probably from *Oesophagostomum* and/or *Trichostrongylus* (R.W. Cooper, pers. comm.). This

Table III.13. Protozoans and Helminth Ova recorded in faecal samples of the CIRMF mandrills

Protozoa	
Balantidium coli, Ciliophora*	trophozoites
Chilomastix mesnili, Mastigophora	cysts, trophozoites
Endolimax nana, Sarcodina	cysts
Entamoeba coli, Sarcodina	cysts, trophozoites
Entamoeba hartmanni, Sarcodina	cysts, trophozoites
Entamoeba histolytica, Sarcodina*	cysts, trophozoites
Giardia lamblia, Mastigophora*	cysts
Pseudolimax bütschlii, Sarcodina	cysts
Trichomonas sp., Mastigophora	trophozoites
Platyhelminthes	
Dicrocoelium-type, Trematoda	ova
Aschelminthes	
Ancylostoma-type, Nematoda, Strongyloidea*	ova
Necator-type, Nematoda, Strongyloidea*	ova
Strongyloides sp., Nematoda, Strongyloidea*	larvae
Trichostrongylus-type, Nematoda, Strongyloidea*	ova
Trichuris, Nematoda, Trichuroidea*	ova

* potentially pathogenic

opinion is supported by the following: the main type of Strongyloidea worms affecting non-human primates are *Oesophagostomum* spp. (Fiennes, 1967); *Oesophagostomum* eggs are reportedly indistinguishable from those of human hookworms (Fiennes, *op. cit.*), and screening was done by technicians who routinely screen human faecal samples in which *Ancylostoma* and *Necator* are common. None of the CIRMF mandrills was positive for microfilaria. *Loa loa* is endemic in the human population of Gabon (Languillat *et al.*, 1978) and Duke (1957) has suggested that mandrills can act as reservoirs for *Loa* in Cameroon. However subsequent evidence from studies in Cameroon suggested that this was unlikely. Although 30% of the human population have microfilaria of *Loa loa* and 96% of wild drills examined were infected with *Loa* sp., the *Chrysops* vectors for each host were different, with different biting habits, and the microfilaria had different periodicity (Duke, 1972). The exchange of parasitic material between human and simian host-vector complexes thus appears to be minimal. *O. bifurcum* has been reported from the large intestine of the mandrill and drill (Graber and Gevrey, 1981) and from savanna baboons (Pettifer, 1984). *Trichuris trichuria* has been reported from the caecum and large intestine of the mandrill (Graber and Gevrey, *op. cit.*).

Arthropods: Unidentified mite eggs (Class Arachnida) were found in two faecal samples but these may have been picked up from the soil. There was no evidence of infection, such as the presence of parasites in the fur, or skin lesions. Fox (1926, cited in Fiennes, 1967) described scabies in a drill.

There have not been any fungal infections in the CIRMF mandrills but the following fatal cases have been reported in zoo mandrills: systemic phycomycosis (Lucke and Linton, 1965), mucormycosis (Lucke and Migaki, 1979), and disseminated entomophthoromycosis (Migaki *et al.*, 1982).

CHAPTER IV. MANDRILL BEHAVIOUR

In this chapter the behaviour of the CIRMF mandrills is described. Behaviour quantified during focal samples is tested for sex differences in behaviour. In addition, the behaviour of the alpha male and alpha female are examined in relation to same-sexed individuals of lower rank. The socioecology of mandrills, synthesised from the few published studies of wild mandrills, is described.

The behaviour of the CIRMF mandrills is described below and is broadly divided into two categories: behaviour which was performed by a solitary individual, and that which occurred in a social context. These data were based on observations of the whole group, i.e., of all age-sex classes. Communication is divided into the visual, acoustic, and olfactory modalities. In some cases behaviour such as solitary play has been included under the broad term play described in the social section to enhance clarity. Tables IV.1 and IV.2 give summary definitions of behaviour scored during systematic data collection. Table IV.3 presents a summary of mandrill vocalisations.

NON-SOCIAL BEHAVIOUR

This was divided into the broad categories stationary, movement, and foraging. Table IV.1 gives a summary of these and other 'maintenance' behaviour which were observed when watching a solitary individual.

Stationary: When the mandrills were stationary and relaxed, their eyes closed or half-closed, they were described as **resting**. The mandrills rested both on the ground and in the trees. When terrestrial, resting was nearly always in a sitting position, sometimes with the back propped against a tree trunk. The mandrills were rarely observed to lie down and did not 'plop themselves down on their back' as savanna baboons frequently do (Smuts, 1985). Perhaps the damp forest floor was

Table IV.1. A summary of categories of non-social behaviour

Activity	
REST:	stationary and relaxed (non-alert)
STILL:	stationary and alert
TRAVEL:	quadrupedal movement over more than one body length at less than one metre height
CLIMB:	quadrupedal movement over more than one body length at greater than a metre height
Alimentary	
FORAGE:	searching for and processing food
REGURGITATE:	bringing up into the mouth of swallowed food
DRINK:	intake of water by sucking
DEFAECATE:	voiding of faeces
URINATE:	voiding of urine
TRUE YAWN:	mouth is opened, the lips cover most of the teeth
SELF GROOM:	picking through the fur with the fingers, occasionally tongue, lips or teeth
SCRATCH:	rapidly and repeatedly raking the skin with a hand or foot
SCENT-MARK:	a behaviour sequence involving sniffing and sternal rubbing, and which may include lipping and chinning
PLAY:	a wide variety of behaviour particularly exploration
MASTURBATE:	manual manipulation of the genitals

uncomfortable to lie on. Mandrills also rested in the trees, both during the day and overnight. They tended to rest at lower levels, 3 to 10 m, during the day than they did at night when they sometimes climbed to 20 to 25 m. At night adult females sat in forks of branches and slept with their most recent infant ventral and older offspring cuddled at their back. Older juvenile sibs sometimes slept or rested in each other's arms. Subadult and adult males slept in various splayed attitudes, sometimes lying horizontally along a branch. Mandrills were described as being **still** when they remained stationary (either arboreal or terrestrial) but were alert, monitoring what was going on around them.

Movement: Subadult and adult males, and adult females, especially those carrying ventral infants, usually travelled on the ground. **Travel** was scored when a movement of greater than one body length occurred at a height of less than one metre. Slow travel often alternated with foraging and was accompanied by contact grunts. **Rapid travel** was terrestrial, apparently purposeful, and silent and occurred in single file along well-worn mandrill paths. Considerable distances, 150 to 200 m, were covered, e.g., the mandrills travelled right across the enclosure. Rapid travel was not preceded by any particular vocalisations (i.e., there did not seem to be rallying cues), the mandrills just suddenly left the area. Wild mandrills and drills also have been observed to travel silently in this way (Jouventin, 1975a; Gartlan, 1970).

Climbing was defined as movement over more than one body length at a height of more than one metre. The mandrills were adept but not graceful climbers. Smooth straight trunks were ascended using a joint pushing movement of the hind legs. Smaller saplings were climbed quadrupedally. In large trees the mandrills walked along the top of branches. Descent was sometimes head-first, sometimes feet-first, depending on the individual and the type of tree it was leaving. Juveniles and older infants frequently climbed (interspersed with play) in the trees and several individuals followed each other over the same arboreal route, both when moving from place to place and also in 'follow-my-leader' play. Youngsters often dangled from a hand or foot and 'ran' along the underside of vines. Locomotion, whether arboreal or terrestrial, was digitigrade (Napier and Napier, 1967). In the genus *Mandrillus* the phalanges of the hand and foot are longer and more slender than in *Papio* and *Theropithecus*. In addition, in mandrills and drills (in contrast to other Papioninae) the foot is organized about an axis which runs between the first and second digits and it possesses a hallux which is particularly long, stout, abductable, and powerfully muscled. These features suggest adaptation for climbing or branch-walking (Hill, 1970; Jolly, 1970).

Foraging: When the mandrills were actively engaged in searching for food and processing it they were described as **foraging**. They were extremely dextrous and exploratory foragers, turning over the leaf litter, splitting open stems, dead branches, and rotting logs, and turning over stones in the streams while sifting through submerged debris. Examples of foraging are given below.

> 30 April 1986
> 1553: Female No. 6 unrolls a dead leaf and eats the ants and ant-eggs inside.
>
> 11 September 1986
> 1041: Female 12 uses her teeth to break open a branch of dead wood and gets a large grub out of a hole in the wood.
>
> 16 October 1986
> 0909: Male No. 14 pulls up a purple orchid and eats the base. He digs for the bulb but does not find it. He then eats the flower and stem.

The long, strong hands of mandrills and drills (Hill, 1970; Jolly, 1970) have well differentiated precision and power grips and a high opposability index (Napier and Napier, 1967). This suggests adaptation of the hands for branch-walking, as well as for good manipulatory and extractive foraging ability. When the mandrills were foraging on the ground **digging** was a frequent behaviour. Roots and corms were excavated with the hands and then pulled out, gripped in the incisor teeth. Roots were scraped clean using the incisors before the pith was eaten. On occasion holes up to 30 cm deep were dug.

> 27 March 1986
> 0850: Female No. 17 digs in a hole. Female 6 displaces her and digs there too, but is displaced in her turn by Male No. 13 who digs, reaching into the hole up to his elbows.

Mandrills stored food in their cheek pouches, particularly when at the feeding site where relatively large amounts of food could rapidly be acquired. Food was retrieved from the cheek pouches by pushing the food into the mouth using the back of the hand.

The mandrills also **regurgitated** their food. The occurrence of regurgitation could be recognised by sound alone. The 'retching' noises were accompanied by heaving of the shoulders. The food was never voided but was masticated (**rapid chew**) by the molars and then reswallowed. Regurgitation was seen in all the founder mandrills except Male No. 3, and in youngsters ranging from 16 to 44 months of age. The function of regurgitation is unclear and this behaviour has not before been reported in mandrills. Mandrills were observed **drinking** from streams and hollows in trees. They sucked water up with their lips and did not lap like a dog.

SOCIAL BEHAVIOUR

Social behaviour was broadly divided into affiliative and agonistic (aggressive and submissive) behaviour.

Affiliative behaviour was divided into three broad categories, described below, all of which contained behaviour which involved positive physical contact between individuals.

Contact: Mandrills touched each other and affiliative contact occurred when individuals **embraced.** One animal, usually an adult female or adolescent female, put her arm round or across another. This behaviour was seen particularly towards younger, juvenile mandrills. Individuals also approached and touched muzzles, a **muzzle-kiss**. This behaviour also has been observed in captive mandrills (Emory, 1975a; Mellen *et al.*, 1981) and drills (Böer, 1987c; Cox unpubl.). It took place between adult females and juveniles, and between adult females. It was unclear whether this was a greeting display or a way of investigating what another individual has just been eating. Cox (unpubl.) has stated that in drills a muzzle-kiss was often followed by allogrooming.

Grooming: Various postures in which a particular part of the body was held stiffly infront of another individual were used to **solicit grooming**. These included presenting the rear, flank, shoulder, neck, or head. If this invitation was successful it was followed by **allogrooming** in which one individual began parting and picking through the fur of the other with the fingers, and occasionally tongue, lips, or teeth. The groomer lipsmacked while grooming. Mandrills also groomed themselves - **autogrooming** - and they also **scratched**, repeatedly raking the skin with a hand or foot.

Play: Particular behaviour used by juveniles and infants to **solicit play** from others who were not playing included going down on their elbows with the rump in the air (in the same manner in which a dog solicits play), bouncing quadrupedally infront of a potential play partner, or ostensibly attempting to steal something. Invitations to play and play itself were accompanied by a smile and the play face (see below). Similar play behaviour has been observed in captive *Mandrillus* (van Hooff, 1967; Emory, 1975a; Davis, 1976; Mellen *et al.*, 1981; Böer, 1987c). Infants and juveniles engaged frequently and vigorously in mutual **social play.** Gnaw wrestling, rough and tumble, follow-my-leader, chases, and stealing objects were among the types of play observed. The young mandrills also played in water, jumping into pools from heights, swinging over water on vines and then letting go to splash into a pool, and jumping on each other. They were good swimmers. Individuals were also seen in **solitary play** and

Table IV.2. Summary of categories of social behaviour

Affiliative behaviour

EMBRACE:	one individual puts its arms round/across another
MUZZLE-KISS:	two individuals touch muzzle to muzzle
SOLICIT GROOM:	various postures which are held in front of the individual being solicited
ALLO-GROOM:	picking through the fur of another individual using fingers, lips or tongue, accompanied by lip-smacking, and divided into give and receive allogroom
SOLICIT PLAY:	crouching with elbows bent, bouncing etc., accompanied by the smile or play face
SOCIAL PLAY:	gnaw wrestling, rough and tumble, chase etc.

Aggressive behaviour

STARE:	a fixed look at another individual
S+CREST-RAISE:	a stare with the sagittal crest raised
HEAD BOB:	a downward jerk of the head
HB+CREST-RAISE:	a downward jerk of the head with the crest raised
HEAD BOB+CALL:	a downward jerk of the head accompanied by a threat grunt
THREAT LUNGE:	a lunge forward of less than a body length, with elbows usually bent
THREAT RUSH:	a rush forward over 2 to 3 m towards another individual, no contact is made
GROUND SLAP:	a threat lunge without the forward motion in which the ground is slapped
CHASE:	an aggressive chase of another
BITE:	high intensity bite, skin is punctured
PUNISH BITE:	fur/skin is held between the teeth, the skin is not punctured

Submissive behaviour

PRESENT:	the hindquarters are oriented and held towards another individual
PRESENT + HAND:	a hand is placed on the animals perineum or rump as it presents
PRESENT CROUCH:	the animal crouches to present with its ventrum almost touching the substrate

Table IV.2. cont. Summary of categories of social behaviour

Sexual behaviour	
SEXUAL PRESENT:	female stands with her sexual swelling oriented towards the male
MOUNT:	male places his hands on the female's hips and makes genito-genital contact in a dorso-ventral position
INTROMISSION:	male's erect penis enters the female's vulva/vagina
EJACULATION:	emission of semen, signalled by cessation of thrusting and body tremor
Displays and facial expressions	
TREE-BOUNCE:	a display in which a bough is bounced on
BRANCH-SHAKE:	a display in which the animal stands bipedally and shakes the trunk of a sapling, or the branch of a tree
DISPLAY YAWN:	mouth is opened wide, head is tilted back, and lips are retracted to expose the teeth
SMILE:	the lips are closed over the incisors and retracted over the canines resulting in a figure of eight
SMILE + SHAKE:	the head is shaken in a lateral plane while smiling
PLAY FACE:	relaxed open mouth face with the teeth exposed
DUCK FACE/POUT:	the upper lip is flared, mouth is closed
LIPSMACKING:	the lips are rapidly smacked together

this frequently involved object exploration and repeated climbing and jumping off the same vine, repeatedly 'attacking' a leaf, and frolic (Emory, 1975a), which was rapid energy expenditure characterised by exuberant racing around, climbing and sliding etc..

Agonistic behaviour is divided into aggressive and submissive components. For both aggression and submission the behaviour is presented in order of increasing intensity. In addition, displacement is included here, although it frequently did not involve overt aggressive or submissive acts.

An indicator of dominance which did not involve a particular threatening gesture was a simple **displacement**. One individual avoided or skirted round another or a mandrill simply left at the approach of another. Displacements were among the behaviour quantified and used to assess relative dominance rank (see Chapter V). Subordinate individuals were displaced from resources such as foraging areas, digging spots, or grooming partners. Examples are given below:

> 14 April 1986
> 1618: Female 17 is foraging - digging in some soft earth and leaf litter. Female 12 approaches, displacing No. 17 and takes over her digging spot. Then Female 6 walks over to Female 12 and displaces her in turn. Female 6 continues digging in the same place and unearths a root which she then eats
>
> 20 May 1986
> 0921: Female 16 is sitting, relaxed on a brach in the sunshine. Female 17 approaches her, displaces her and sits in exactly the same place.
>
> 1434: Female 12 is grooming Female 2. Female 5 approaches, presents to No. 2 and displaces Female 12. Then Female 5 starts grooming Female 2.

Aggression: The least intense threat was a **stare** in which one individual looked fixedly at another. Sometimes the sagittal crest was erected (**stare+crest-raise**). A downward jerk of the head, a **head bob**, with a fixed look, was the most common threat behaviour. Sometimes the sagittal crest was raised too (**head bob+crest-raise**). A more intense threat than a head bob+crest-raise was the **head bob+call**, in which the downward jerk of the head was accompanied by a threat grunt. In a **threat lunge** the aggressing individual lunged forward less than a body length, its arms were usually bent, so that the front half of the body was lower than the rear. Mandrills also did a **ground slap**, which could be described as a threat lunge without the forward motion in which the ground was slapped. This behaviour could be followed by a **threat rush** in which the threatened animal was rushed towards over a short distance of about two to three metres, although no contact was made. This behaviour corresponded to the 'charge' described in Emory (1975a) and Mellen *et al.* (1981). Frequently the threatened animal did not retreat. An aggressive **chase** occurred when the threatened animal avoided and the other mandrill pursued it. A chase occured over a greater distance than a threat rush. Usually no contact was made but if it was, a **bite** resulted, in which the skin was punctured and the bitten animal reacted by screaming (see vocalisation section below), and often also by defaecating.

> 26 August 1986
> 0852: Adolescent female 5A bites adolescent female 10A. 10A crouches screaming.

This high intensity bite could be distinguished from a **punish bite** in which the fur/skin was held between the teeth but the skin was not broken. Punish bites were usually directed at the small of the back and the 'punished' mandrill frequently remained silent.

Submission: In a **present** one individual swivelled its hips towards another individual and held the posture, with its tail flattened against its back. The presenting mandrill frequently turned its head to look at the animal to whom it was presenting. [It was difficult to differentiate presenting as a sign of submission from presenting as an invitation for copulation. As generally all females were subordinate to subadult and adult males (but see Chapter V) a submissive signal may be a component of all presents. Degree of intensity could be inferred from tail carriage; the more fearful and submissive the closer the tail lay against the back. Solicitations for grooming in which the rear was presented could be distinguished from submissive presents by the confidence characteristic of the former.] Generally presenting indicated submission towards a more dominant individual. In a more intense present the individual placed a hand on its perineum as it presented. This submissive **present+hand** was observed mainly in youngsters and also in the most subordinate subadult male No. 18. A **present crouch** in which an animal bent its arms or crouched with its ventrum pressed to the substrate indicated extreme submission and fear, and was frequently used by infants and juveniles when presenting to subadult and adult males. Sometimes a present by a youngster was accompanied by smiling (see below).

SEXUAL BEHAVIOUR

As described in Chapter III, sexual behaviour was almost entirely confined to periods of maximum sexual swelling, which lasted about 14 days in the year during the months July to October, for any one female. As well as heterosexual mounting in a sexual context of oestrous females by subadult and adult males (described below), juveniles and infants also were observed to mount oestrous females. Mounting in an apparently non-sexual context occurred between juveniles (in whom it may have a function connected to dominance), and very rarely between subadult males. An adult female (No. 5) occasionally attempted to mount other oestrous females.

Females sometimes initiated sexual behaviour by a **sexual present**. The female faced away from the male and stood with all limbs extended. Sometimes she flexed her hindlimbs or backed up towards the male. Occasionally the female looked fixedly into the male's eyes before swivelling her hips and adopting a presentation posture. This was equivalent to 'eye-contact proceptivity' as described for *Papio ursinus* by Bielert (1986). In sexual presents initiated by females the tail was carried in a relatively upright plane (see above). Female-initiated copulations were rare (n = 12, 11% of intromitted mounts where the initiator was clearly identifiable) and only were observed in four of the seven females (Nos. 2, 6, 10, and 12). Examples from field notes are given below.

> 13th September 1986
> 0938: Female 2 is travelling slowly through the undergrowth, Male 7 is following her in a relaxed manner. She stops and then approaches 7 to less than a metre, looks directly at him, turns, presents to him, and moves on. 7 immediately follows smiling, head-shaking, and lip-smacking,
> 0940: She moves away fast and then stops and stands so that 7 mounts her, intromits, and thrusts to ejaculation.
>
> 9th October 1986
> 1722: Female 2 climbs, Male 7 follows, he is relaxed
> 1726: Another mandrill screams and 2 climbs to investigate, 7 moves after her
> 1727: 2 climbs slowly onto a sturdy bough, she stands and then presents, looking back at 7. He then approaches smiling and head-shaking and mounts, intromits, and thrusts to ejaculation.

Of the 113 intromitted mounts where the initiator of the interaction was clearly identifiable, 89.4% were initiated by the male. Females also presented to males in response to their precopulatory behaviour, which involved persistent following and the smile and head-shake displays, and sometimes lipsmacking (see below). The male usually developed an erection during this period. Frequently the female moved away as the male approached, but often this did not appear to be clear avoidance behaviour as she moved only a short distance or led him round and round a bush before stopping and letting him mount. An example of this 'teasing' behaviour is given below.

> 30th September 1986
> 0839: Male 7 follows Female 5A smiling and shaking and lipsmacking. She moves away and he follows. She goes behind a bush and then trots round and round it. He follows her.
> 0841: 5A climbs into an old vine tangle 1.5 m above the ground, and 7 starts to follow. She descends and resumes circling the bush. 7 is always 1 to 2 m behind her.
> 0844: She finally stands still, so he catches up with her, mounts, intromits, and thrusts to ejaculation.

This behaviour was typical of an adolescent female experiencing her first oestrus. My interpretation was that she was ambivalent about the approach and close proximity of the alpha male, fearful of his status yet attracted to him also.

In a **mount** the male placed his hands just anterior to the female's pelvis. In subadult and adult males the feet remained on the ground, but juveniles clasped the female's calves in the 'double foot clasp' mount of macaques, baboons, and many other species, to lever themselves high enough to reach her perineum. **Intromission** was followed by pelvic **thrusting** and defined as **copulation**. Repeated thrusts in a single mount culminated in **ejaculation** which was characterised by cessation of thrusting and the occurrence of body tremor (defined as an ejaculatory pause). Ejaculate could be seen immediately the male dismounted and it coagulated rapidly on the female's perineum. The appearance of fresh semen was used to define ejaculation. Although the female occasionally looked back at the male during copulation, neither sex showed distinctive changes in facial expression or vocalised during copulation (cf. copulation call of *Papio anubis* (Smuts, 1985) and *P. ursinus* (Hamilton and Arrowood, 1978)) and there was no indication of female orgasm. The female ran a few metres from the male immediately he dismounted (as also was observed in zoo mandrills by Mellen *et al.*, 1981). Females avoided copulation attempts by running away or by climbing. If mounted by a juvenile they simply sat down and the juvenile slid off, or they turned and threatened him. Females also interrupted copulation by moving out from under the male.

All age classes of males were observed to **masturbate**. Juvenile males tended to hold their penis in one hand and then make pelvic thrusting movements. Subadult and adult males masturbated by holding the penis and making single-handed back and forward movements. They rarely masturbated to ejaculation but if they did the emission was eaten. Masturbation by females was extremely rare, however one female occasionally rubbed her clitoris on a stick.

COMMUNICATION

Mandrills have rich communicative repertoires and the visual, acoustic, and olfactory modalities are each described in turn below.

Visual communication

Mandrills communicated visually by their appearance, posture, and facial expression. Male mandrills, with their red and blue muzzles, yellow beard, colourful rump, and white sparsely-haired region behind the ears, are among the most colourful of monkeys (see Frontispiece) and the function of their colouration and its possible significance are discussed in Chapter VII.

Postural displays: Mandrills, particularly subadult and adult males, communicated visually by postural displays such as **tree-bounce** in which the mandrill stiff-leggedly bounced on a horizontal branch. In another display, **branch-shaking,** the bough was grasped and shaken vigorously. When a male was on the ground this latter display involved becoming bipedal and shaking the trunk of a sapling. Both these displays occurred in situations of high arousal such as during male-male chases, or in response to low-flying aircraft and were often followed by roaring (described below). Both these displays have been seen in captive mandrills (Mellen *et al.*, 1981) who used the chain link fence as a substrate.

Facial expressions: **Display/tension yawns** were seen exclusively in subadult and adult male mandrills. Display yawns were of longer duration (about 6 secs) than 'true' yawns (see below), the head was always raised, the lips were retracted to expose the teeth, and the face was turned away from the recipient who saw the mouth and canines in profile. Display yawns usually occurred when the male was seated and this was also reported by Baenniger (1987) who never observed a mandrill standing while yawning. Display yawns do not have a clear threat function (contrary to suggestions by Hill, 1970 and Fiedler, 1972) since zoo mandrills did not combine yawning with other threat gestures, nor did they yawn while staring at a potential opponent (Mellen *et al.*, 1981). Display yawns also were indicative of tension. Occasionally they were given in response to direct scrutiny by the observer, for example during a focal sample. Adjustment in observer behaviour, such as avoiding prolonged gaze, or turning away from the mandrill tended to reduce the response. Further details of the display yawn in relation to interactions between males are given in Chapter V. **True yawns** were seen in all age- and sex-classes. They were of short duration (about 3 to 4 secs) (Baenniger, 1987), no special head posture was evident, and the lips were not retracted so the teeth remained largely covered. They were seen in the early morning and evening and in rest periods during the day.

Although not strictly a facial expression, pilo-erection of the sagittal crest (**crest-raise**) indicated arousal. It was seen accompanying aggressive behaviour such as a stare or head-bob as well as submissive behaviour. It also accompanied affiliative behaviour such as the smile (see below).

The grin face or **smile** is a facial expression unique to the genus *Mandrillus* (van Hooff, 1967; Bernstein, 1970). The lips are retracted over the canines but closed over the incisors so that a figure of eight (∞) shape results. It was seen in animals of all age-sex classes. In mandrills it has been described both as an aggressive display (Andrew, 1963; Jouventin, 1975b, 1987; Spassov, 1979) and as an affiliative or distance-reducing display (van Hooff, 1967; Hill, 1970; Davis, 1976). The latter is a more accurate description, and in fact the smile functions as a reassurance gesture. This interpretation is supported by the following: (1) the behaviour develops early, at about three weeks of age, whereas threat behaviour is not seen until about 20 weeks and friendly rather than threatening behaviour is to be expected from a very young infant (Mellen *et al.*, 1981, p.217); (2) smiling often precedes and accompanies play behaviour (van Hooff, 1967; Mellen *et al.*, op. cit.; Davis, 1976). About 40% of play bouts (n = 881) contained smiling displays, yet threat displays such as head bobs and threat grunts never occurred during play even during chasing and rough and tumble interactions (Feistner and Dixson, in prep.); (3) study of a captive group indicated that infants threatened at a low rate and adult males at a high rate yet both smiled at about the same rate (Mellen *et al.*, 1981); and (4) the smile sometimes functions as an appeasement gesture in response to threat, although most threats did not provoke a smile. Affiliative behaviour - approach, sitting together, grooming - rather than agonistic behaviour was the most common sequel to the smile display, occurring in about 97% of cases (Feistner and Dixson, in prep.), and van Hooff (1967) reported that the smile was never followed by attack. Smiling was sometimes accompanied by lateral movements of the head - **smile and shake.** This display was accompanied by pilo-erection of the sagittal crest and was a more intense form of smile. The horizontal movements contrast strongly with the vertical head bobs given during threat, and this difference supports the evidence cited above for the friendly motivation of the smile display. Although the smile was given in a 'submissive' context, e.g., it sometimes accompanied presents by juveniles and infants, it was not used on its own as an indicator of relative status. In dyadic interactions which involved smiling, both the dominant and subordinate individual were observed to initiate by smiling. For example, in a situation where a young juvenile is near the alpha male at the feeding site - (a) sometimes the alpha male initiated by smiling at the youngster, who responded by presenting. This could be interpreted as the male 'reassuring' the juvenile; (b) sometimes the youngster initiated by smilng with head-shaking and crest-raise at the alpha male. This could be interpreted as the juvenile 'placating' the male. Both examples emphasise the friendly distance-reducing function of this facial expression.

The **play face** was a frequent expression in young mandrills and was basically a 'relaxed open mouth' face (van Hooff, 1967). However in mandrills the lips were retracted exposing the teeth. This expression was described as a laugh and illustrated by Davis (1976, p.5). It accompanied most types of play, particularly gnaw-wrestling (as was also observed by van Hooff, 1967; Davis, 1976; and Mellen *et al.*, 1981).

The facial expression **duck face/pout,** in which the upper lip was protruded and flared (illustrated in Davis, 1976, p.10), was indicative of a state of high anxiety. This behaviour was seen in juveniles and subordinate adult females in response to a stare or threat by another more dominant individual and was often followed by the animal turning round and presenting.

Lipsmacking behaviour is rare and infrequently observed in the genus *Mandrillus* in comparison to *Papio* baboons, except in relation to grooming (van Hooff, 1967; Bernstein, 1970) when the individual giving the grooming lipsmacks. Lipsmacking also formed part of pre-copulatory behaviour in the male mandrill (van Hooff, 1967; Mellen *et al.*, 1981; Feistner and Dixson, in prep.) and drill (Cox unpubl.).

Vocal Communication

Mandrills have a rich vocal repertoire which contains a number of calls unique to the genus as well as those whose analogues can be found in other baboon species. Kudo (1987) studied vocalisations of wild mandrills in Campo and identified 11 calls: three long-distance (audible over several hundred metres) and eight short-distance calls (audible over 10 to 30 metres). Kudo's study is further discussed in Chapter VII. Although some of the calls heard in the CIRMF mandrill group correspond to those recorded by Kudo, others have not before been reported. A list and description of calls is given in Table IV.3.

Table IV.3. Summary of mandrill vocalisations

Short distance calls	
CONTACT GRUNT:	soft low-pitched grunt audible only over a few metres
THREAT GRUNT:	short intense grunt given with a head bob
WARNING GRUNT:	a very low-pitched grunt
PLAY PANT:	staccato pant heard during social play
GEK:	repeated short sharp call given by infants and young juveniles
MOAN:	low continuous moaning sound
SQUEAK:	short high-pitched call
INCITE SCREAM:	similar to but more prolonged than a squeak
SCREAM:	high-pitched loud shrill call
ALARM BARK:	a short sharp two-syllable grunt, accent on 2nd syllable
YAK:	repeated middle-pitch yaks
PANT-GRUNT:	repeated calls similar to yaks but of lower pitch
Long-distance calls	
CROW:	trilled crowing call
TWO-PHASE GRUNT:	low-pitch breathy grunt of two syllables, only given by dominant male
ROAR:	continuous low-pitch call given exclusively by males
YELL:	similar to roar but higher-pitch, given mostly by adult females
TOOTH GRIND:	grinding of teeth

Contact grunt: This short-distance soft grunt was frequently emitted by the study mandrills, especially by adult females and older juveniles, and particularly while foraging. When one mandrill grunted other individuals within five to seven metres grunted in reply, resulting in a chorus of grunts. Grunts were also heard when there was a change of behaviour, for example when foraging ended and travel began, and on the approach of another individual. This contact grunt was conspicuous by its absence from Kudo's study. She stated that 'grunts ... do not function in group integration because they are given only in an aggressive context ... the mandrills have a low rate of vocal exchange and lacks a short distance contact call' (p.301). Kudo made several inferences about mandrill social organisation based on this 'lack' of a short-distance contact call, which are discussed further in Chapter VII. The 'absence' of this call in her study was probably due to the fact that (1) Kudo spent only a third of her observation time at less than 20 metres from mandrills and (2) that these grunts were barely audible over ten metres.

Threat Grunt: This was equivalent to the 'grunt' of Kudo. It was given in aggressive situations by all age-sex classes and was always combined with a head bob (see above) thus forming the threat head bob + call (HBC).

> 24 May 1986
> 1036: Female 5 head bob+call (HBC) Female 17 who leaves; 5 takes over her foraging site
>
> 27 May 1986
> 1505: Female 5 HBC then chases Female 6; 6 runs away then stops and presents
>
> 3 June1986
> 1137: Female 2 HBC Female 5; 5 presents

Warning grunt: This low-pitched grunt was given only by the alpha male in the context of mate-guarding a female in oestrus; neither the vocalisation nor behaviour have been reported before. The warning grunt was not accompanied by other threat behaviour such as a head bob, although it was effective as a threat in that other males distanced themselves from the female if the alpha male gave this type of grunt. The 'message' seemed to be 'I'm watching you, be careful'.

> 19 November 1986
> 1025: Female 10 who is in oestrus climbs a tree. Male 9 also ascends the same tree, climbing towards 10. Male 7 gives warning grunts and 9 continues climbing and passes 10.

Play pant: This pant was described by Mellen *et al.* (1981) as occurring during social play, particularly gnaw wrestling. It was also heard in the CIRMF mandrills, but it is unclear whether this is a specific vocalisation or simply 'fast rhythmic staccato breathing' associated with exertion (van Hooff, 1967, p.49).

Gek: This repeated short sharp call was given by infants and young juveniles when distressed e.g., when the mother moved away, or when rejected during weaning. The infant stood twitching with distress and was usually retrieved, or then ran rapidly and jerkily to its caretaker and clung tightly. In very young infants violent spasmodic movements of the limbs and body were seen when the infant lost contact with the nipple. These movements were not accompanied by the gek vocalisation.

> 5 December 1987
> 1140: 2 rejects 8-month old 2D, who geckers madly; 2C (2D's older sister) retrieves 2D.

Moan: This call (the 'girney' of Kudo) had a low moaning/grumbling sound and indicated unwillingness and mild distress, for example when given by an infant or juvenile following its departing mother i.e., the sound was often made while the animal was on the move, whereas the gek (above) was usually given while the infant was stationary.

Squeak: This short high-pitched call was given by youngsters in situations of sudden fright or mild fear, and was sometimes preliminary to a scream. It always instantly drew a mother's attention.

Incite scream: This call was similar to though slightly more prolonged than a squeak, and was used in triadic interactions. The incite scream was directed at an animal being 'threatened' and was accompanied by repeated eye contact between it and a third individual whose aid was being enlisted. The facial expression resembled the staring or frowning bared-teeth scream face (van Hooff, 1967). Sometimes no sound was emitted but the effect on the animal at whom the 'scream' was directed was the same.

Scream: This loud shrill vocalisation was given in situations of fear and escape, for example during attack. It was given by most age-sex classes except adult males. It corresponded to the squeal (Gartlan, 1970) and shriek, squeal, or screech (Struhsaker, 1969) of drills. It was often accompanied by defaecation.

Alarm bark: This was the 'oomph-a' warning (Tate, 1941), 'mbé-mbé' call (Jouventin, 1975a), and 'K-alarm' (Kudo, 1987) previously reported in mandrills, and the 'two-syllable alarm bark' reported in drills (Gartlan, 1970). It was given in response to some birds flying over, branch falls, and other situations in which I could not identify the stimulus. As the mandrill response varied there probably was more than one type of alarm call (as has been reported in vervet monkeys, *Cercopithecus aethiops*, (Seyfarth and Cheney, 1982), although I could not distinguish alarm calls. Sometimes mandrills descended in response to a call, and sometimes they climbed. A particularly common response was to leap onto a nearby sapling and cling to the trunk only a metre above the ground. This would be an effective way to avoid a ground hazard such as a snake, and snakes were present in the enclosure. Alarm barks by adults were always responded to, whereas those given by infants were sometimes ignored.

Yak: This call may correspond to the 'K-sound' of Kudo. It was given by all individuals except subadult and adult males, but especially by juveniles and was particularly associated with movement by the alpha male. When he entered a clearing where juveniles were playing or moved slowly down a path the juveniles emitted this call. It seemed as though they were constantly monitoring his movement. The intensity at which this call was given varied with context. Arrivals of other males and sometimes of the observer were also greeted in this fashion.

Pant-grunt: This call (perhaps the 'growl' of Kudo) was given by subadults and adults of both sexes (although usually not by the alpha male). It was similar to though of lower pitch than the yak more characteristic of juveniles. Arrivals were sometimes greeted by pant-grunts. This call probably corresponds to the panting grunts (Struhsaker, 1969) and pant-threats (Gartlan, 1970) reported in drills.

Crow: Reported in both wild mandrills (Sabater Pi, 1972; 'ka-ka-ka', Jouventin, 1975a; Kudo, 1987) and drills (Struhsaker, 1969; Gartlan, 1970) the function of this long-distance trilled call seems to be that of communicating between separated individuals, e.g., different subgroups or lost individuals, and thus facilitating group cohesion. Very intense emotive crow calls were given by adolescent females who had lost the corpse of their infant (see below). It was particularly noticeable that 5A gave calls when she was settling down for the night since she was the only animal vocalising at this time. It was the crow calls of 10A which enabled me to pinpoint the date of her late abortion (see Chapter III). Male 18 gave long crow calls, 'lost calls' on occasions when he was far behind the group.

20 March 1987
5A is carrying a rotting corpse

24 March 1987
She continues to carry the corpse, flies follow

25 March 1987
11.45: 5A is still carrying what is left of the corpse

14.58: 5A is no longer carrying the remains
15.06: 5A gives three very long and emotive crow calls
15.28: She gives a long crow call
16.56: "   "   "   "   "
17.15: The alpha male goes to sleeping site 1A and females including 5A follow
17.17: 5A gives a crow call
17.19: 5A gives a crow call
17.20: 5A gives two crow calls
17.24: 5A gives a crow call
17.26: 5A gives a crow call
17.28: 5A gives a crow call
17.32: 5A gives a crow call
17.34: 5A gives a crow call
17.35: 5A gives a crow call
17.40: 5A gives a crow call

8 February 1988
Female 10A gives emotive crow calls

Two-phase grunt: This call is characteristic of the genus *Mandrillus* although 'according to its acoustic structure it corresponds to the "wahoo" bark (Byrne, 1981)' of *Papio* baboons (Kudo, 1987, p.291). The two-phase grunt ('oomp-oomp', Tate, 1941; Sabater Pi, 1972; 'oum-oum', Jouventin, 1975a; Hoshino *et al.*, 1984; Kudo, 1987) is characteristic of mature 'leader' (Jouventin, 1975a) males in both mandrills and drills (Struhsaker, 1969; Gartlan, 1970). In the latter species this Type A call was associated with movement and was not given when the male was foraging, sitting, or resting. Its function was to initiate and promote movement of dispersed group members (Gartlan, 1970). This seems also to be true for wild mandrills in whom the call was heard regularly and frequently at the time of change of movement by the group and at the beginning and end of travel (Hoshino *et al.*, 1984). Its function seemed to be to maintain group cohesion during travel when the call was emitted continuously (Sabater Pi, 1972; Jouventin, 1975a) and it was not heard during periods of foraging

(Jouventin, 1975a). Surprisingly, given the prevalence in wild mandrills of the two-phase grunt, it was almost never given by the alpha male in the CIRMF group. Probably the enclosure was so familiar to them that the need for cohesion and long-distance movement in relatively unfamiliar areas was lacking. The mandrills had worn travel paths in the enclosure.

Roar: In the CIRMF mandrills the roar was a loud long-distance call given only by males. All subadult and adult males in the group emitted this call and were individually recognizeable to me by their voice alone. The difference was chiefly in pitch, and the alpha male had the deepest voice. The call was also given by older male juveniles, and was first heard in Male 2A at the age of 35 months before his voice had 'broken'. It was given in contexts of relatively high arousal, for example just at the beginning of a storm; following displays after a tractor or low-flying helicopter had gone by; or after a chase between males. If one male called, especially one of the subadult males such as No. 15, other males responded. Kudo also identified a roar which she stated was emitted only by adult males and during group movement, had a common origin with the two-phase grunt and was thus acoustically similar to the savanna baboon 'wahoo'. It is unclear if this was the same call as the roar of the present study, which more closely resembles the two-phase huffing grunt Type B identified by Gartlan (1970) which was emitted by adult, subadult, and possibly older juvenile male drills.

> 14 March 1986
> 0912: The mandrills are foraging in a grove of *Uapaca* trees near the edge of the enclosure. A noisy truck full of workmen goes by. Males 9, 15, and 14 climb rapidly. Male 14 roars, Male 3 roars and does a branch-shaking display. Male 7 is in the undergrowth, then climbs to 2 m, and roars (his voice is deeper than the others). Male 3 roars, then Male 7. In the same tree are Male 7 at 4 m height, Male 3 at 11 m, and Male 9 at 12 m. Male 3 roars again.

2 April 1986
1415: The sky is clouding over
1422: Thunder becomes louder and closer
1430: It gets darker and the wind rises. Rain starts suddenly and two males roar as it starts.

Yell: This call was given exclusively by adult females and only when chasing subadult or adult males. It resembled a male roar but was of much higher pitch. The chases were intense and the male and vocalising female in pursuit could be heard over relatively large distances (over 100 m).

5 December 1987
1035: Male 15 threatens (head-bobs) 12A1; 12A1 screams;
12A attacks 15 who runs away; 12A follows yelling

Tooth grind: This sound was heard only on the infrequent occasions when the alpha male was shut in the small enclosure at the feeding site. Jouventin (1975a) reported that angry adult males ground and snapped their teeth. Kudo reported it in all age- and sex-classes in situations of tension (which corresponds to Male 7's captive situation above) or non-tense scratching.

Olfactory communication

Another feature characteristic of the genus *Mandrillus* is the possession of a sternal scent gland. **Scent-marking** was seen in all age- and sex-classes, except very young infants. It comprised a sequence of behaviour as follows. A terrestrial mandrill approached a trunk and **sniffed** it, sometimes rearing up bipedally to do so. The lower lip was often rubbed against the bark (**lipping**). Then, clasping the trunk with both arms, the upper middle portion of the chest was rubbed vigorously from top to bottom against the substrate, i.e., in an upward and then downward motion, a few times. Before and/or after **sternal rubbing**, the chin may be rubbed against the bark

(chinning). Sometimes a damp stain was left on the bark.

Mandrill behaviour

The following section describes the results of the analyses of data from one-zero focal samples in Part 1 of the study (see Chapter II). Analyses of behaviour were done to answer the following questions:

(1) Do males and females differ in their behaviour?

(2) Is the alpha male different from other males?

(3) Is the alpha female different from other females?

(4) Does behaviour correlate with dominance rank within sex?

The behaviour of each founder individual (n = 14) was analysed as follows. For each behaviour the number of intervals in which the behaviour occurred was totalled for each focal sample. These totals were then summed over all focal samples and divided by the total number of samples to give a mean number of intervals in which the behaviour occurred per sample. This mean number of intervals was converted to a percentage by dividing by 30/100 (since there were 30 intervals per 15-minute sample). The following statistical tests were done using these mean percentage intervals, which are presented in Table IV.4. [The percentages of behaviour do not sum to 100% since more than one behaviour could occur in any 30-second sampling interval.]

Planned comparison t-tests were used to test for differences, in the mean percentage of intervals in which a behaviour occurred, between males and females. One-sample t-tests were used within sex to see if the alpha individual was different from the others in the mean percentage of intervals in which a particular behaviour occurred. Spearman rank order correlations were used to test whether the rank proportion of intervals in which a behaviour occurred correlated with dominance rank within each sex. Since the alpha individual was predicted to differ from others the

Table IV.4. Mean percentage intervals in which behaviour occurred

Identity	Rest	Still	Travel	Climb	Forage	PlayΔ	Groom*		Aggro©	Submit†	T
							Give	Receive			
Females											
No. 2	0.30	59.57	23.47	7.67	45.50	1.27	2.40	11.60	0.44	0.70	1410
No. 5	7.43	46.04	25.83	5.00	59.10	0.43	3.97	4.03	0.32	0.70	1440
No. 6	9.80	67.67	26.40	6.20	50.13	0.00	1.67	0.53	0.24	0.07	1500
No. 10	1.50	65.46	18.23	12.34	39.50	0.13	2.33	3.83	0.26	0.63	1410
No. 12	3.13	63.46	23.33	7.78	45.95	0.13	2.93	3.47	0.04	1.40	1530
No. 17	6.00	54.86	24.42	10.14	52.97	0.93	5.50	0.23	0.00	0.87	1380
No. 16	14.10	69.79	17.43	9.93	33.47	0.50	0.43	0.50	0.00	0.33	1440
Mean	6.04	60.98	22.73	8.44	46.66	0.48	2.75	3.45	0.19	0.67	10110
Males											
No. 7	8.57	87.30	13.05	1.49	17.94	0.00	0.00	0.50	0.57	0.00	1410
No. 3	11.57	75.58	22.48	4.26	34.34	0.00	0.00	0.00	0.33	0.00	1290
No. 14	0.57	81.21	25.18	5.74	42.34	0.00	0.00	0.00	0.54	0.00	1410
No. 9	8.07	72.71	25.00	7.29	39.31	1.17	0.07	0.00	0.02	0.20	1440
No. 13	7.37	65.35	25.83	5.83	42.29	1.23	0.56	4.38	0.17	0.13	1440
No. 15	1.90	77.01	27.69	8.50	47.14	0.27	0.00	0.00	0.63	0.27	1470
No. 18	4.87	63.68	17.08	19.17	50.90	5.97	0.35	0.00	0.00	0.20	1440
Mean	6.13	74.69	22.33	7.47	39.18	1.44#	0.16#	0.81#	0.32#	0.13#	9900

Mandrills are listed in order of decreasing dominance rank

Δ Play was with all other individuals

* Grooming was restricted to grooming with other founders (offspring, juveniles and adolescents were excluded)

© Aggression was a composite of head-bob, head-bob and threat grunt, and threat rush (see text)

† Submit was defined as presenting

T total number of intervals

Male 3's data were excluded from calculation of the mean (see text)

Spearman correlations were done in two ways: (a) excluding the data of the alpha individual and (b) with this individual's data included. The results of the Spearman tests are shown in Tables IV.5 for males and Table IV.6 for females. In all figures mandrills are shown in order of decreasing dominance rank within sex.
Determination of dominance rank is described in Chapter V.

Rest

Overall the founder mandrills rested in 6% of intervals. The mean proportion of intervals spent resting by each individual is illustrated in Figure IV.1. There was no difference in the proportion of intervals spent resting by males (6.1%) and females (6.0%) ($t = 0.038$, $df = 12$, NS). Although the alpha male rested in a greater proportion of intervals (8.6%) than other males (5.7%) this difference was not significant ($t = 1.701$, $df = 5$, NS). However, the alpha female rested in significantly fewer intervals (0.3%) than all other females (7.0%) ($t = 3.577$, $df = 5$, $p < 0.02$). In neither sex was there a significant correlation between dominance rank and mean percentage of intervals in which resting occurred (see Tables IV.5 and IV.6).

Still

In contrast to resting, the behaviour *still*, i.e., being stationary and alert, was a common behaviour and occurred in 68% of intervals. There was no significant difference between males and females ($t = 1.190$, $df = 12$, NS), although males were *still* in more intervals (74.7%) than females (61.0%) and this is illustrated in Figure IV.2. The alpha male was significantly different from other males ($t = 5.130$, $df = 5$, $p < 0.01$) and was *still* in a greater proportion of intervals (87.3%) than other males (72.9%). Among males there was no significant correlation of dominance rank with mean percentage of intervals in which they were *still* (Table IV.5). The alpha female was not different from other females (59.6% vs. 61.2%) ($t = 0.439$, $df = 5$, NS) nor was there a significant correlation of *still* with dominance rank among females (see Table IV.6).

Table IV.5. Spearman Rank Order Correlations of rank mean percentage intervals of behaviour and dominance rank in male mandrills

Behaviour	Alpha male excluded [a]	Alpha male included [b]
Rest	0.37	0.57
Still	0.54	0.71
Travel	-0.14	-0.46
Climb	-0.94*	-0.96**
Forage	-0.87	-0.92*
Aggression$	0.30	0.37

a: n = 6, b: n = 7
$ Male No. 3 excluded, n = 5, n = 6
* $p < 0.05$, ** $p < 0.01$

Table IV.6. Spearman Rank Order Correlations of rank mean percentage intervals of behaviour with dominance rank in female mandrills

Behaviour	Alpha female excluded [a]	Alpha female included [b]
Rest	-0.14	-0.46
Still	-0.43	-0.43
Travel	0.71	0.54
Climb	-0.60	-0.64
Forage	0.60	0.32
Play	-0.56	0.03
Give grooming	0.20	0.14
Receive grooming	0.77	0.86*
Aggression	0.93*	0.95**
Submission	-0.14	-0.05

a: n = 6, b: n = 7
* $p < 0.05$, ** $p < 0.01$

Figure IV.1. Mean proportion of intervals in which the behaviour REST occurred

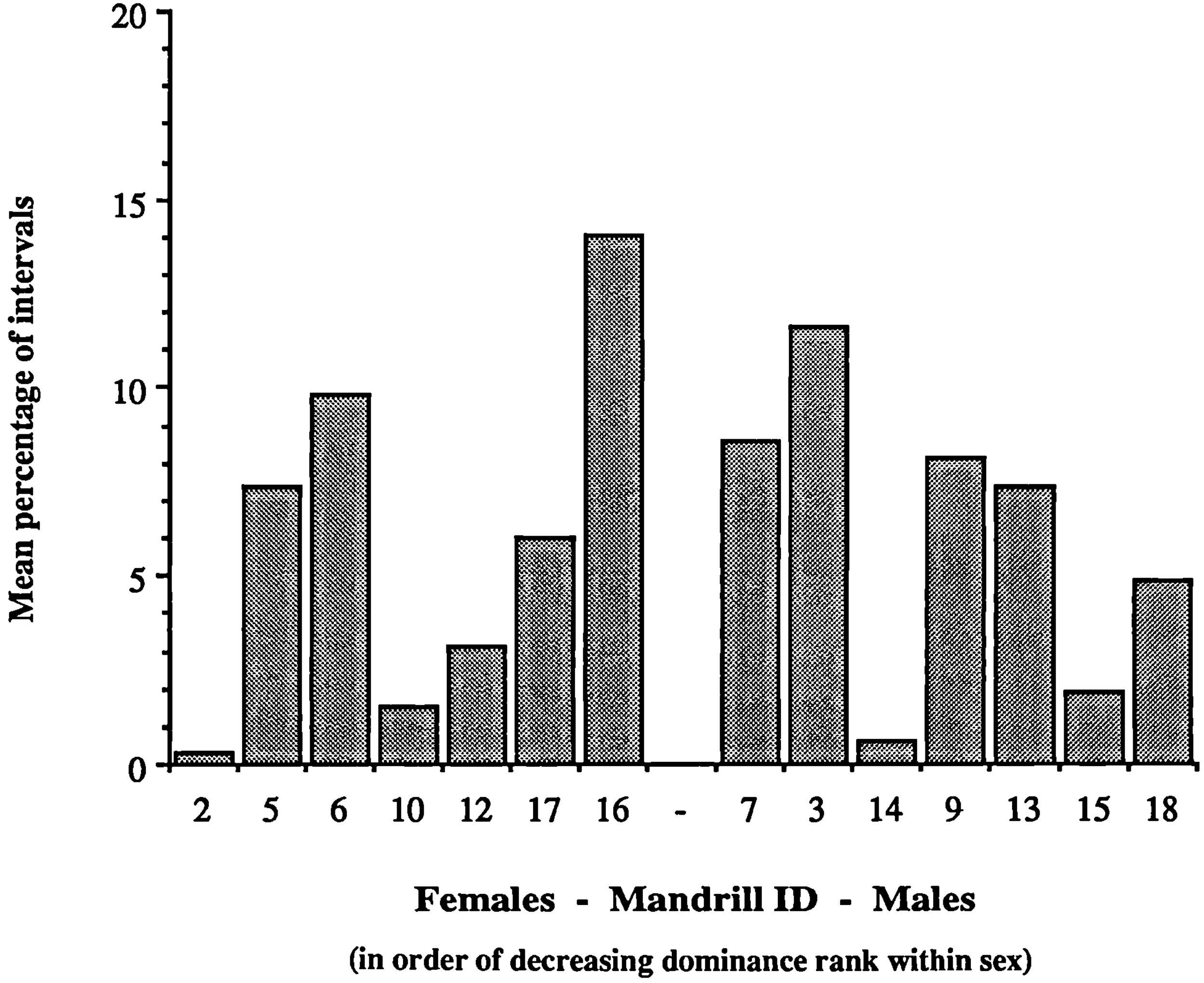
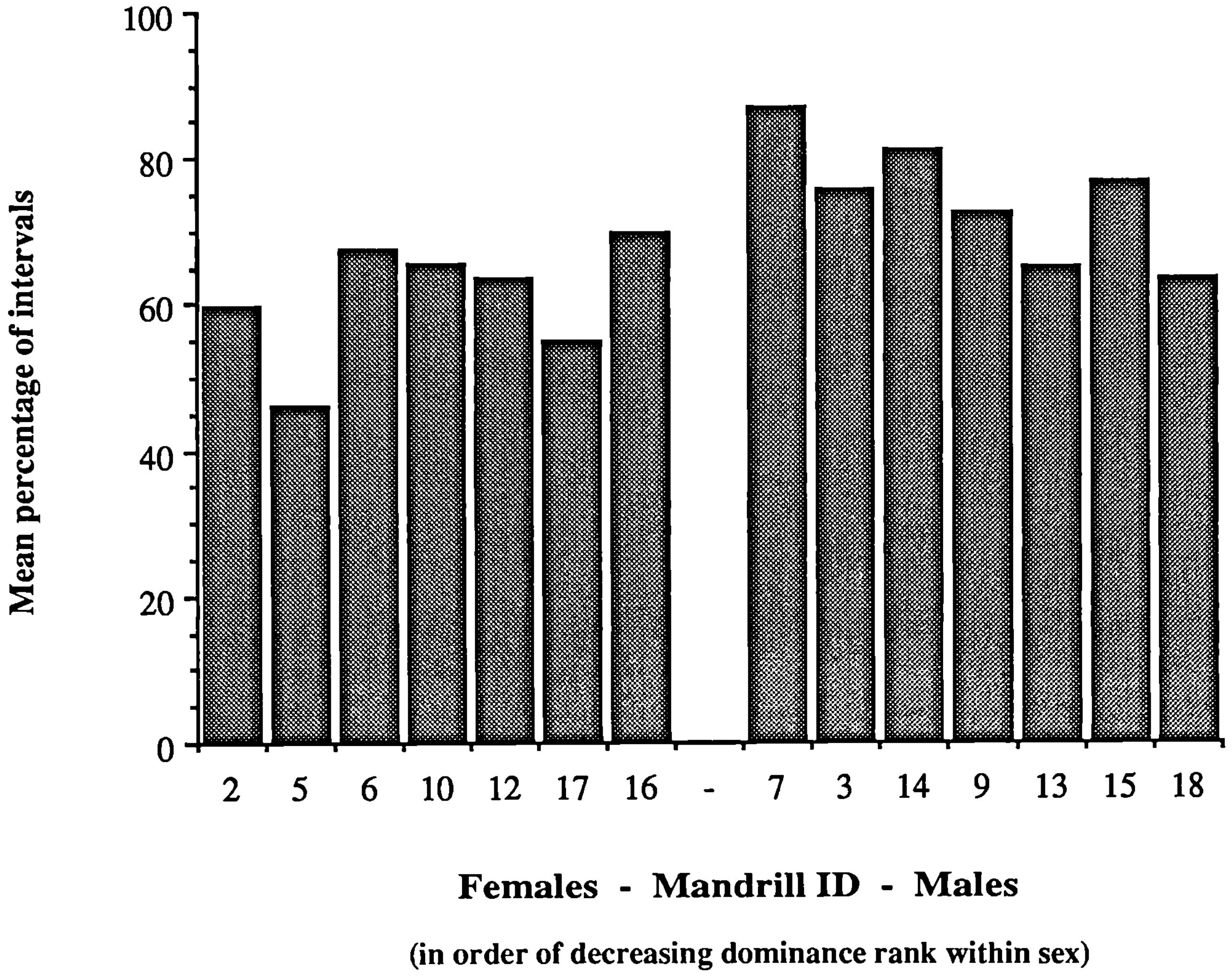


Figure IV.2. Mean proportion of intervals in which the behaviour STILL occurred



Travel

Mandrills travelled in 22% of intervals and males (22.7%) and females (22.3%) did not differ in the proportion of intervals in which travel occurred ($t = 0.153$, $df = 12$, NS). The alpha male travelled in significantly fewer intervals (13.1%) than all other males (23.9%) ($t = 7.046$, $df = 5$, $p < 0.001$) and this is shown in Figure IV.3. This difference was not observed in the female mandrills; the alpha female did not differ from the other females (23.5% vs. 22.6%, $t = 0.579$, $df = 5$, NS). There were no significant correlations of travel with dominance rank in males (Table IV.5) but in females a strong but nonsignificant correlation ($r_s = 0.71$) indicated that dominant females travelled more than subordinate ones (Table IV.6).

Climb

Climbing occurred in about 8% of intervals. There was no significant difference between males and females ($t = 0.410$, $df = 12$, NS). Among males, the alpha male climbed significantly less (1.5%) than the other males (8.5%) ($t = 3.140$, $df = 5$, $p < 0.05$). There was a strong significant negative correlation of amount of climbing with dominance rank ($r_s = -0.94$, $n = 6$, $p < 0.05$) with subordinate males climbing in a greater proportion of intervals than more dominant individuals. This is clearly illustrated in Figure IV.4. In particular the most subordinate male, No. 18, climbed in nearly 20% of intervals (Figure IV.4). Among females, the alpha female did not differ significantly from other females (7.7% vs. 8.5%, $t = 0.678$, $df = 5$, NS). A similar trend of climb with dominance to that described for males was seen in females, with a nonsignificant negative correlation indicating a tendency for dominant females to climb less than subordinate females (see Table IV.6).

Figure IV.3. Mean proportion of intervals in which the behaviour TRAVEL occurred

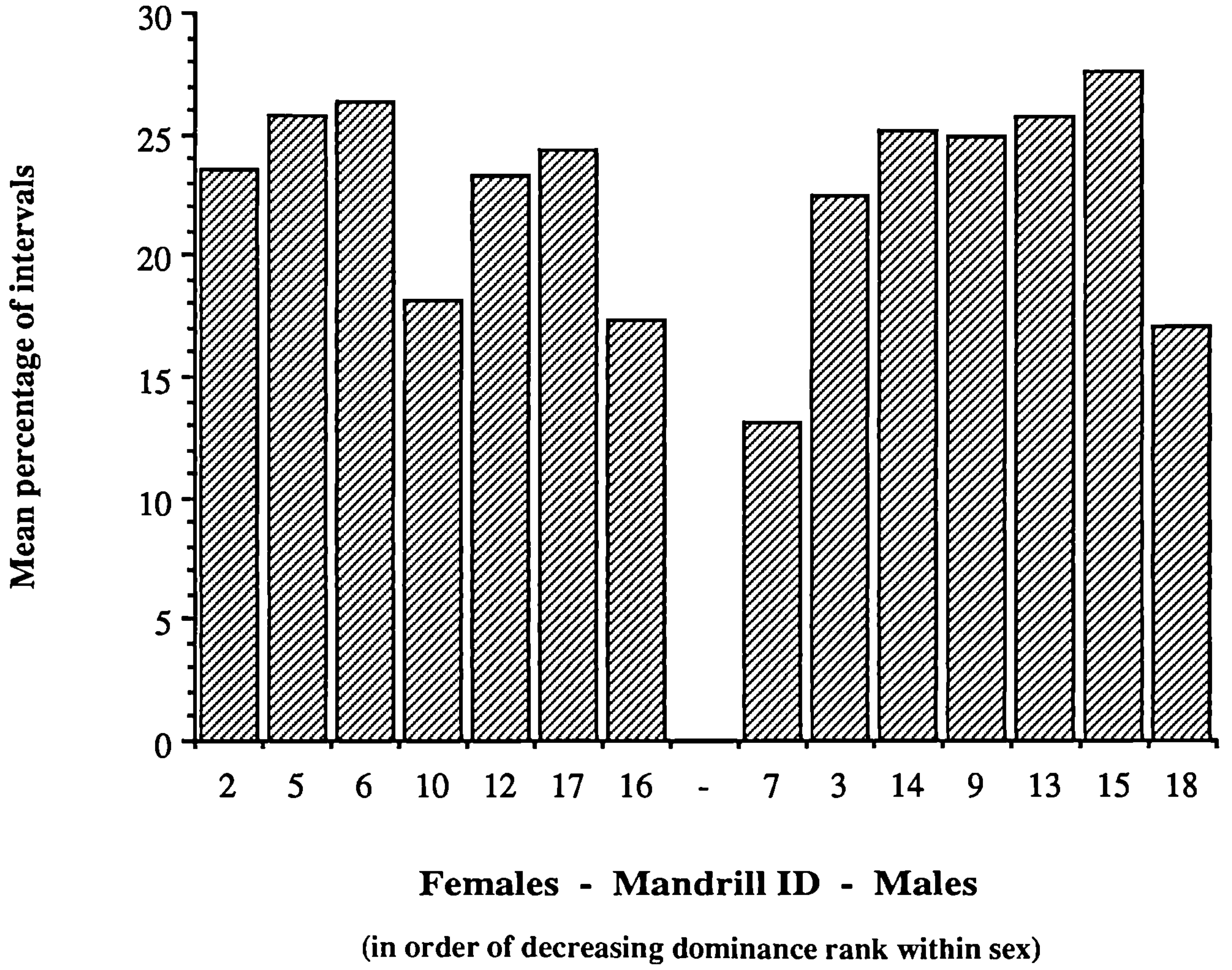
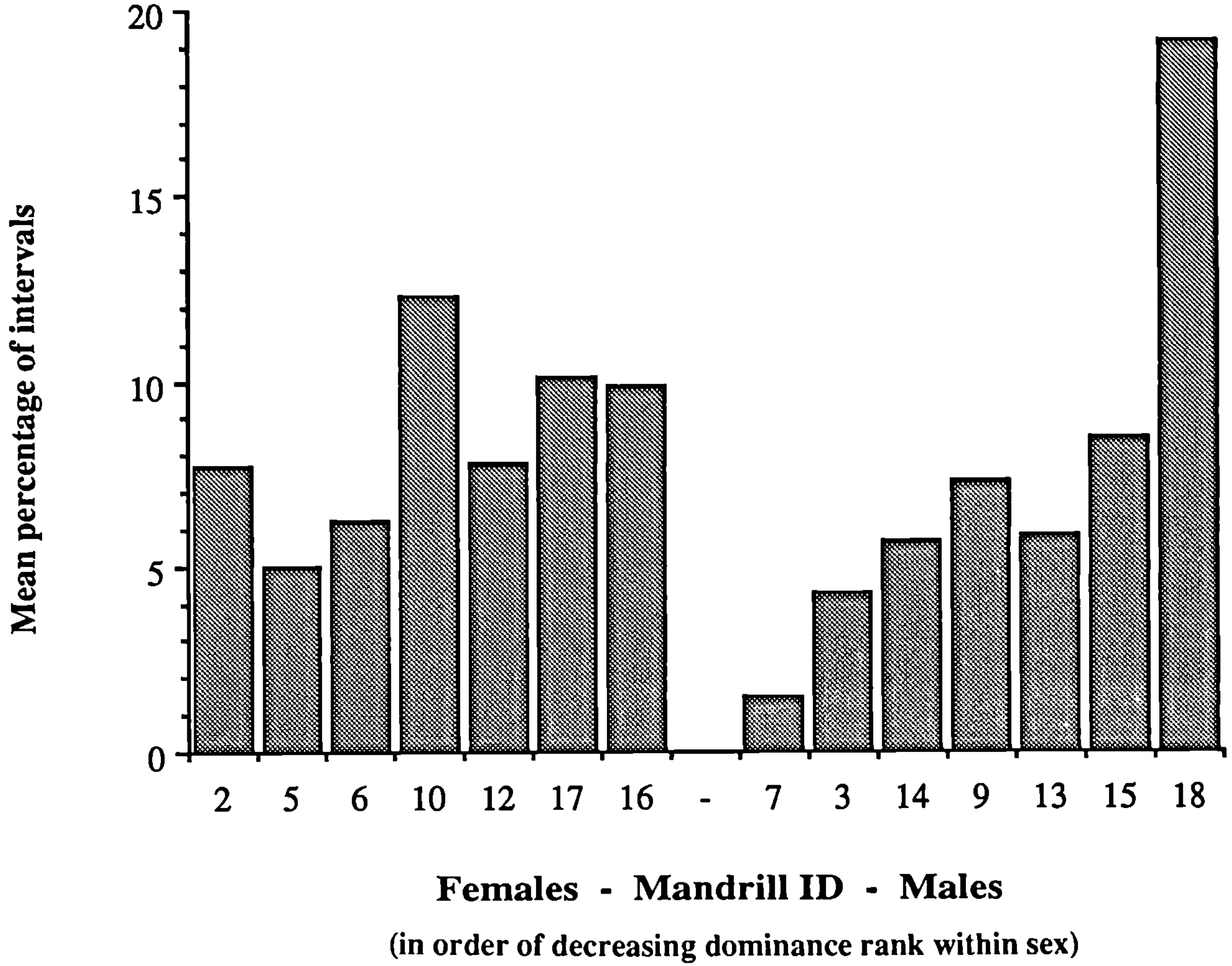


Figure IV.4. Mean proportion of intervals in which the behaviour CLIMB occurred



Forage

Foraging occurred in about 43% of intervals. Males and females did not differ significantly in the mean percentage of intervals in which foraging occurred ($t = 1.544$, $df = 12$, NS), but there was a tendency for males to forage less (39.2%) than females (46.7%). The alpha male foraged in fewer intervals (17.9%) than other males (42.7%) and this difference was highly significant ($t = 10.464$, $df = 5$, $p < 0.001$) and is clearly seen in Figure IV.5. This difference between the alpha individual and the others was not seen in females (45.5% vs. 46.9%, $t = 0.518$, $df = 5$, NS). Dominance rank and forage correlated strongly negatively in males (see Table IV.5), with dominant individuals foraging in fewer intervals than subordinate ones, but this relationship was only significant when Male 7's data were included ($rs = -0.92$, $n = 7$, $p < 0.01$). Correlations between foraging and dominance rank in females were positive but non-significant (see Table IV.6).

The solitary male, No. 3, was excluded from analyses of the following behaviour categories described below - play, allogrooming, aggression, and submission. As he was nearly always alone, he was unable to participate in social interaction. His low scores reflected this solitariness and lack of opportunity to interact with others, rather than indicating that these behaviours were rarely performed by him despite having the opportunity to do so. His data were thus excluded.

Play

The play behaviour analysed here included play with all individuals (cf. grooming with other individuals, below). As might be expected in adult individuals, the founder mandrills played rarely; play was recorded in less than 1% of intervals. Males played more (1.4%) than females (0.5%) but this was largely due to Male 18, the most subordinate and youngest founder male, who played in 6% of intervals (see Figure IV.6). The difference between males and females was not significant ($t = 1.087$, $df = 11$, NS). None of the three highest ranking males was observed to play, and a rank

Figure IV.5. Mean proportion of intervals in which the behaviour FORAGE occurred

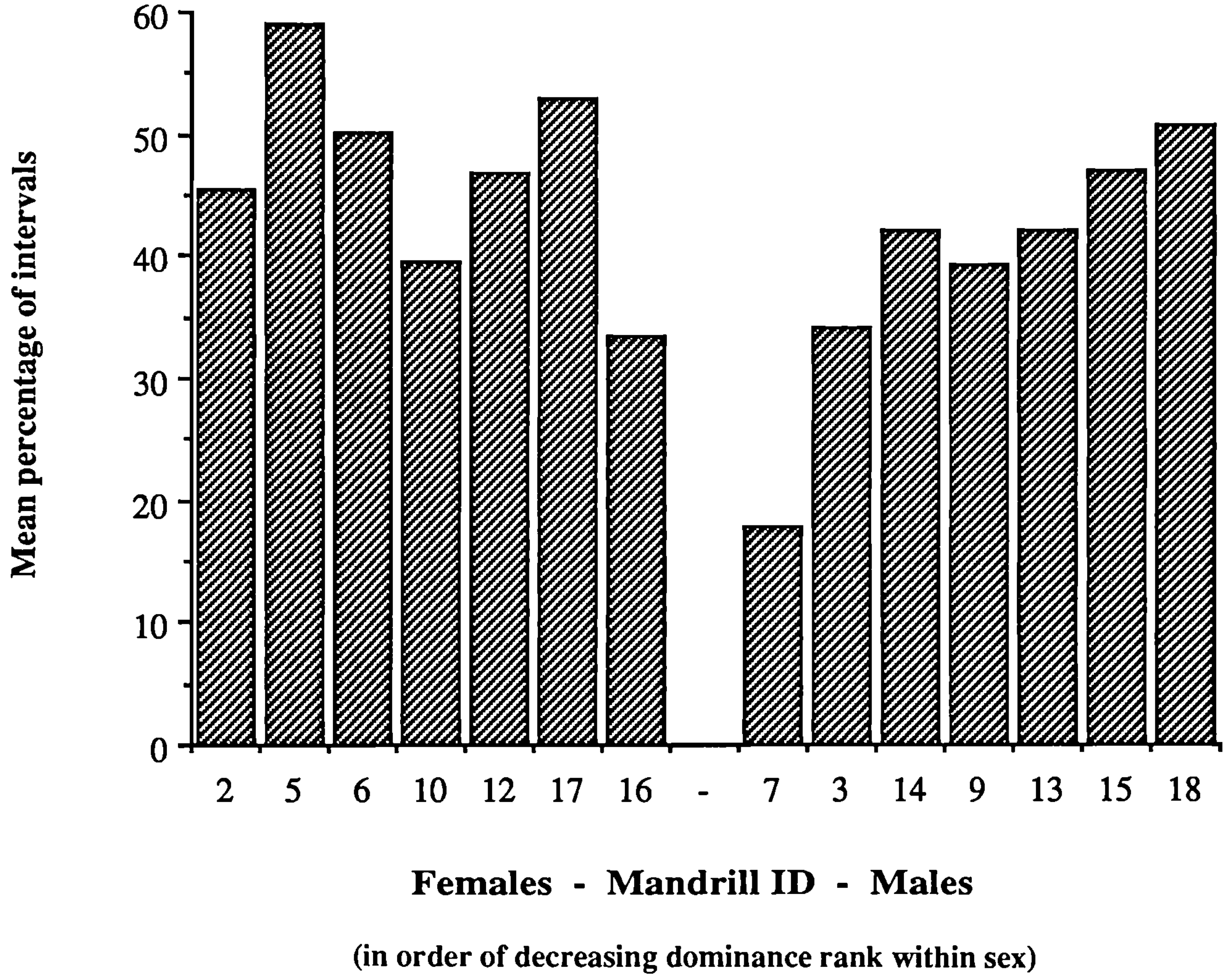
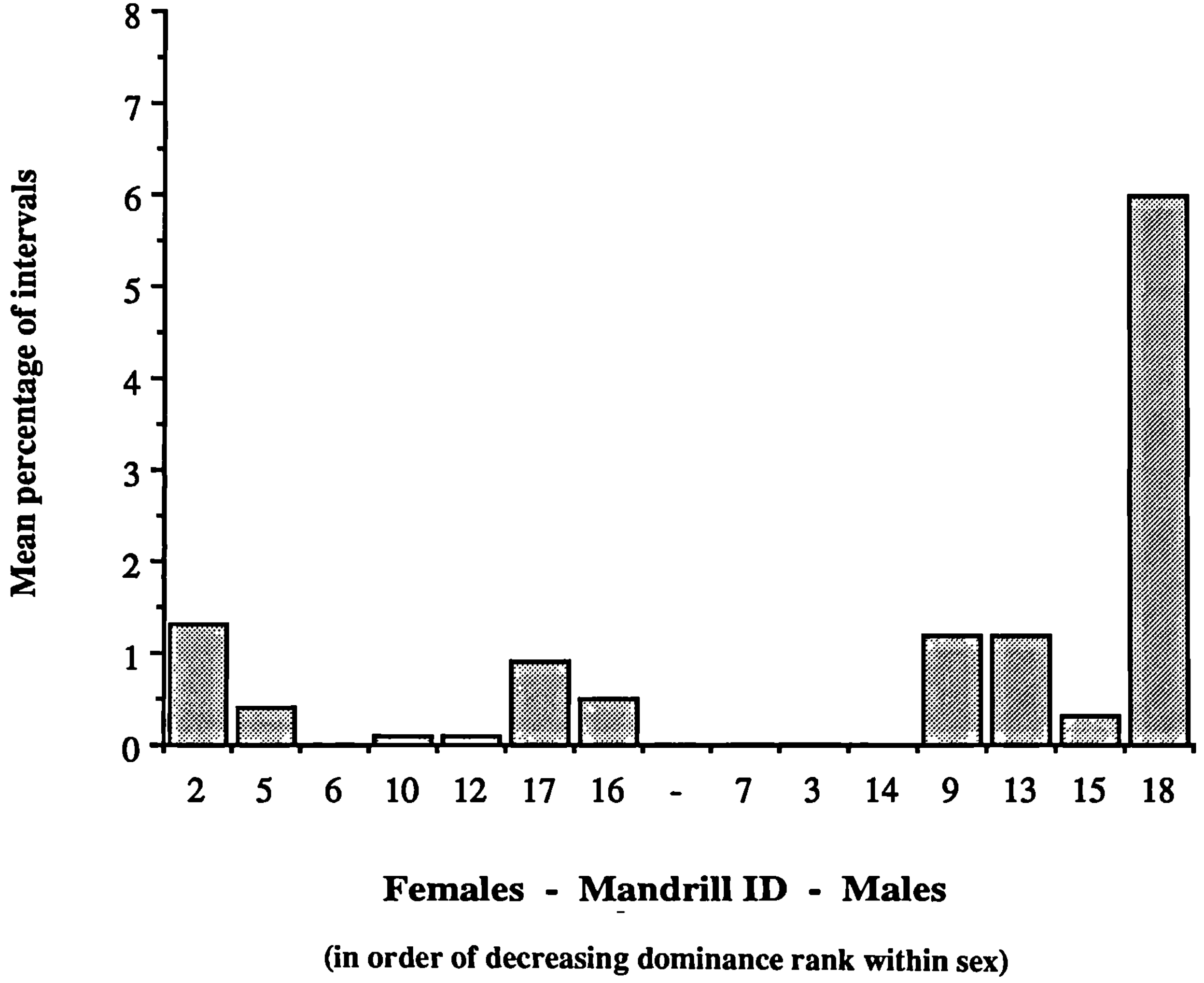


Figure IV.6. Mean proportion of intervals in which the behaviour PLAY occurred



correlation was not done for males due to the large number of ties. In females, the alpha female, No. 2, played significantly more (1%) than other females (0.3%) (t = 6.57, df = 5, p < 0.002) but there was no significant correlation with dominance rank (see Table IV.6).

Give grooming

The following analyses are of the mean percentage of intervals in which the focal founder individual groomed another founder, i.e., grooming with offspring and other juveniles and adolescents was excluded. Grooming occurred in less than 3% of intervals. All females groomed others and groomed more often (2.7%) than males (0.1%), among whom only three of the group males were recorded grooming others. The sex difference in giving grooming was significant (t = 3.820, df = 11, p < 0.01) and is clearly seen in Figure IV.7. There was no correlation of giving grooming with dominance rank in females (Table IV.6) neither did the alpha female give significantly less grooming (2.4%) than other females (2.8%) (t = 0.569, df = 5, NS). Rank correlation was not calculated in males since three males were not recorded grooming others.

Receive grooming

These analyses were also restricted to grooming received by focal individuals from other founders. Mandrills received grooming in about 2% of intervals. Females received more (3.5%) than males (0.8%) but this difference was not significant (t = 1.499, df = 11, NS). All females were groomed by other founders, but only two males received grooming as is illustrated in Figure IV.8. Male 13's grooming (Figure IV.8) was received from Female 2, with whom he appeared to have a friendship during this part of the study. The alpha female was groomed in a significantly greater proportion of intervals than other females (11.6% vs. 2.1%, t = 12.616, df = 5, p < 0.001). In females, being groomed correlated strongly and positively with dominance rank (rs =

Figure IV.7. Mean proportion of intervals in which the behaviour GIVE GROOMING occurred

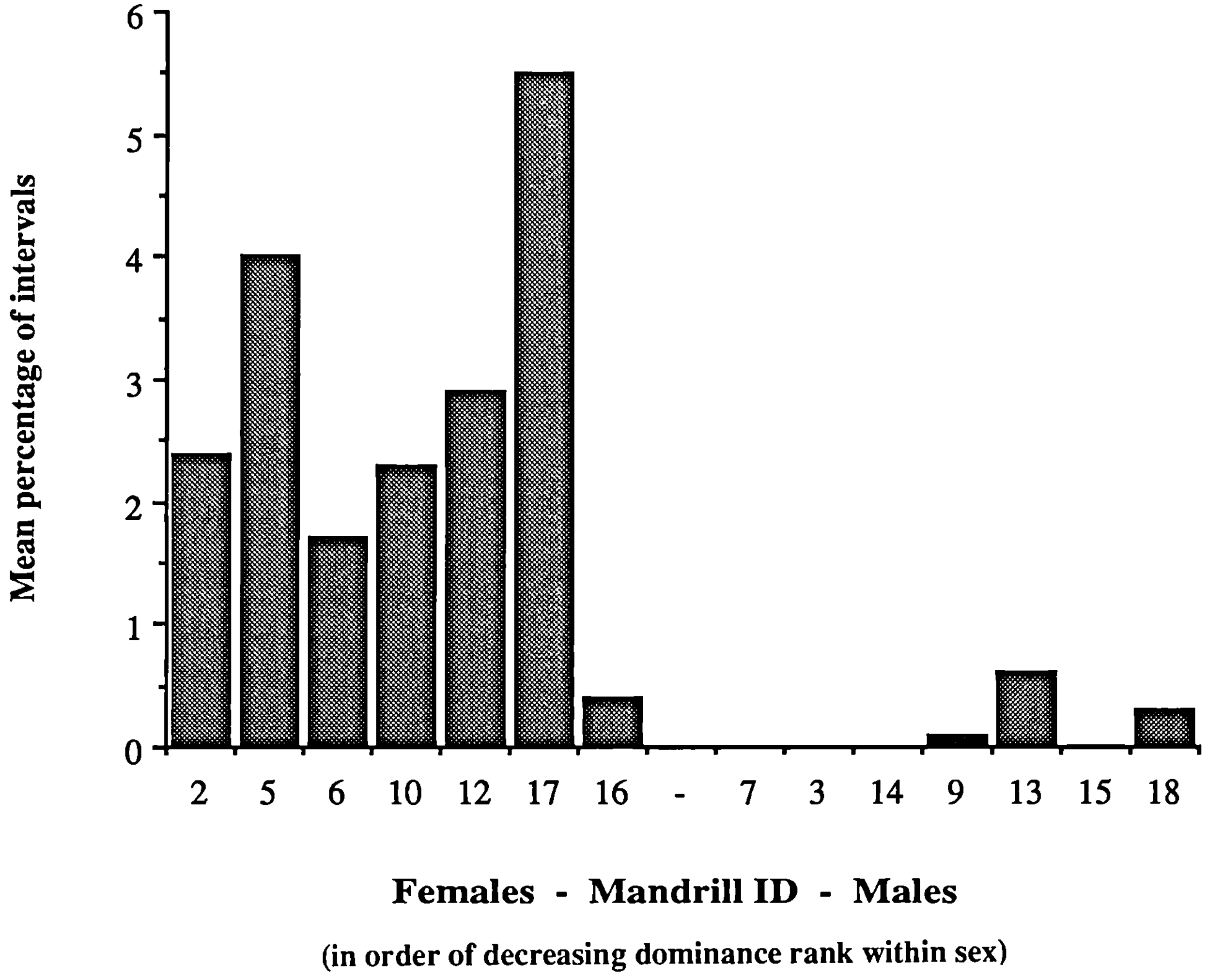
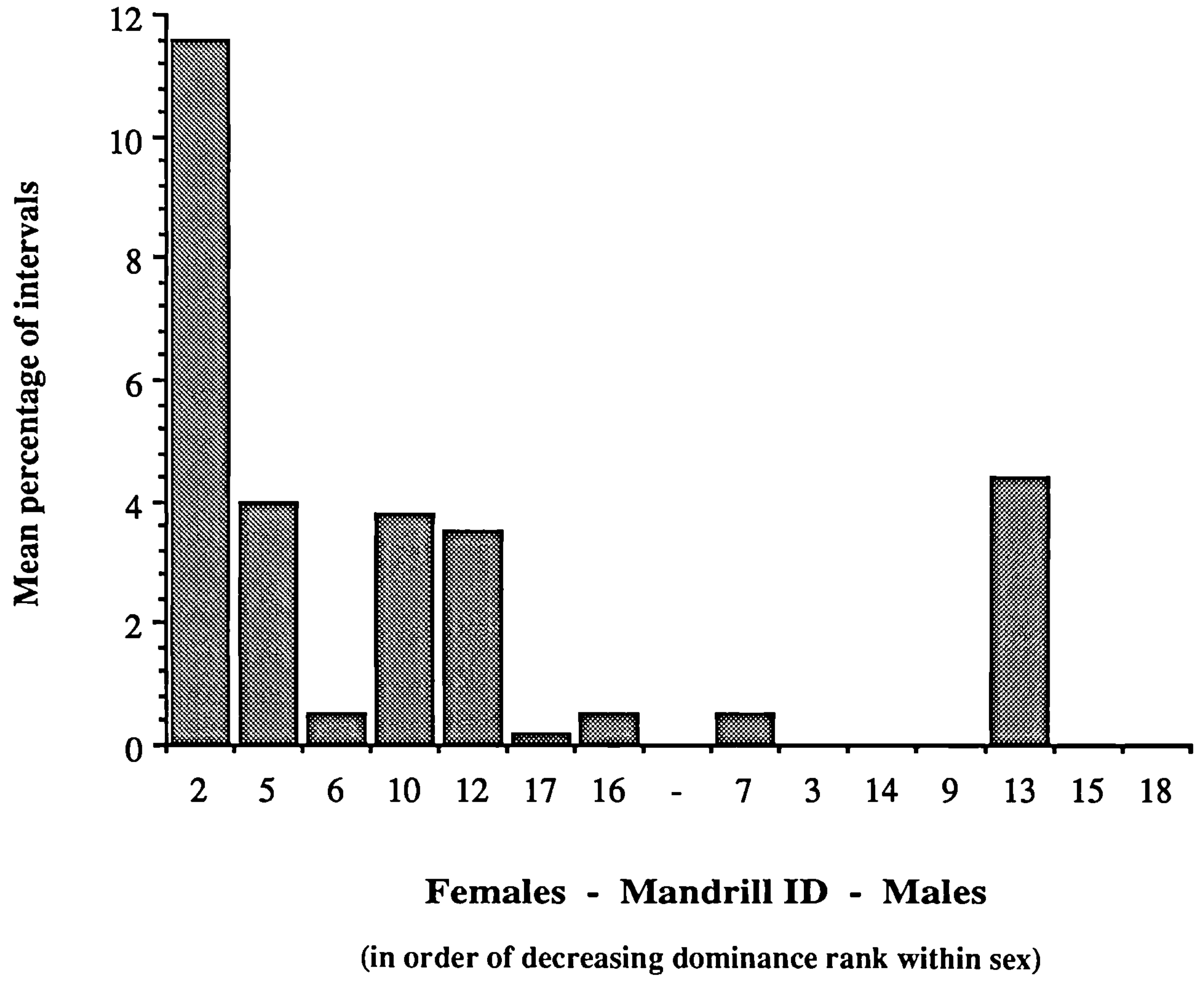


Figure IV.8. Mean proportion of intervals in which the behaviour RECEIVE GROOMING occurred



0.77, n = 6, NS) with more dominant individuals receiving more grooming than females of lower rank, but this was only significant when the alpha female's data were included (see Table IV.6).

Aggression

A composite measure of aggression was used since individual behaviours occurred infrequently. The totals for head-bob, head-bob and threat grunt, and threat rush were summed and the mean percentage interval calculated as described above. This percentage was then divided by three (since there were three behaviours).

Overall, aggression was recorded in only 0.2% of intervals. The mean proportion of intervals in which aggressive behaviour occurred is illustrated in Figure IV.9. Males were aggressive in slightly more intervals (0.3%) than females (0.2%) but this difference was not significant ($t = 1.077$, $df = 11$, NS). Male No. 7, the alpha male, was significantly more aggressive (0.6%) than other males (0.3%) ($t = 3.425$, $df = 4$, $p < 0.05$) but there was no significant correlation of aggressive behaviour with dominance rank in males (see Table IV.5). In contrast, among females aggressive behaviour correlated significantly positively with dominance rank ($rs = 0.93$, $n = 6$, $p < 0.05$) with dominant females being aggressive in a greater proportion of intervals than more subordinate individuals. In addition, the alpha female was aggressive in significantly more intervals (0.4%) than other females (0.1%) ($t = 5.000$, $df = 5$, $p < 0.01$).

Submission

Presenting was used by the mandrills as an indication of submission. Presenting occurred in less than 1% of intervals (see Figure IV.10). Presenting by females occurred in significantly more intervals (0.7%) than presenting by males (0.1%) ($t = 2.222$, $df = 11$, $p < 0.05$). This can partly be explained by the fact that in general females were subordinate to males (see Chapter V) so presenting scores for

Figure IV.9. Mean proportion of intervals in which AGGRESSION occurred

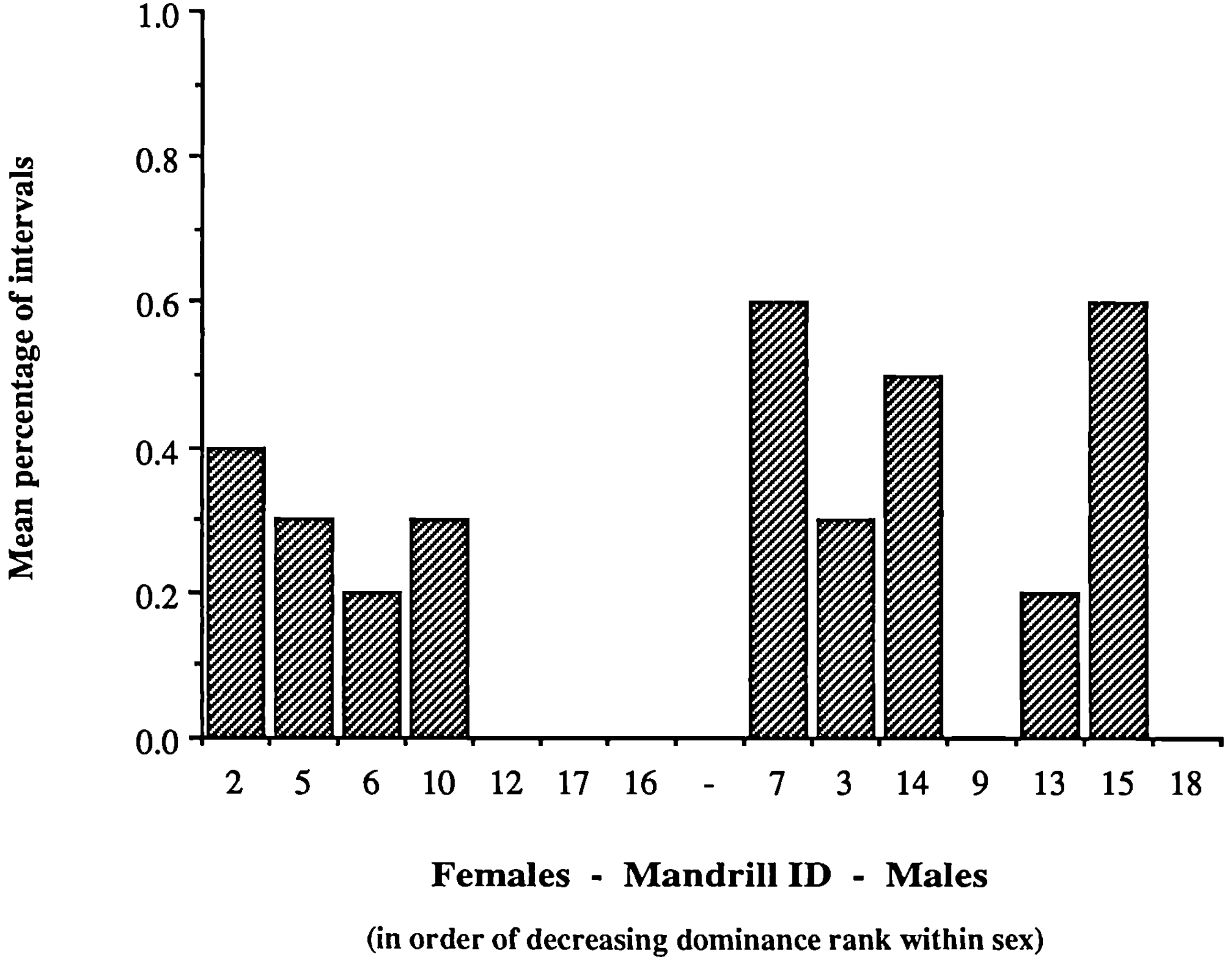
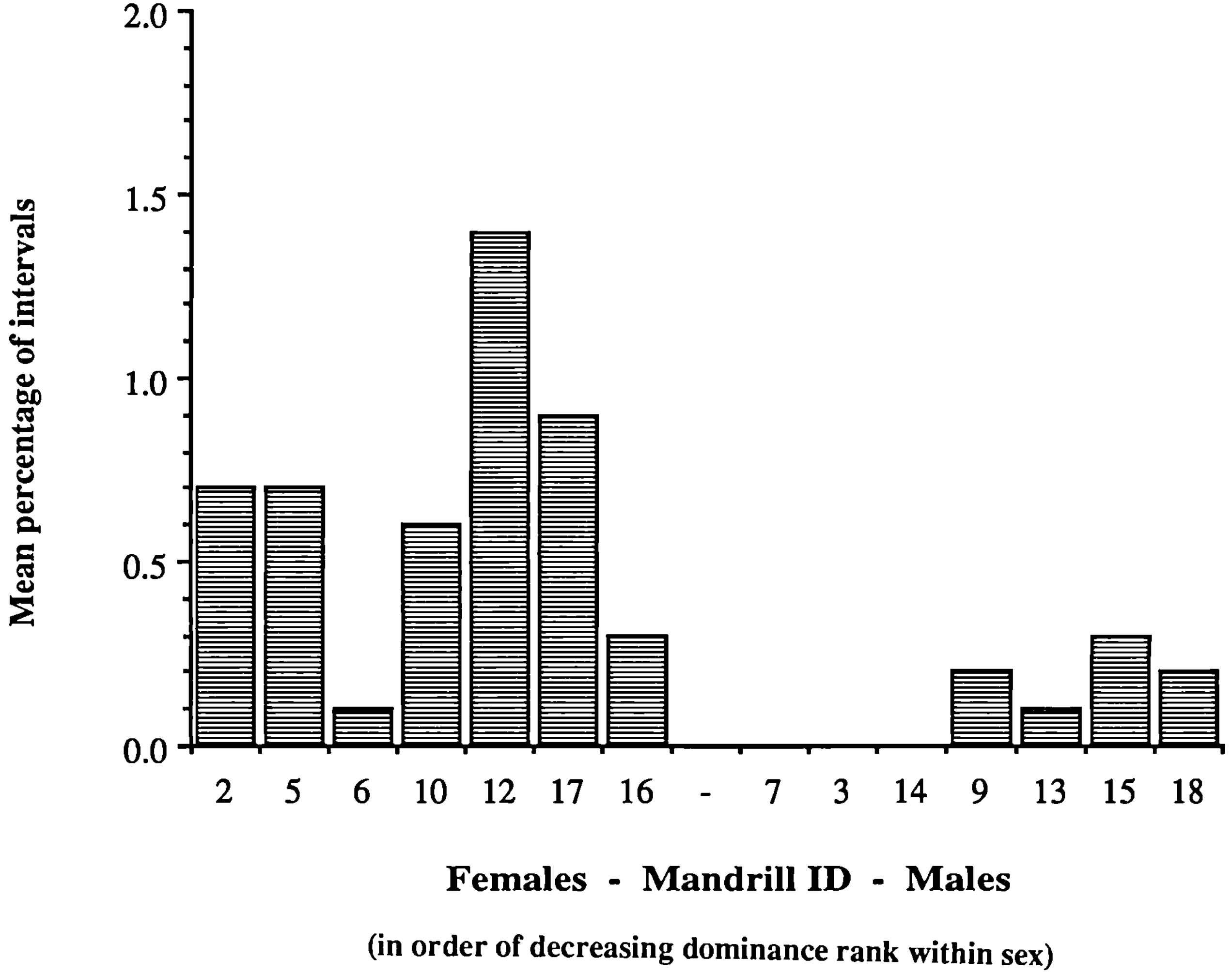


Figure IV.10. Mean proportion of intervals in which SUBMISSION (presents) occurred



females were presents to male and females, whereas those by males were only directed at other males. Direction of present was not analysed separately. Presenting was not recorded in the three highest ranking males, whereas all females were recorded presenting (illustrated in Figure IV.10). The alpha female did not differ from other females in presenting (0.7% vs. 0.7%, t = 1.500, df = 5, NS) nor was there a correlation of mean percentage intervals in which a present occurred with dominance rank in females (see Table IV.6). This somewhat unexpected result may be due to the confounding of presenting to other females and to males and the influence of male-female relationships. The relatively high proportion of presenting by Female No. 2 can be attributed to her relatively close proximity to males, and the alpha male in particular (see Chapter V). Close spatial proximity of a female to a male was often preceded by presenting on the part of the female. Thus the relatively high rate of presenting in female No. 2 may actually be an indication of her high dominance status in terms of her 'confidence' and ability to be close to males rather than an indication of her subordination.

Scent-marking

Since there are no previous quantitative reports on scent-marking, further details of scent-marking behaviour in the group of mandills at CIRMF are reported below.

As described in Chapter II scent marking was recorded by behaviour sampling. The identity of the individual, time of day, height of the mark, diameter at breast height (dbh) of the trunk or the diameter of the branch where rubbed, and the sequence of behaviours making up a scent-marking sequence, were recorded on a check-sheet. Other individuals less than five metres from the scent-marker were also recorded as was the general activity and 'atmosphere' in the group at the time.

Sometimes individuals just sniffed and rubbed their chin against the bark, without following this by sternal rubs, as if checking a deposited scent. However, 114 sequences which ended in rubs were seen. The supports marked were nearly always vertical (occasionally a side branch was rubbed) and varied from 4 to 55 cm (mean = 22 cm) in diameter where marked. A sternal secretion was deposited at heights varying from 0.5 m to 17 m (mean = 4, mode = 0 to 1 m; Figure IV.11) by vigorous sternal rubs (range = 1 to 14, mean = 3.25, mode = 2; Figure IV.12). Sometimes a damp stain was left on the bark. There were several marks in the enclosure which were re-marked repeatedly, by different individuals, and these were visible as yellowish stains. Youngsters sometimes rubbed marks left immediately prior by other individuals. Unless the scent mark was just deposited I did not find that the stain had a strong characteristic odour.

Mandrills seven months and older, and both males and females scent-marked (Table IV.7). All subadult and adult male founders were observed scent-marking. They were more frequently observed scent-marking (mean 8.6) than female founders (mean 2.4) and this sex difference was statistically significant ($t = 4.514$, $df = 11$, $p < 0.001$). The alpha male (No. 7) accounted for 30% of the sternal marking by founder males and he scent-marked significantly more frequently than all other males (18 times vs. mean 7 times, $t = 8.352$, $df = 5$, $p < 0.001$). There was a positive but non-significant correlation of frequency of scent-marking with dominance rank among males ($rs = 0.71$, $n = 7$, NS) with more dominant males more frequently observed marking than subordinates. Only four of the seven founder females were observed to scent-mark. Similar to the relative frequencies seen in males, the alpha female (No. 2) scent-marked significantly more frequently (11 times) than other females (mean = 1 time) ($t = 19.342$, $df = 5$, $p < 0.001$). A rank correlation with dominance was not calculated due to the large number of ties.

The youngest animal in which scent-marking was seen was an infant male of seven months. At this age the sternal gland was not even visible and the chest hair was dry and fluffy. The behaviour pattern was observable before the animal was physiologically able to deposit a scent mark. Juvenile males were more frequently observed scent-marking (mean 4.5 times) than juvenile females (mean 1.8 times) (t =

Figure IV.11. Height (in metres) at which mandrills scent-marked

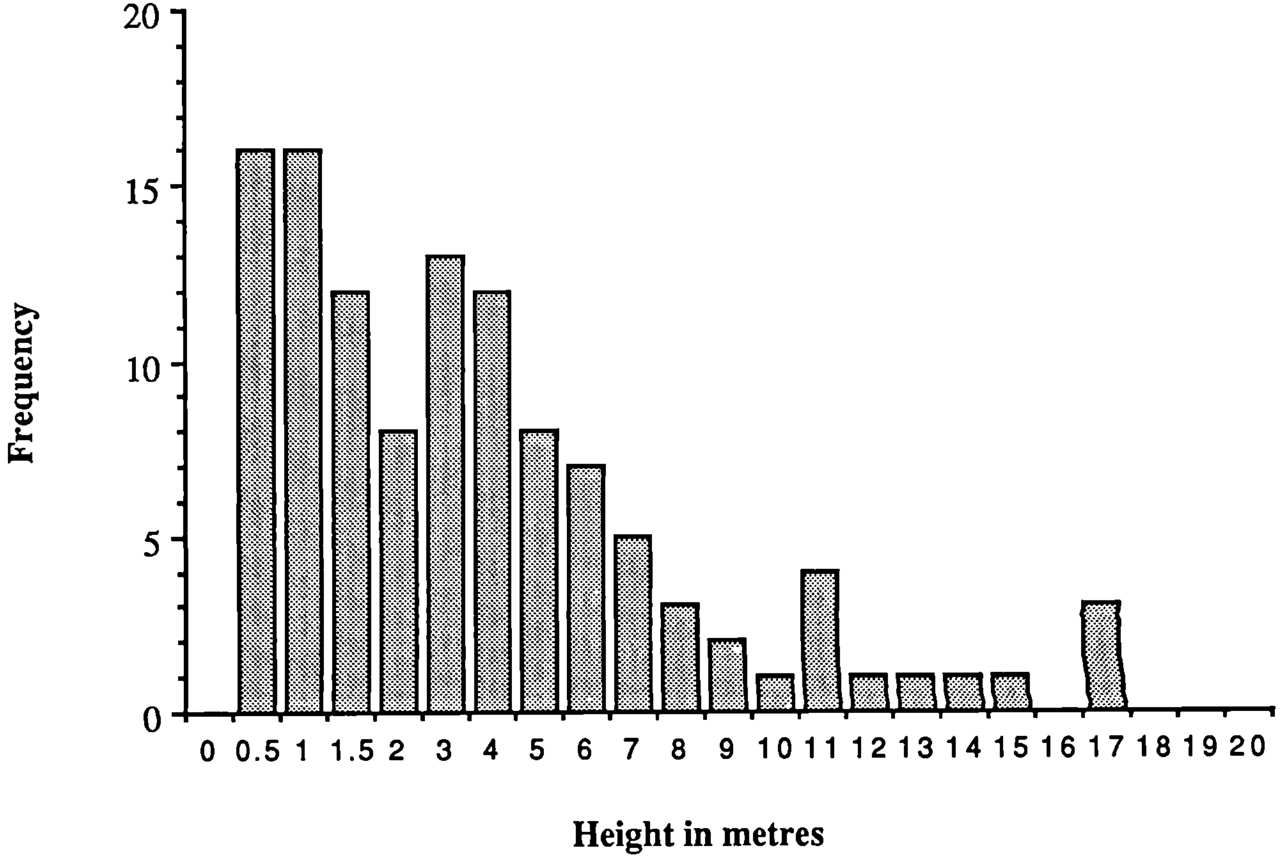


Figure IV.12. Number of sternal rubs per sequence

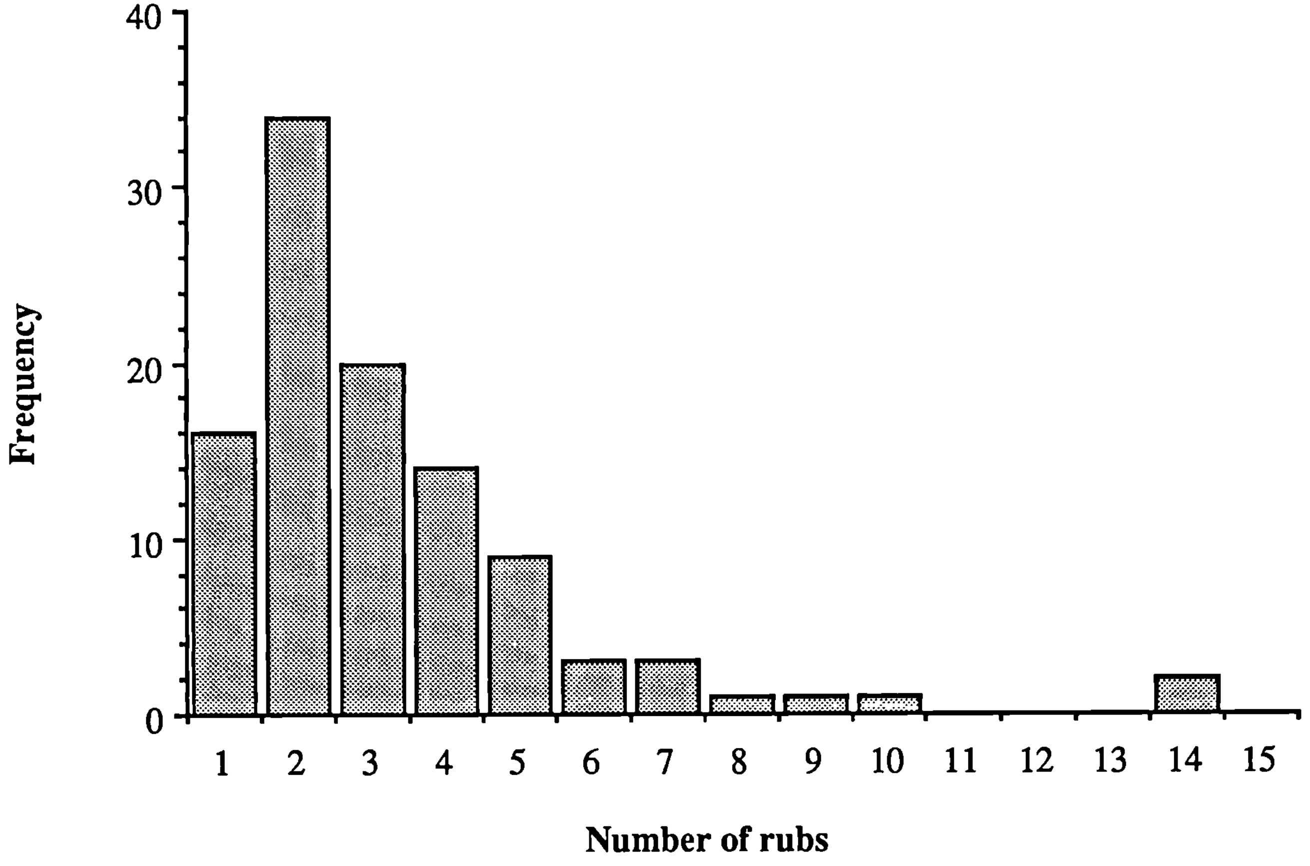


Table IV.7. Frequency of scent-marking by the CIRMF mandrills

Identity	Total Frequency
Immatures* Males : Females	27 : 11
Founder Females (n = 7)	17 (1)
Male 7	18 (1)
Male 3	8 (7)
Male 14	10 (0)
Male 9	11 (3)
Male 13	3 (1)
Male 15	4 (1)
Male 18	6 (1)

* Immatures include adolescents, juveniles, and infants

Male founders are shown in order of decreasing dominance rank

Numbers in brackets are observations which occurred during focal sampling

(NB no data were collected on immatures by focal sampling)

3.243, df = 10, $p < 0.01$). The sex ratio of immatures old enough to scent-mark (i.e., older than 7 months) was 1:1. Marking was seen in five of the six male juveniles but 63% of sternal rubbing sequences (total = 27, Table IV.7) were performed by the two oldest males, 2A and 6A. Among juvenile females two individuals, 5A and 10A, accounted for all the scent-marking. These were the second and third oldest female juveniles. It seems likely that initially frequency of scent-marking may be related to age and then later to dominance status. However, it was not possible to test this since (a) scent-marking was not observed frequently enough during focal sampling and (b) among founders the alpha individual in each sex was also the oldest animal.

In older individuals the pores of the glandular area were enlarged and the elongated hairs were sometimes stained and slightly greasy. A strong musky odour was discernable on sniffing the chest of anaesthetised mandrills, and was sometimes noticeable when I was standing close to a male. Even in adult individuals, although it could always be distinguished, the sternal gland was not always greasy-looking. I had the impression that a difference existed between the sexes in gland development, which paralleled other differences. Females first had greasy 'active' looking glands around puberty, at three to four years of age, whereas in males greasy glands appeared later, at four to five years old. This period corresponded to the onset of the adolescent growth spurt in males, during which a sex difference in size first became apparent.

Although some marking sites seemed random, some of the sites and circumstances in which scent-marking occurred may give clues as to its functional significance. Sleeping sites were often marked. On occasions when I was alone with Male No. 14, as he was walking past sleeping site 3, he stopped, climbed, and marked a trunk less than 10 m from the sleeping place that Male No. 7 habitually used, before continuing to another part of the enclosure. Scent-marking was sometimes associated with tension, both between individuals (see Chapter V) and in the group as a whole after disturbance. Approximately 12% of scent-marking occurred during or immediately following situations of tension.The functional significance of scent-marking is discussed in Chapter VII.

In summary, the behavioural data presented above showed that the alpha individuals in each sex differed significantly in their behaviour from others. These data in addition to more subjective and qualitative assessments contribute to an overall impression of the alpha individuals in terms of both their role and personality.

The alpha male

The alpha male, No. 7, was extreme among males in the behaviour still, travel, climb, forage, and scent-marking. He spent significantly more intervals being still and aggressive, and he scent-marked more, and significantly fewer intervals travelling, climbing, and foraging than other males. Inclusion of his data in the correlations of dominance rank and behaviour (Table IV.5) strengthened every relationship. He spent much time sitting quietly, often somewhat to one side of the main grouping of females and youngsters, monitoring the group. He was largely terrestrial, travelling little and rarely climbing. He did not have the highest frequency of aggression, despite playing a policing role in the group and 'breaking-up' disputes between females (see Chapter V). These data, together with *ad lib.* observations, give a general picture of a calm, confident, controlling individual. This was in contrast to the more 'exuberant' style of younger subadult mandrills such as Male No. 15, who moved about, chasing and threatening juveniles, displaying, and climbing readily.

The alpha female

The alpha female, No.2, was extreme among females in the behaviour rest, play, receiving grooming from other founders, aggression, and scent-marking. She spent significantly more intervals playing, being groomed, threatening others, and she scent-marked more frequently. She rested significantly less than others. This reduced resting may be linked to her being groomed more - when other females were sitting by themselves resting, Female 2 was being groomed. In contrast to the alpha male, who differed from other males on a number of maintenance behaviours, the alpha female was not distinguishable from other females in foraging, climbing, travelling, or being still. Instead she differed in an array of social behaviour, including both affiliative and aggressive components. Inclusion of her data to rank correlations of dominance status and behaviour (Table IV.6.) did not consistently increase the correlation as it did in males. Female 2 could be described as confident and rather aggressive. She asserted her status frequently, in contrast to the alpha male, for example by displacing others from desired resources, soliciting grooming, and she seemed always to be at the centre of the group (see Chapter V). She sometimes initiated travel.

Some of the behavioural features described above are examined in more detail in Chapters V and VI.

This chapter has provided an introduction to the behaviour of the CIRMF mandrills. This is the first description of behaviour from a group of mandrills approximating in size that of wild mandrills (see Chapter II) and maintained in naturalistic conditions in a habitat country. To complement the behavioural data described and quantified above and in later chapters, a description of the socioecology of mandrills based on field study is presented below. In Chapter VII the behavioural and ecological information will be integrated in an attempt to provide a more complete understanding of this species.

Field studies of *Mandrillus*

There have been five published field studies of mandrills totalling only 73 months of fieldwork and presenting largely ecological data, and only one study specifically on drills. In contrast the savanna baboons of the genus *Papio* have been well-studied, as has the gelada baboon - there have been several long-term behavioural studies of habituated individuals observable from distances of only a few metres. The field studies on *Mandrillus* are all characterised by a lack of behavioural observation.

This has led to a paucity of quantified information, and much of the published work is descriptive.The field studies on mandrills and drills are described below.

Sabater Pi's study, carried out in Rio Muni, Equatorial Guinea in 1967 and 1968, was part of a collecting trip and general study on primates. The ecological data presented (Sabater Pi, 1972) were from the capture sites of 101 mandrills, augmented by just over 11 hours of observation from 16 contacts with wild mandrills in a period of 21 months.

Jouventin's broad ecological study of mandrills was conducted for three months in each of two areas in Gabon (near Makokou in the northeast in 1973 and near Booué in central Gabon in 1974, see map in Figure II.1). During this time he made 39 contacts with mandrills which resulted in 48 hours of observation. Data were obtained from chance contacts with mandrills while walking through the forest. Attempts at habituating them (by sitting quietly on travel routes) were unsuccessful because visibility through the vegetation was less than their flight distance (Jouventin, 1975a), so that approach to a distance from which they were observable elicited a flight reaction.

Hoshino and coworkers carried out a 27-month field study (1979 to 1983) on mandrills in the Campo Reserve, Cameroon (Hoshino *et al.*, 1984; Hoshino, 1985; Kudo and Mitani, 1985; Kudo, 1987). For this largely ecological study a network of over 100 km of paths was cut in 25 km^2 of forest to facilitate the location of mandrills. They were found 187 times but no information was presented on the amount of observation. When mandrills were located they were followed at a distance of 40 to 100 m. The data presented result from analyses of fresh feeding remains and 752 faecal samples. Kudo's 14-month study of vocalisations was based on 39 encounters and 89.6 hours of direct observation, although only 30% of following time was within 20 m (1987, p.290).

Harrison's study was carried out in northeastern and central Gabon for six months in 1982 to 1983. He made only one observation (lasting a few hours) of a group of mandrills in this period, however he also saw solitary males. Ten further contacts with mandrills during five weeks in August and September 1983 were also reported (Harrison, 1988).

Lahm's field study of mandrills was carried out in northeastern and central Gabon (at the same sites as Jouventin and Harrison) for 12 months in 1982 and 1983. Due to severely limited observation (mandrills were contacted only 14 times and observed for a total of nearly 17 hours) feeding ecology was the main emphasis of the project. Fresh food remnants, 63 faecal samples, and the contents of 12 stomachs provided the data base (Lahm, 1986).

Gartlan (1970) studied drills in the Bakundu Forest Reserve, West Cameroon, for 15 months from October 1967 to December 1968. Paths were cut in the 155 ha study area to facilitate quiet travel when following groups of drills. Drills were encountered 32 times for a total of almost 78 hours contact and for nearly half of this time (about 37 hours) the drills were in clear view.

Information on wild drills was also collected by **Struhsaker** during a 19-month study of West African forest cercopithecines in Cameroon (Struhsaker, 1969; Gartlan and Struhsaker, 1972). Drills were sighted 22 times in 1095 hours of contact with primates. There was no information on the amount of time spent observing drills.

The above summaries give an indication of how little work has been done on either species. The nature of tropical forest, coupled with the semi-terrestrial habits of mandrills and drills, enables them to elude attempts at sustained observation and habituation. Visibility is frequently less than 20 metres (Hoshino *et al.*, 1984; Lahm, 1985) yet following distances are from 20 to 100 m (Hoshino *et al.*, *op. cit.*, 1984; Lahm, *op. cit.*; Kudo, 1987), so observation of these animals is notoriously difficult. From the studies described above, per month of study an average of only 3.6 contacts with mandrills, and 1.6 with drills were made. The following description of the socioecology of mandrills and drills is based largely on the data resulting from the field studies outlined above.

Both mandrills and drills have been observed as solitary individuals and in groups of various sizes (Struhsaker, 1969; Gartlan, 1970; Sabater Pi, 1972; Jouventin, 1975a; Hoshino *et al.*, 1984; Lahm, 1985; Harrison, 1988; pers. obs.). Nearly 30% of Jouventin's observations were of groups numbering over a hundred individuals and groups of over 300 mandrills have been recorded (J.-P. Coupin, C.E.G. Tutin, pers. comm.). Gartlan (1970) observed three groups of drills containing more than 100 animals; the largest group numbered 179 individuals. Accurate counts of individuals are difficult to make under field conditions. In the dense forest understorey adult males, due to their large size, flamboyant colouring, and characteristic two-phase grunt rallying vocalisation (Gartlan, 1970), are the most conspicuous individuals of the group, and it is clear that mandrills and drills are found in groups which contain a single male and in groups containing multiple males. Given the relative ease of observing adult males, some workers (e.g., Sabater Pi, 1972; Jouventin, 1975a) used Struhsaker's (1969) and Gartlan's (1970) estimates for drills of 20 individuals per adult male as a basis for estimating group size from adult male counts in mandrills. However from direct observation Hoshino *et al.*, (1984) reported an average adult male to individual ratio of 1: 13.9, and Lahm of 1: 14.7 (range 1: 12.5 to 1: 17.5, Lahm, 1985). Harrison (1988) cited a ratio of 1: 27 to 32 (from Tutin and Fernandez, unpubl.), and from ten reliable observations (Jouventin, 1975a, p.523-524) a ratio of 1: 22.5 can be calculated. All workers found that small groups of about 20 or fewer individuals contained only one adult male, and that groups of over 20 individuals contained more than one adult male. In groups numbering more than a hundred, four to eight adult males were present in mandrill groups, and three to five in groups of drills (Gartlan, 1970).

Mandrills and drills in the wild thus have the highest ratio of males to group members of any of the baboons. This skewed ratio suggests that males experience high mortality and/or that they emigrate from their natal groups. The latter suggestion is supported by field observations from which an average of 15% (range 5% to 75%) of mandrill sightings were of solitary males; (75% of 4 sightings, Harrison, 1988; 5% of 187, Hoshino *et al.*, 1984; 26% of 39, Jouventin, 1975a; 21% of 14, Lahm, 1985; 31% of 16, Sabater Pi, 1972; 45% of 31, C.E.G. Tutin, pers. comm.), and 17% of drill observations (6% of 32 sightings, Gartlan, 1970; 27% of 22, Struhsaker, 1969). Although solitary individuals were invariably males, no all-male bands have been reported in either species, though occasionally two male mandrills have been observed together (Jouventin, 1975a; Rogers, in Harrison, 1988). It appears then that mandrills and drills are polygynous, that a one-male unit is the basic unit of social organisation, and that large groups, the 'grandes hordes bruyantes' (cited for drills in Gabon) of Malbrant and Maclatchy (1949, p.56) and observed by others, consist of one-male units which have coalesced (Jouventin, 1975a; Spassov, 1979). However, Kudo (1987) suggested that a multi-male organisation occurs in the mandrill.

In mandrills the coalescing of one-male units into large groups appears to have a temporal pattern. However, neither at Idenau nor Bakunda in Cameroon was a seasonal pattern in occurrence or density of drills evident (Gartlan and Struhsaker, 1972). In Gabon very large groups of mandrills were more frequently observed from June to September (Jouventin, 1975a; A.Gautier-Hion, C.E.G.Tutin, pers. comm.). Harrison observed groups of up to 200 mandrills over five weeks in August and September, but made no further contacts during the following eight months (1988, p.221). June to September are the months of the long dry season in Gabon (IPN, 1983), and this is a period of relative fruit scarcity in the forest (Gautier-Hion, 1980; Gautier-Hion *et al.*, 1985; Williamson, 1988). Hoshino *et al.*, (1984) found no significant differences in the frequency of observation of one-male and multiple-male groups between the wet and dry season in Cameroon, but did find a significant difference related to fruiting pattern. Large multiple-male groups were more frequently observed in the minor fruiting season

(May to August). For mandrills the data from Gabon and Cameroon concur: large aggregations of mandrills coincide with periods of relatively low availability of fruit. So it seems that mandrills have a flexible social system, possibly a fission-fusion type, which varies with the ecological conditions in the forest, and which is most probably influenced by food supply.

Very little is known about the ranging behaviour of either species, although all authors agree that home ranges for mandrills are likely to be very large. Sabater Pi (1972) reported two groups each containing two adult males in a joint home range of 1000 ha over five months. Jouventin (1975a) estimated ranges to be of 40 to 50 km^2 with average daily travel distances of 8 km. Based on observation, Hoshino *et al.*, (1984) estimated a range of 5 km^2 for a group of 15 individuals, and calculated minimum home range size from group size for three other groups, giving ranges up to 30 km^2. Harrison (1988) estimated the range of a single group to be 36 to 45 km^2 over nine months.

All field workers reported that mandrills, especially the adult males, were largely terrestrial, although juveniles and adult females also used the higher strata of the forest. This terrestriality was corroborated in Sabater Pi's collecting trip where 93% of captures occurred on the ground, either in traps set for catching antelope or by shooting the mothers. At Campo in 67% of sightings all observed mandrills were at less than five metres height (Hoshino, 1985). Strong terrestriality was also observed in wild drills; 70% of feeding sightings (n = 55) were at less than three metres height, and 80% of all activities in the mature forest at Idenau were at less than eight metres height (Gartlan and Struhsaker, 1972). Both species flee terrestrially (a reliable characteristic of semi-terrestrial forest primates, Struhsaker, 1969; Gartlan and Struhsaker, 1972) except when chased up trees by dogs. Mandrills and drills invariably climb up trees to sleep at night and Jouventin (1975a) reported mandrills at heights of 30 to 40 m.

Mandrills are omnivorous and eclectic feeders. Fruit constitutes the major food category and other plant parts (bark, buds, flowers, leaves, roots, stems, shoots, tubers), and invertebrates are also important (Hoshino, 1985; Lahm, 1986; pers. obs.). At Campo, mandrills ate parts of 113 species of plants. For 89% of the species the fruit and seeds were eaten. Hoshino (1985) classified mandrills as 'seed and monocotyledonous plant leaf eaters' in contrast to arboreal *Cercopithecus* monkeys which he termed 'pulp and tree leaf eaters' (p.265). Lahm's (1986) study corroborated the finding that fruit, mostly from 1 to 8 cm in diameter, was a major portion of the diet; for example 88% of dry weight of the contents of 12 stomachs consisted of fruit. Trees were the major (77%) source of fruit. Fungi and earth were also consumed (Hoshino, 1985; Lahm, 1986; pers. obs.).

Invertebrate remains (especially those of social Hymenoptera and Isoptera) were found consistently in mandrill faecal samples and stomach contents, and they probably constitute an important part of the diet. Ants, beetles, caterpillars, crabs, crickets, grasshoppers, mantids, moths, prawns, scorpions, snails, spiders, termites, and worms were preyed on (Sabater Pi, 1972; Jouventin, 1975a; Haltenorth and Diller, 1980; Hoshino, 1985; Lahm, 1986; pers. obs.). Among vertebrate prey mandrills were reported to eat tortoises, frogs, porcupines, shrews, and swamp rats as identified from remains in faecal samples (Lahm, 1986). Birds and their eggs, fish, lizards, and also medium-sized mammals such as the blue duiker (*Cephalophus monticola*), the young of the bay duiker (*C. dorsalis*) and other cephalophinae have been reported as mandrill prey by native hunters (Jouventin, 1975a; Harrison, 1988). Kudo and Mitani (1985) reported a predatory episode on a juvenile bay duiker at Campo. Although the actual attack was not witnessed, indirect evidence, such as mandrill vocalisations and a pattern of damage to the skull which matched inter-canine distances for adult mandrills, strongly suggested a predation by mandrills. Jouventin (1975a) reported that when he imitated the whistle alarm call of a duiker a mandrill approached.

Confirmed natural predators of mandrills are the leopard *Panthera pardus* and the crowned hawk eagle *Stephanoaetus coronatus*. Jouventin (1975a) observed a leopard eating a young mandrill, came across one stalking mandrills, and was shown an adult male mandrill who had been slashed, disembowelled, and partly consumed by a leopard. Harrison (1988) observed the reaction of a group of mandrills to a leopard and classified the response as one of fear towards a predator. There has been only one report of an observed attack on mandrills by a crowned hawk eagle; on a subadult male who subsequently died from wounds to the eyes and skull (illustrated in Jouventin, 1975a, p.510). Eagles also attack live mandrills caught in snares (Lahm, 1985; Harrison, 1988). It is conceivable that chimpanzees *Pan troglodytes troglodytes* hunt young mandrills and that large pythons (*Python sebae*) or vipers (*Bitis gabonica*) occasionally take small mandrills (Jouventin, 1975a, 1987; Harrison, 1988).

Mandrills in Gabon seem to be seasonal breeders (see Chapter III), as are the other diurnal monkeys, although the field evidence for reproductive seasonality is scanty. Jouventin (1975a) stated that although young mandrills could be observed as pets in villages all year round, it was very easy to obtain neonates in March. For six group counts ratios of neonates to individuals ranged from 1: 2.6 to 1: 8. Of three groups detailed by age-sex class 80%, 83%, and 40% of the females carried neonates in March, April, and June respectively. However, Jouventin's study only covered six months of the year, split over two years, so conclusions drawn from these data are tentative. In Rio Muni, Equatorial Guinea, Sabater Pi collected six suckling infants (which he classifed as being from one to three months old); two each in December and February, the others in March and June .

Associations of mandrills with other animals are shown in Table IV.8. These polyspecific associations are not of the same type as those reported for arboreal cercopithecines in Gabon which are stable over days and years (Gautier and Gautier-Hion, 1969; Gautier-Hion and Gautier, 1974). Most associations involving mandrills lasted but a few hours. The most common appears to be between mandrills, especially solitary males, and spot-nosed guenons (*C. nictitans*) (Table IV.8). Jouventin (1975a, p.513) reported seeing what he assumed was the same male mandrill with the same group of guenons for three consecutive days. Associations of groups of

Table IV.8. Reported polyspecific associations involving mandrills.

Species	Mandrill Grouping	Comments	Source
C. nictitans	not reported	6% of contacts	Sabater Pi, 1972
"	solitary and group	31% of contacts	Jouventin, 1975a
"	solitary male		Harrison, 1988
"	group		Norris, 1988
C. cephus	group	6% of contacts mandrills terrestrial	Sabater Pi, 1972
"	not reported	8% of contacts	Jouventin, 1975a
"	solitary male		Harrison, 1988
"	group		Norris, 1988
C. pogonias	solitary male	6% of contacts mandrill arboreal	Sabater Pi, 1972
"	not reported	3% of contacts	Jouventin, 1975a
"	solitary male		Harrison, 1988
L. albigena	solitary male		"
Colobus satanas	solitary male	6% of contacts mandrill arboreal	Sabater Pi, 1972
P. troglodytes	group	6% of contacts both species terrestrial	Sabater Pi, 1972
G. gorilla	group	"perhaps"	Norris, 1988
Cephalophus callipygus (Peter's duiker)	not reported	18% of contacts one or more indivs.	Jouventin, 1975a
C. monticola (blue duiker)	group	hunter's report	"
Tragelaphus sylvanicus (bush buck)	group		Norris, 1988
Potamochoerus porcus	not reported	5% of contacts	Jouventin, 1975a
Tropicranua albocristatus	not reported	13% of contacts	Sabater Pi, 1972
(white-crested hornbill)	not reported	18% of contacts	Jouventin, 1975a
Guttera plumifera (plumed guinea fowl)	group	hunter's report	"

mandrills with other guenons, chimpanzees, and with forest pigs were of short duration and assumed to be fortuitous, with both species attracted to the same fruiting tree. However, in one of the two pig-mandrill associations Jouventin reported (1975a, p.513) that he observed mandrills eating the fibrous outer coverings of palm nuts (*Elaeis guineensis*) and pigs following the mandrills and cracking the nuts to eat the kernels. Association of other artiodactyls with mandrills were relatively frequent and frugivorous duikers were reported to forage on mandrill left-overs. Jouventin speculated that an association between Peter's duiker *C. callipygus* and mandrills might be analagous to that reported between savanna baboons and impala antelope (Altmann and Altmann, 1970). However the latter association was suggested to enhance detection of predators, whereas the association involving mandrills seems more likely to be a feeding association. Jouventin recorded one instance when an alarm call given by a duiker on seeing the observer was immediately followed by alarm calls from subadult mandrills, whereupon the group fled.

Polyspecific associations involving drills are shown in Tables IV.9 and IV.10. In Cameroon, as in Gabon, arboreal cercopithecines are often in association with each other (Gartlan and Struhsaker, 1972). Drills however were infrequently observed with other species and their association was transient.

Table IV.9. Observations of polyspecific associations involving drills (from Gartlan and Struhsaker, 1972).

Site	Single species	Association	Total	Percentage in association
Idenau, mature forest	4	1	5	20.0%
S. Bakundu A, 2^{o} forest	9	2	11	18.2%
S. Bakundu B, mature and 2^{o} forest	17	4	21	19.0%
Idenau (excl. main site), mature and old 2^{o}	2	1	3	33.3%
W. Cameroon (excl. Idenau), mature	2	1	3	33.3%

Table IV.10. Species groups seen in association with drills (from Gartlan and Struhsaker, 1972).

Species	Observations
C. pogonias pogonias	1
C. nictitans martini, C. p. pogonias	1
C. erythrotis camerunensis, C. mona	1
C. n. martini, C. e. camerunensis, C. mona	2
C. n. martini, C. e. camerunensis, C. p. pogonias	2
C. n. martini, C. e. camerunensis, C. p. pogonias, C. mona	2

CHAPTER V.

RELATIONSHIPS DURING ANOESTRUS

In this chapter various types of relationship between the subadult and adult founder mandrills are described. These relationships are divided into spatial relationships, affiliative relationships, and agonistic relationships.

Various measures of spatial proximity were used to describe the position of mandrills in relation to each other. The spatial relationship of individuals can be thought of as resulting from a balance of factors attracting the individuals to each other and factors repelling them. Thus indices of these two factors were also measured. Attractive force - affiliation - was measured by grooming behaviour and repulsive force by agonistic behaviour.

SPATIAL RELATIONSHIPS

Data about proximity were collected during focal samples in Part 2 of the study (see Chapter II). At point samples every minute the identity and distance of every founder individual within 5 m of the focal individual was recorded. Within 5 m, distance categories were divided as follows: I: 0-1 m, within arm's length; II: 1-2 m, just outside arm's length; and III: 2-5 m. At point samples every five minutes the identity of founders at IV: 5-10 m was recorded. This category represented distances greater than 5 m, and 10 m was the limit of reliable visibility (see Chapter II). For each individual, the number of times it was recorded at a particular distance was divided by the total number of point samples for that focal animal. This figure was then converted to a percentage to give the percentage of point samples at a particular distance category. Percentage point samples is taken to represent and to be proportional to percentage time spent at a particular distance category. The number of focal samples and the total number of point samples in each category are given in Appendix V.1.

The four distance categories can be represented as a series of concentric rings round the focal individual. The area in which another individual could be found was greater the larger the distance category. If distance scores were simply added together across distance categories, those from the larger categories would outweigh the contribution of the scores from the smaller distance categories. Additionally, being within arm's length of another individual is probably a stronger indication of affiliation than being at 5 m distance. For this reason I decided to weight the proximity scores such that distance category I > II > III > IV. Following Smuts (1985) the reciprocal of the mid-point of the distance was used as a weighting factor. The percentage score was multiplied by this factor (see Table V.1).

The method of calculating the composite proximity score is shown in Table V.2 using proximity data collected in focal samples on Female No. 5 when she was lactating. The data are shown for two individuals, Female No. 2 and Male No. 15. The score was the percentage of point samples in which each mandrill was present at a given distance category. Each score was multiplied by the weighting factor for that distance, and then the weighted scores for all four distances were summed to produce the mandrill's composite score. To obtain a general measure of sociability, for each focal individual the composite scores of the 13 other founder mandrills were summed to produce a sociability index. The higher the number the more 'sociable' the focal individual.

Data for males were categorised into two sets. One in which the data were collected on days when there was no oestrous female in the group, the other from days on which a female was in oestrus. These data were analysed separately and the latter data set will be examined in the following chapter. The proximity measures for males presented below are based on analyses of 6,764 point samples. For females the data

Table V.1. Weighting Scores

Distance category	Distance category limits (m)	Mid-point	Reciprocal of mid-point
I	0 - 1	0.5	2.0000
II	1 - 2	1.5	0.6667
III	2 - 5	3.5	0.2857
IV	5 - 10	7.5	0.1333

Table V.2. Calculating composite proximity score for Female No. 5 when lactating

		Female No. 2		Male No. 15	
Distance category	Weighting factor	Score	Score x Wt. factor	Score	Score x Wt. factor
I	2.000	4.93	9.86	0.00	0.00
II	0.667	2.67	1.78	0.62	0.41
III	0.286	12.53	3.58	4.72	1.35
IV	0.133	8.57	1.14	14.29	1.90
C score			16.36		3.66

were divided by reproductive state - pregnant, lactating, and oestrus. These data were also analysed separately and data on oestrous females will be presented in Chapter VI. The proximity measures for females described below are based on analyses of 7,970 point samples (pregnant 4,972; lactating 2,998). Thus, the data presented below describe spatial relationships during periods of anoestrus, which is the state in which female mandrills spend most of their lives.

Planned comparison t-tests were used to test for differences between males and females. One-sample t-tests were used within sex to see if the alpha individual was different from the others. Paired t-tests were used to test for differences between reproductive states within individuals. Spearman rank order correlations were used to test whether the rank sociability, proximity, etc. correlated with dominance within each sex. The Spearman statistic was not reported if there was more than one tie. Since the alpha individual was predicted to differ from others the Spearman correlations were done in two ways: (a) excluding the data of the alpha individual and (b) with this individual's data included. All probabilities were two-tailed and alpha was set at 0.05. In all figures and tables mandrills are shown in order of decreasing dominance rank within sex.

Due to the small number of individuals the Spearman coefficient rarely reached statistical significance. No significance level was reported with an n less than five. However, calculation of the coefficient of determination (r_S^2) indicates the variance in one measure which is accounted for statistically by the variation in the other (Martin and Bateson, 1986). Hence, for an $r_S = 0.70$, nearly 50% of the variance in one set of scores is accounted for statistically by variation in the other ($r_S^2 = 0.49$). This degree of relationship may have biological significance even if small sample sizes preclude the achievement of statistical significance. Furthermore, as Harcum (1989) emphasized, it is important to differentiate between the magnitude of an effect, and its associated probability value, which provides a measure of confidence that we are dealing with a nonchance phenomenon.

General sociability

The sociability indices for males are illustrated in Figure V.1. The mandrills are shown in order of decreasing dominance, as stated above, with the exception of Male No. 3. He held the second dominance rank but is shown at the end because no other founder mandrill was recorded in 92% of his point samples at <5 m or in 88% of point samples at 5-10 m. These data provided further confirmation of his solitary status, described in Chapter II. His data were excluded from all further analyses.

It is readily apparent in Figure V.1 that Male No. 7, the alpha male, had the highest index. He was significantly more sociable than the other males (58.2 vs. mean = 21.7, $t = 15.736$, $df = 4$, $p < 0.001$) and their scores averaged only 37% of his score. Male 14's index was low. He was the next most mature and biggest male after No. 3 and seemed to be becoming increasingly solitary at the time these data were collected. Excluding Males 3 and 7, there was a nonsignificant but strong negative correlation of sociability with dominance rank ($r_S = -0.70$, $n = 5$, NS) with subordinate males having higher indices, indicating that they were more sociable than more dominant males.

Figure V.2 illustrates the sociability indices for the female mandrills at times when they were pregnant and lactating. Females were significantly more sociable than males, both when pregnant (64.2 vs. 27.7, $t = 3.834$, $df = 10$, $p < 0.01$) and when lactating (76.0 vs. 27.7, $t = 3.129$, $df = 9$, $p < 0.02$). On average female indices were 2.5 times higher than those of males. In comparison to the position of the alpha male in relation to other males, the alpha female (No. 2) was not significantly different from other females (pregnant: $t = 2.268$, $df = 4$, NS; lactating: $t = 0.352$, $df = 3$, NS) although her index was higher than that of the average of the other females in both

Figure V.1. Sociability indices of male mandrills

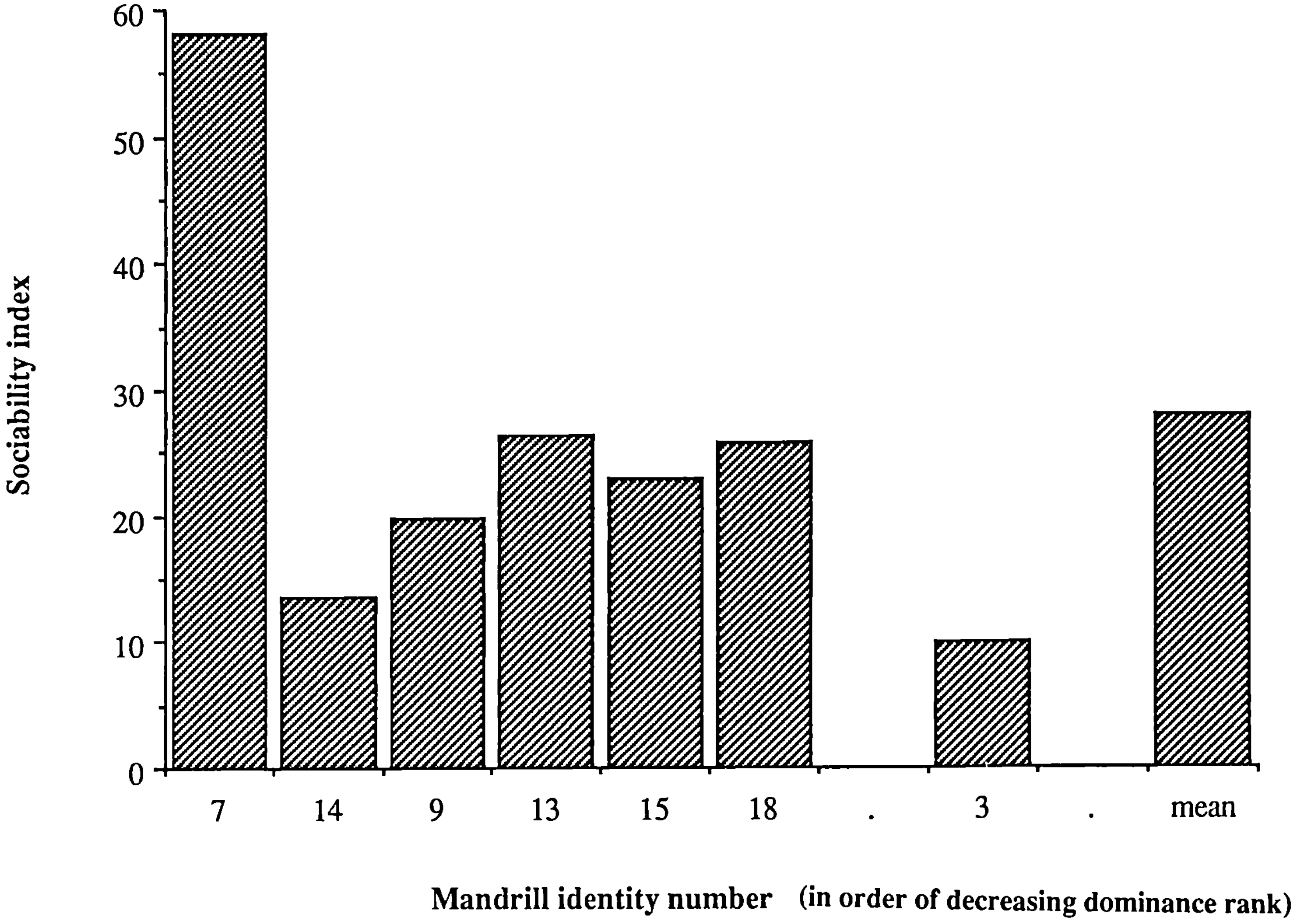
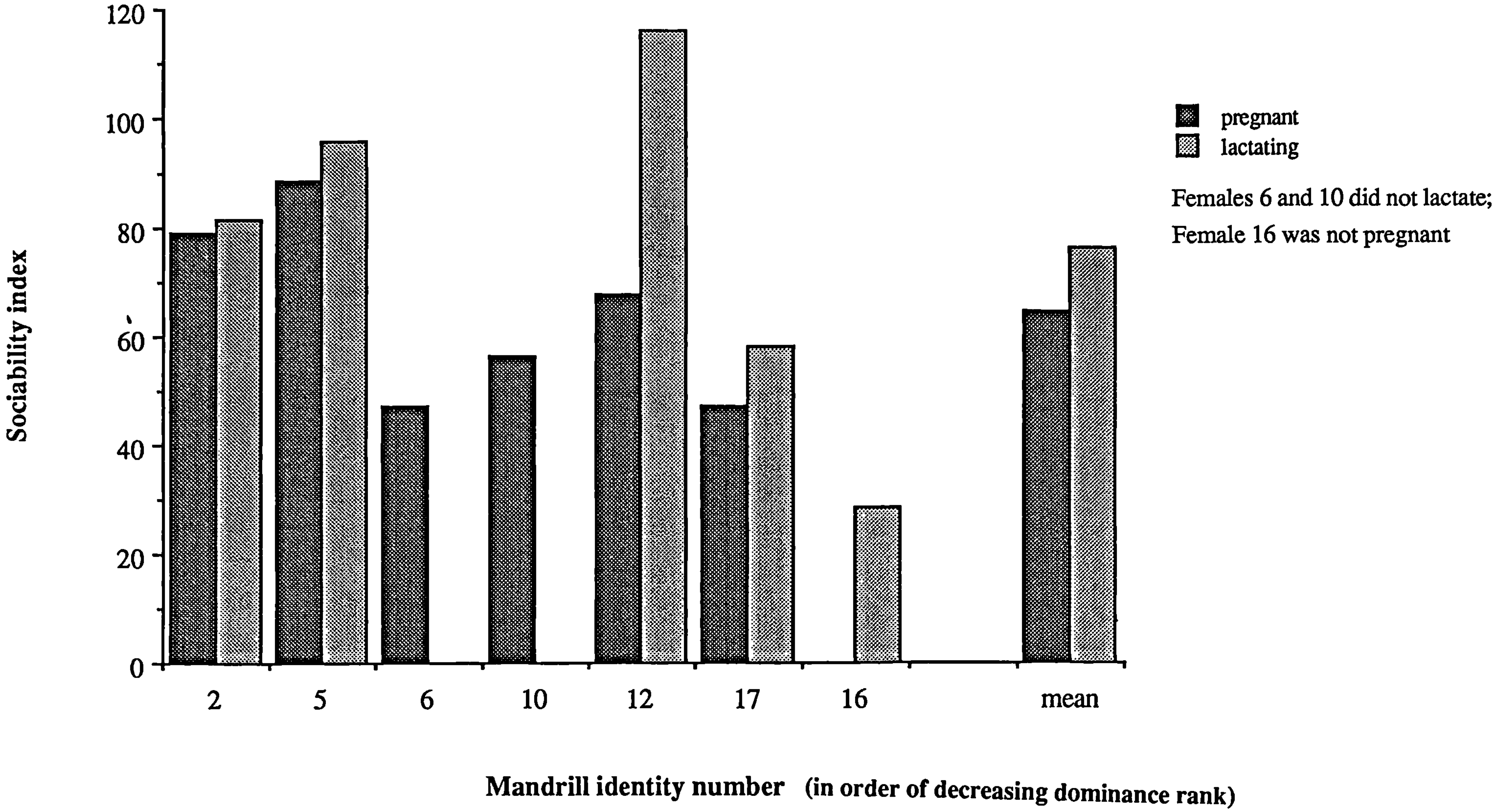


Figure V.2. Sociability indices of female mandrills when pregnant and lactating



Females 6 and 10 did not lactate;
Female 16 was not pregnant

reproductive states (pregnant: 79.0 vs. mean = 61.2; lactating: 81.5 vs. mean = 74.6). There were no clear trends with dominance in either reproductive state (pregnant: r_s = 0.64, n = 6, NS; lactating: r_s = 0.60, n = 5, NS). The most subordinate female (No. 16) had the lowest sociability index (Figure V.2). For all four females for whom there were comparable data, the sociability index was higher when they were lactating (mean = 87.9) than when pregnant (mean = 70.5, Figure V.2) but the difference in the indices was not significant (t = 1.650, df = 3, NS).

In order to examine in more detail the spatial relationships between individuals, the 0-5 m distance categories were examined separately. The analyses reported below used the unweighted percentage scores.

In some cases particular individuals were never recorded within a specific distance category in relation to a focal individual, i.e., their score was 0% of the possible point samples. These 0% scores were termed 'empty slots'. In relation to each founder focal individual there was a total of 13 possible empty slots at each distance category. For example, in relation to a focal female there were potentially six female empty slots and seven male empty slots. Analysis of these empty slots is described overleaf and in Table V.3. Empty slots were powerful measures of absence, since, for example, an average of 66% empty slots meant that on average two-thirds of individuals of a specified sex were NEVER recorded at that distance from a focal animal; 100% empty slots meant that no mandrills of that sex were ever recorded at that distance. Mean percentage empty slots also showed the general use of a distance category by members of a specified sex and allowed comparisons of spatial relationships between males and females.

To assess whether dominance rank correlated with proximity, Spearman rank correlations of rank proximity score (percentage time) and dominance rank were done for distance categories where on average < 33% of slots were empty and there was no

Calculation of empty slots

In relation to each focal female there was a total of six males who could spend some or no time in close proximity at 0-1 m. Column M in Table V.3. below shows the number of males who were never recorded at 0-1 m from each focal female. Column E gives this number expressed at a percentage of a possible six males. The individual identity of these males may vary between females but over all pregnant females on average nearly half the males (mean = 44%) were never within a metre of a pregnant female.

Table V.3. Calculation of empty slots. Proximity of males at 0-1 m in relation to focal pregnant females

Focal female	Male ID						M No.males never seen i.e., score 0% time (i.e. no.empty)	E % empty (of 6)
	7	14	9	13	15	18		
2	7.3	0	0	0.29	0.14	0	3	50
5	0.22	0	0.22	0.22	1.12	0	2	33
6	0	0	0	0	0.1	0	5	83
10	3.68	0	0.86	0	0	0.25	3	50
12	0.21	0.21	0.21	0.21	0.43	0	1	17
17	0.31	0	2.65	0	0.47	0.62	2	33
							mean =	44

more than one tie. Since the alpha individual was predicted to differ from others the Spearman correlations were done in two ways: (a) excluding the data of the alpha individual and (b) with this individual's data included.

Relationships of Pregnant females.

The data from a total of 259 focal samples on six pregnant females (Nos. 2, 5, 6, 10, 12, and 17) are reported below.

A) Female - Male Proximity

In examining the proximity data for pregnant females, the following questions were considered.

> In relation to pregnant females, is the alpha male extreme among males in his proximity?
>
> Does the dominance rank of males influence their spatial proximity to pregnant females?

a) At 0-1 m, over the six pregnant females an average of 44% of male slots was empty (Table V.4 and Figure V.3) - i.e., nearly half the males were never within a metre of a pregnant female. The alpha male had the extreme high score in only two of the six females.

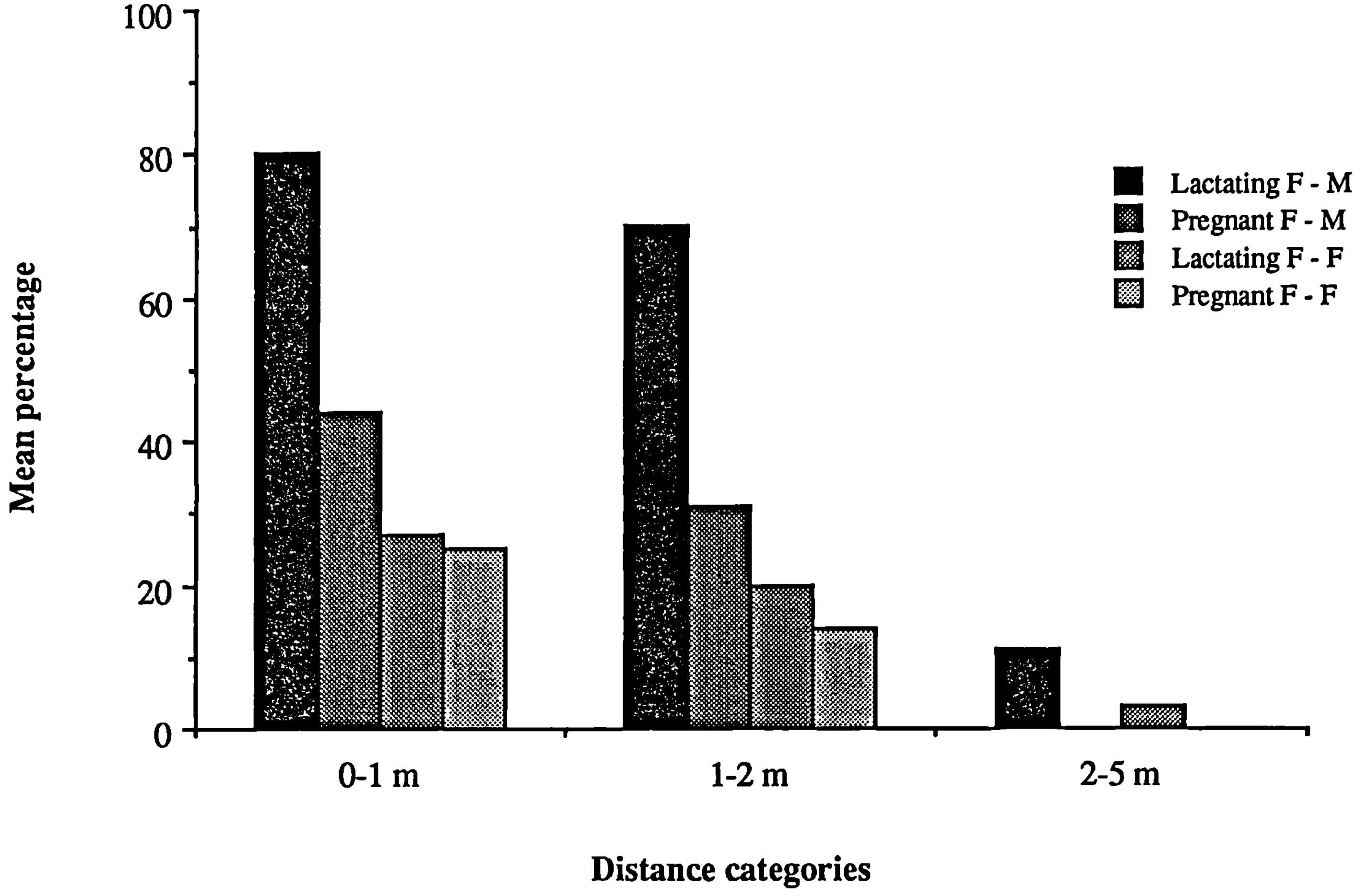
b) At 1-2 m on average two-thirds of the males were recorded at this distance (Table V.4 and Figure V.3), although they generally spent less than 1% of the time there. In four of the females the alpha male had the extreme (high) score.

c) There were no empty slots at 2-5 m, indicating that all males spent some time at this distance from a pregnant female, although on average males only spent about 5% of the time near females. For five females the alpha male had the highest score, i.e., he spent the greatest percentage of time near the female. Among other males nonsignificant

Table V.4. Mean percentage empty slots in relation to focal females

	0-1 m	1-2 m	2-5 m
Pregnant female - male			
No. 2	50	50	0
No. 5	33	33	0
No. 6	83	50	0
No. 10	50	33	0
No. 12	17	17	0
No. 17	33	0	0
Mean	44	31	0
Pregnant female - female			
No. 2	17	17	0
No. 5	0	33	0
No. 6	17	0	0
No. 10	0	0	0
No. 12	33	17	0
No. 17	83	17	0
Mean	25	14	0
Lactating female - male			
No. 2	83	67	50
No. 5	83	50	17
No. 12	83	67	0
No. 17	83	83	0
No. 16	67	83	0
Mean	80	70	11
Lactating female - female			
No. 2	17	33	17
No. 5	17	17	0
No. 12	0	17	0
No. 17	17	33	0
No. 16	83	50	0
Mean	27	20	3

Figure V.3. Mean percentage empty slots for focal females



negative correlations with dominance (median $r_S = -0.61$, $n = 5$, NS, Table V.5) for five of the six females indicated a tendency for subordinate males to spend more time in proximity to pregnant females than more dominant males. Inclusion of the data of the alpha male substantially changed the correlations (Table V.5) because his extreme high scores were in the opposite direction of the general trend for time in proximity to increase with decreasing dominance rank.

Summary

The overall picture of the spatial relationship of males in relation to pregnant females is one in which males were rarely within arms' length (<1 m) of pregnant females. Even at greater distances males rarely spent more than a small percentage of their time near pregnant females. The alpha male spent markedly more time near pregnant females than did other males; in 11 of the 18 cases (61%) he spent the most time in proximity. This skew increased with distance, i.e., the greater the distance from the focal animal the more likely it was that he had the extreme score.

B) Female - Female Proximity

Similar questions were asked about relationships between females.

> Is the alpha female extreme in her proximity to pregnant females?
>
> Does dominance rank influence spatial proximity of females to pregnant females?

Empty slots occurred less than 25% at all distance categories (Table V.4 and Figure V.3) indicating that females were generally close to each other; most females spent some time within two metres of a pregnant conspecific and all females spent some time at 2-5 m of a pregnant female.

Table V.5. Spearman rank correlations between dominance rank and rank spatial proximity

Distance:	0-1 m		1-2 m		2-5 m	
Alpha:	Excl.	Incl.	Excl.	Incl.	Excl.	Incl.
	n = 5	n = 6	n = 5	n = 6	n = 5	n = 6
Pregnant female - male						
No. 2	Δ	-	Δ	-	**-0.93Δ**	-0.10
No. 5	-	-	**0.77Δ**	**0.93***	0.10Δ	0.49
No. 6	-	-	Δ	-	-0.43Δ	0.24
No. 10	Δ	-	Δ	-	-0.63Δ	0.07
No. 12	-	-	-	-	**-0.93Δ**	-0.10
No. 17	-	-	-0.30	-0.36	-0.60	-0.43
Pregnant female - female						
No. 2	0.17	0.64	**0.70**	0.60	**0.70**	**0.77**
No. 5	**0.70**	0.13	-	-	0.20	0.10
No. 6	**0.70**	0.66	**0.97**	0.64	0.30	0.60
No. 10	-0.63	-0.36	-	Δ	0.30	-0.03
No. 12	-	Δ	-0.03	-0.44	0.30	-0.26
No. 17	-	-	-	-	-0.30	-0.60
Lactating female - male						
No. 2	-	-	-	-	Δ	-
No. 5	-	-	-	-	**-0.93Δ**	-0.10
No. 12	-	-	-	-	-0.57Δ	0.27
No. 17	-	-	-	-	**-0.93**	-
No. 16	-	-	-	-	**-0.77Δ**	**-0.94***
Lactating female - female						
No. 2	0.20	0.37	-	-	0.40	0.66Δ
No. 5	**0.70**	0.66	-	-	0.30	0.60Δ
No. 12	0.60	0.49	0.40	0.37	0.60	0.20
No. 17	0.00	0.03	-0.07	-0.09	-0.30	-0.26
No. 16	-	-	-	-	-0.30	-0.60Δ
Male - anoestrus female (n = 6, n = 7)						
No. 7	-	-	-	-	**0.71**	**0.79***
No. 14	-	-	-	-	-0.09	-0.11
No. 9	-	-	-	-	-0.54	-0.57
No. 13	-	-	-	-	0.31	0.36
No. 15	-	-	-	-	-0.37	-0.07
No. 18	-	-	-	-	-0.43	-0.64Δ
Male - male (n = 4, n = 5)						
No.7	-	-	-	-	**-0.80Δ**	**-0.90**
No. 14	-	-	-	-	-0.40Δ	**-0.70**
No. 9	-	-	-	-	**-0.80**	**-0.80**
No. 13	-	-	-	-	0.00	0.10
No. 15	-	-	-	-	**-0.80Δ**	0.10
No. 18	-	-	-	-	0.60	0.10

No rs reported when > 33% slots empty or > 1 tie. Δ alpha individual extreme
Coefficients in bold type are those accounting for at least 50% of the variance (see text)
* $p < 0.05$ Mandrills presented in order of decreasing dominance rank within sex

a) At <1 m the alpha female had an extreme high score for only one of the five focal females. For Females 5 and 6, strong correlations of rank time in proximity with dominance rank (r_S = 0.70, n =5, NS) indicated that more dominant females spent more time in proximity to them than did subordinates. Inclusion of the alpha female weakened most correlations (Table V.5).

b) At 1-2 m the alpha female was not extreme and there were no consistent trends with dominance. In two females there were strong positive nonsignificant correlations of time in proximity with dominance (Table V.5).

c) At 2-5 m the alpha female did not have extreme scores and there was no relation of dominance and spatial proximity, with one exception. Only for the alpha female was there a strong nonsignificant correlation (r_S = 0.77) indicating that other dominant females spent more time near her than did subordinate females.

Summary

An overall view of spatial relationships between females indicates that although pregnant females were more sociable with other females than they were with males (see the comparison in Figure V.3), the association of pregnant females with males and females was similar in that both sexes spent similarly small proportions of time (about 1%) in very close proximity (< 1 m) to them. The alpha female did not have extreme values, in contrast to her male counterpart. Correlations between dominance rank and proximity seemed to depend on the rank of the focal female.

Relationships of Lactating females.

The data from 159 focal samples on five lactating females (Nos. 2, 5, 12, 17, and 16) are reported below.

A) Female - Male Proximity

The data were examined to see whether the dominance rank of a male could be used to predict spatial relationships with lactating females.

Does the alpha male hold an extreme position with males with relation to spatial proximity to lactating females?

Does male dominance rank influence spatial proximity of other males to lactating females?

Do spatial relationships of males and lactating females differ from those of males and pregnant females?

a) At <1 m there were on average twice as many empty male slots (80%) for lactating females than for pregnant females (44%) (see Table V.4 and Figure V.3). When this comparison was restricted to those females (n = 4, Nos. 2, 5, 12, and 17) for whom data were available for both reproductive states, the comparison was 33% versus 83%. This indicated that most males were very rarely near females with young infants.

b) The situation was similar at 1-2 m (see Figure V.3) with 70% empty as opposed to 31% during pregnancy (25% versus 67% for the four females recorded in both reproductive states).

c) At 2-5 m on average a tenth of the slots were empty. In four of the five females the alpha male had the extreme score. In the three most dominant females the score was high, i.e., he spent more time close to them than did other males, but for the most subordinate female he had the extreme low score. In all cases there was a strong negative correlation with dominance among the other males (median $r_S = -0.85$, $n = 5$, NS), i.e., subordinate males spent more time close to lactating females than did more dominant males (Table V.5). However this relationship was not statistically significant.

Summary

The overall picture of spatial relationships between lactating females and males was one in which females with infants were 50% less likely to be in proximity to males than were pregnant females. On average males were near lactating females only 2% of the time. The alpha male had an extreme value for most females, but whether this was extremely high or low seemed to depend on the dominance rank of the female.

B) Female - Female Proximity

Female spatial relationships were examined as follows:

Is the alpha female extreme in her proximity to lactating females?

Does female dominance rank predict spatial relationships of females to lactating females?

Do female - female spatial relationships differ between pregnancy and lactation?

At all distance categories most females (>66%) spent some time near females with small infants (Table V.4 and Figure V.3).

a) At <1 m the alpha female never had an extreme score and there were no significant correlations with dominance although all the correlations were positive (Table V.5). Female 12 had the highest score in each case. On average females spent more time (4%) very close to lactating females than to pregnant females (1%).

b) At 1-2 m a similar situation occurred with no trends relating to dominance. Females spent little time (about 2%) near lactating females, but more than when pregnant (<1%).

c) At 2-5 m dominance seemed to predict proximity. For the two highest-ranking females proximity scores correlated strongly and positively with dominance, suggesting that dominant lactating females spent time together (Table V.5). For the most subordinate female the correlation was strongly negative indicating that she spent time near other subordinate females. Correlations in the two intermediate females were weak (Table V.5) but their directions were consistent with the above, i.e., the correlation of the more dominant female of the two had a positive sign, the more subordinate a negative one. On average females spent less time at this distance from lactating mothers (7%) than they did from pregnant females (9%).

Summary

In general the amount of time females spent near other females depended on whether those females were pregnant or lactating. When females were lactating the time was greater at small distances but similar at greater distances. There was an absence of strong correlations of rank time in proximity with dominance rank in relation to lactating females, suggesting that relationships between mothers of small infants were perhaps less structured around dominance status than they were around individual preferences. For example, as mentioned above, Female 12 (rank 5) had the highest score for proximity in relation to each of the five lactating females. It was noticeable that females of very disparate ranks associated more when they both had small infants than they did at other times. This association was often initiated by the more dominant female approaching to look at and sit near a more subordinate female with a young baby, e.g., Female 5 (rank 2) approached and was very interested in Female 12 (rank 5) and Female 17 (rank 6) after their infants were born. Some examples of interactions between mothers, which show the relaxed and intimate contact between females with very young infants, are given below.

17 March 1987
1512: Female 6 approaches lactating Female 17 to <1 m, touches her one-month old infant daughter 17B and then grooms 17 briefly.
1513: 17 walks away after Female 6 touches 17B again and she geks in alarm.
1518: Female 12 and her two-month old infant 12D approach 17 to <1 m, then 12 grooms 17. 17 forages while 12 grooms her
1519: 12's adolescent daughter 12A approaches the duo to <1 m and handles 17B.

1520: 12D climbs above 17.
1521: 12A moves to 3 m, 17 handles 12D. 12D and 17B play together.
1522: Female 12 picks up 17B; Female 5, carrying two-month old infant 5C, approaches and muzzle-kisses 17 then touches 17B.
1532: Female 17 moves away with 17B ventral.

25 March 1987
0905: Female 12 (with infant 12D) is grooming her adolescent daughter 12A, Female 17 sits at <1 m and Female 10 sits at 3 m.
0906: Female 12 approaches 17 to contact.
0907: 12 picks up and walks off withs 17B, 17 appears unconcerned. Female 10 approaches 12 to contact and cuddles 12D.

1445: Female 12 approaches 17+17B and picks up and walks off with 17B, 17 appears unworried.
1448: 12D and 17B play on and near Female 12.

1503: Female 12+12D approaches 17+17B to 1 m. 12D and 17B climb on 12's head. 17 moves to 2 m.
1505: 12 picks up and walks off with 17B, Female 17 appears unconcerned.

Relationships of Males

The data from 297 focal samples on six males (Nos. 7, 14, 9, 13, 15, and 18) on days in which no female was in oestrus are described below.

A) Male - Male Proximity

Similar questions about the effects of dominance on proximity of individuals to focal males were examined.

Is the alpha male extreme in his proximity to other males?

Does male dominance rank predict spatial proximity between males?

a) At 0-1 m an average of 80% of the male slots were empty (Table V.6 and Figure V.4) indicating that most males were never recorded very close to another male.

b) At 1-2 m the situation was similar with most males (73%) never recorded at this distance from another male (see Table V.6 and Figure V.4).

c) On average all males spent some time 2-5 m from another male. For half the males the alpha male had the extreme score. When the alpha male was the focal subject the next most dominant group male (No. 14) spent the least time in proximity to him. In relation to Male 14's focal data, Male No. 7 spent the least time in proximity to him. This may have been an indication of male-male avoidance since 14 was the next biggest male in the group, excepting the solitary male. Male 7 had the extreme high score in relation to Male 15.

Summary

In general males spent little time together. They were hardly ever within two metres of each other and on average spent only 3% of time at 2-5 m.

B) Male - Female Proximity

The data below describe spatial relationships between males and females who were anoestrus (i.e., they were pregnant and/or lactating).

Similar questions concerning the role of dominance were framed

Is the alpha female extreme in her proximity to males?

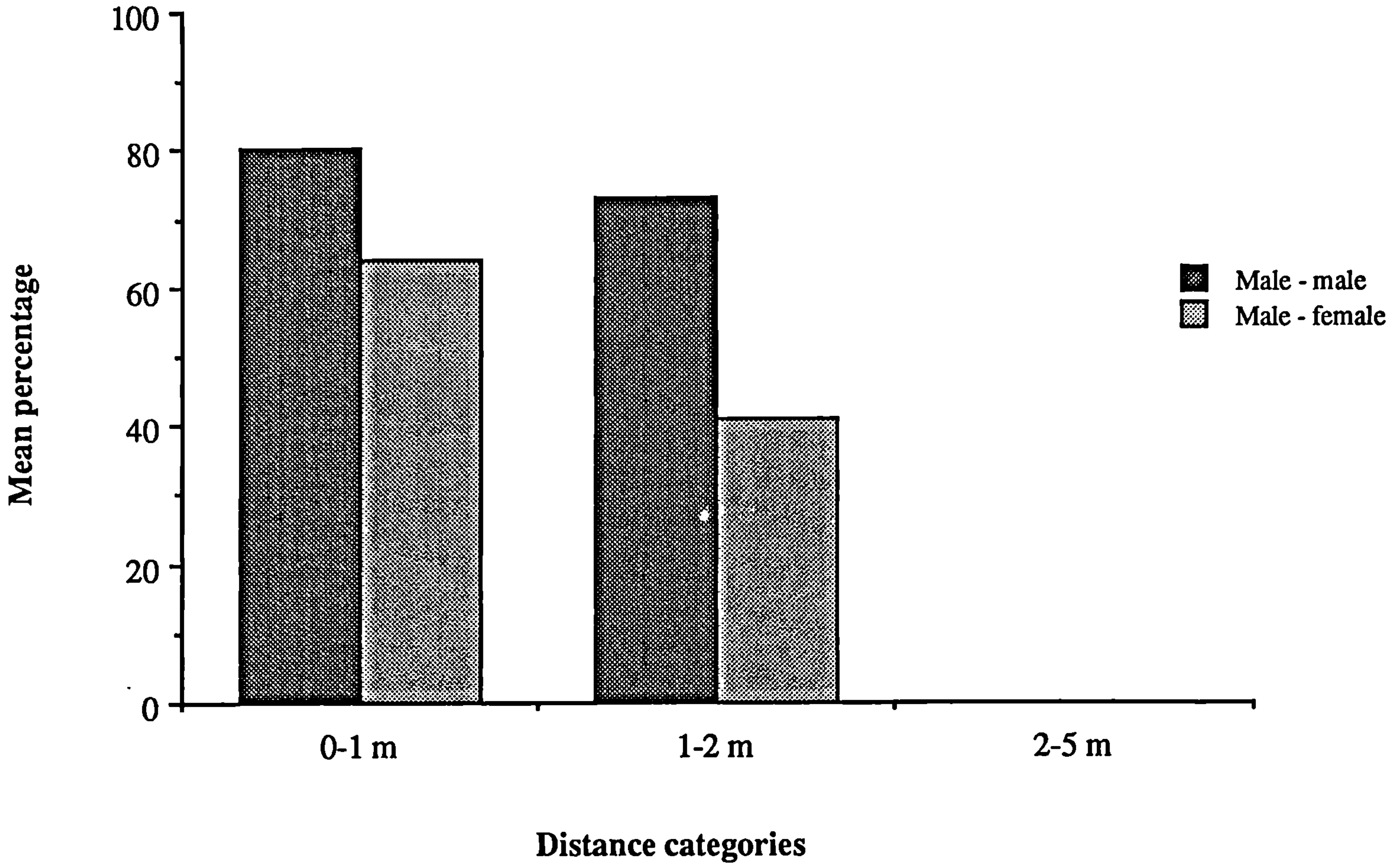
Does female dominance rank predict the proximity of anoestrous females to males?

a) At <1 m an average of over two-thirds of the slots were empty, i.e., most

Table V.6. Mean percentage empty slots in relation to focal males

Identity	0-1 m	1-2 m	2-5 m
Males - anoestrous females			
No. 7	29	29	0
No. 14	86	43	0
No. 9	43	29	0
No. 13	71	57	0
No. 15	86	57	0
No. 18	71	29	0
Mean	64	41	0
Males - males			
No. 7	80	60	0
No. 14	100	100	0
No. 9	80	80	0
No. 13	40	40	0
No. 15	100	60	0
No. 18	80	100	0
Mean	80	73	0

Figure V.4. Mean percentage empty slots for focal males



anoestrous females were never recorded in close proximity to focal males (Table V.6 and Figure V.4). The alpha male was extreme in having fewer empty slots (29%) than the other males (mean = 71%).

b) At 1-2 m 41% of the female slots were empty indicating that on average just under half the females were never recorded at this distance from a male.

c) At 2-5 m on average all anoestrous females spent some time within 5 m of a male. The alpha female was not extreme among females in her proximity to males. For the alpha male only there was a strong positive correlation ($r_S = 0.71$, $n = 6$, NS) between female dominance rank and proximity (irrespective of whether or not the alpha female was included, Table V.5), such that more dominant females spent more time close to him than did subordinate females. For the other males correlations with dominance were negative and/or weak (Table V.5).

Summary

In general there was little close proximity between males and females. Females spent more time close to the alpha male (mean = 6%) than to other males (mean = 2%) and there was a perfect positive correlation with rank total time all females spent near (2-5 m) a male (excluding No. 7) and his dominance rank ($r_S = 1.00$, $n = 5$, $p < 0.05$).

Conclusions

In relation to spatial proximity of males to both pregnant and lactating focal females, the alpha male was extreme among males and spent the most time near founder females. In contrast, in relation to proximity of females to other focal females, the alpha female was not extreme among females. With reference to spatial proximity to focal males, the alpha female was not extreme and female dominance rank did not predict spatial relationships between anoestrous females and focal males. There were no consistent correlations between male dominance and spatial proximity to focal males.

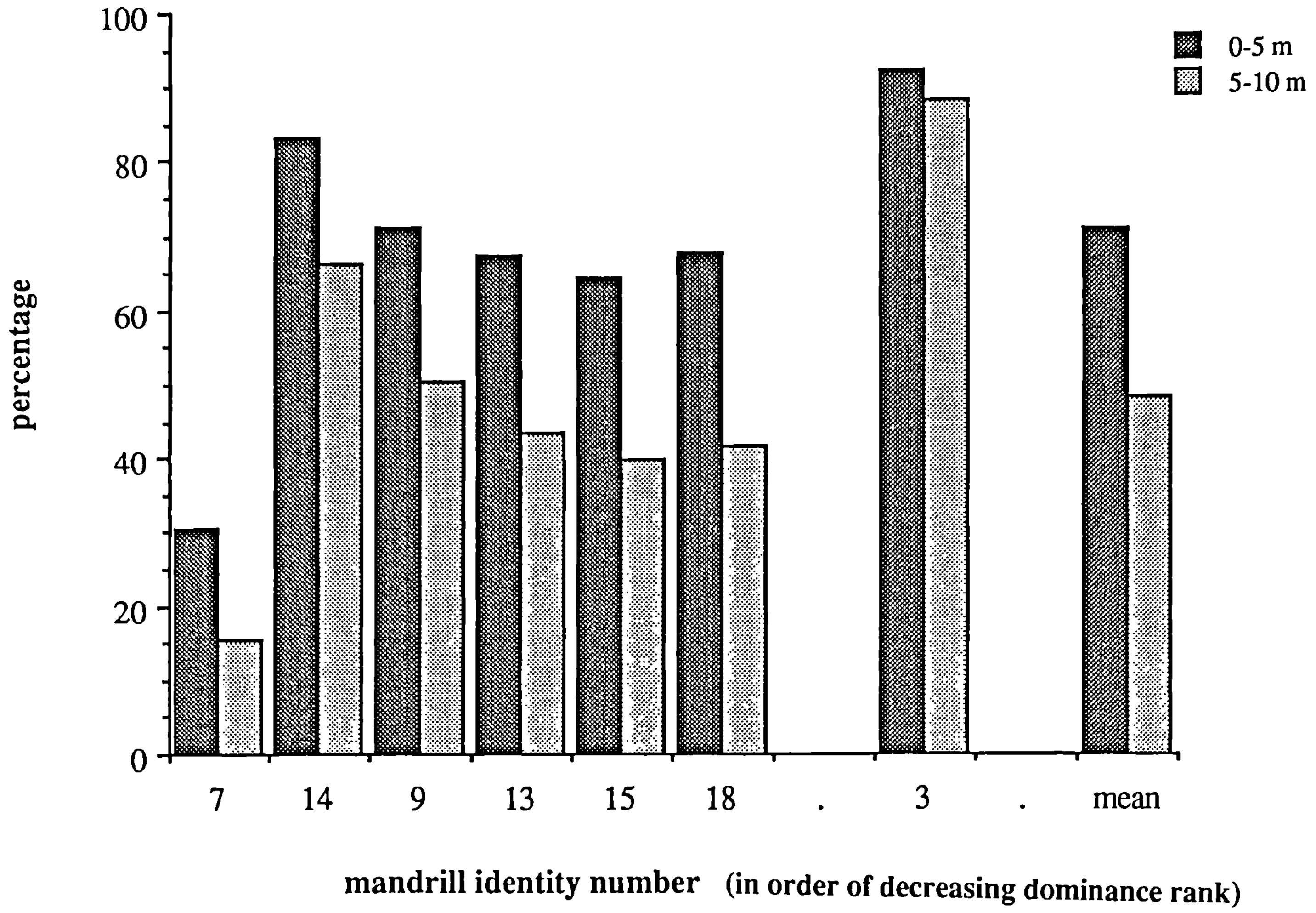
In general the above information suggests that mandrills, particularly males, do not spend much time in close proximity to each other. However, the above analysis was based on individual records in relation to a focal individual, i.e., how much time (proportion of point samples) a particular individual spent within 5 m of a specified other focal individual. In other words the spatial data presented above were based on a dyadic analysis of relationships. The fact that, for example, Female 17 was near Female 2 for only 7% of the time, did not mean that Female 2 was without neighbours. In order to get a more general measure of dispersion, measures of absence were analysed.

For each individual the number of point samples in which no other founder mandrill was recorded in proximity was summed and divided by the total number of point samples. This figure was then converted to a percentage to give the percentage time a focal individual had no founder neighbours at a certain distance category. The categories were combined to give two measures - 0-5 m and 5-10 m.

Planned comparison t-tests were used to test for differences between males and females. One-sample t-tests were used within sex to see if the alpha individual was different from the others. Spearman rank order correlations were used to test whether the rank percentage time with no neighbours correlated with dominance rank within each sex. The Spearman statistic was not reported if there was more than one tie. Since the alpha individual was predicted to differ from others the Spearman correlations were done in two ways: (a) excluding the data of the alpha individual and (b) with this alpha individual's data included. All probabilities were two-tailed and alpha was set at 0.05. In all figures mandrills are shown in order of decreasing dominance rank within sex. Male No. 3 was excluded from analysis.

Male mandrills. Figure V.5 shows the percentage time with no neighbours of male mandrills. The second ranking male is shown at the end. It is clear that the

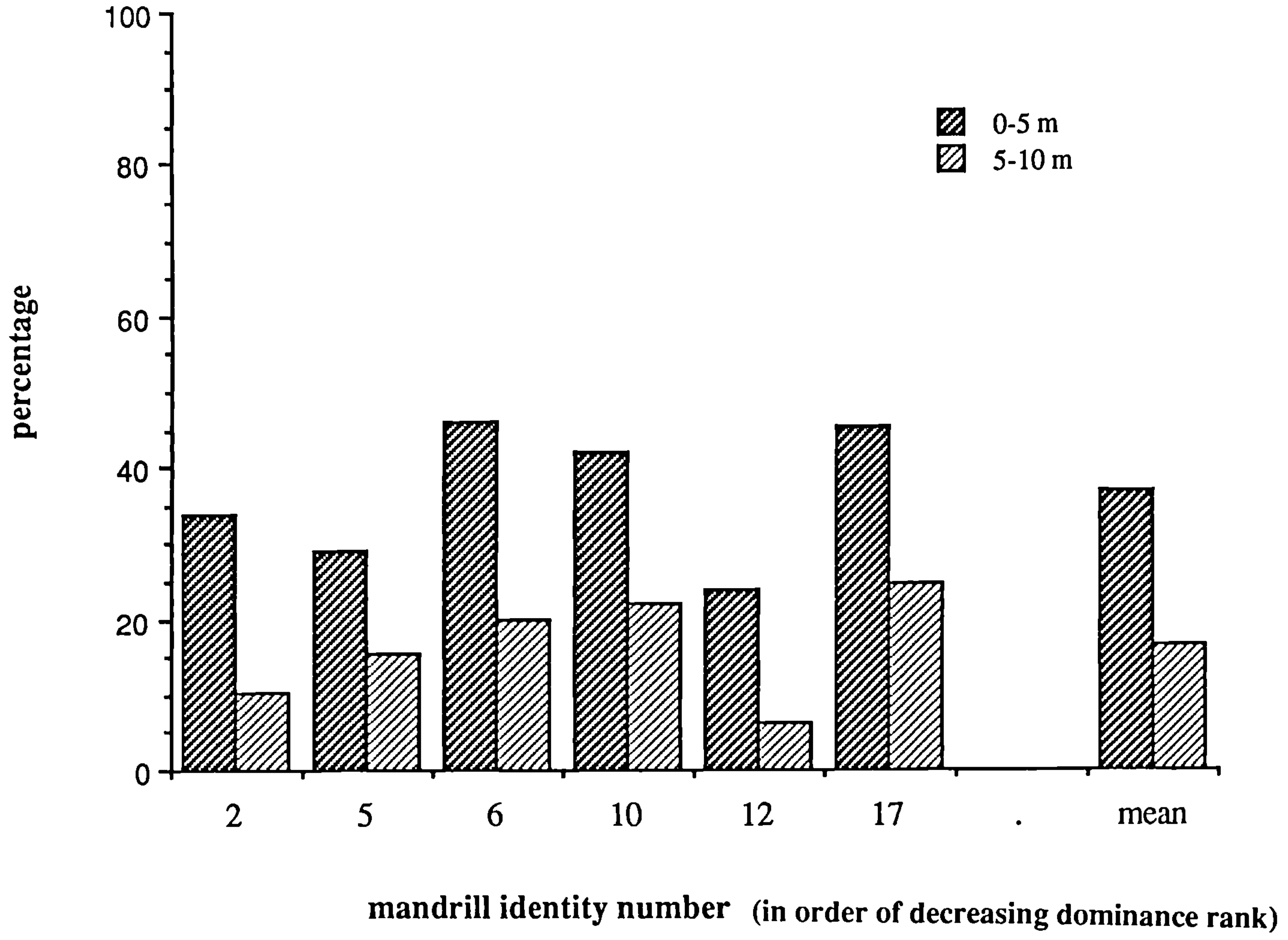
Figure V.5. Percentage time with no neighbours in male mandrills



alpha male, No. 7, had the lowest percentage at both distance categories, indicating that he was without neighbours on significantly fewer occasions than other males (0-5 m: t = 12.730, df = 4, $p < 0.001$; 5-10 m: t = 6.840, df = 4, $p < 0.01$). At the 0-5 m category he was over twice as likely to have no neighbours than other males (No. 7 vs. other males 30.5% vs. 70.6%) and at the 5-10 m category he was three times as likely (15.4% vs. 48.3%). It is also shown in Figure V.5 that Male No. 3, the solitary male, had the most time with no neighbours. Additionally the next male, No. 14 (rank 3), was the next most extreme. This was perhaps an indication of impending peripheralisation. It was certainly my impression that Male 14 spent progressively less time with the group and interacted less with individuals during the course of the study. I predict that he will become solitary. In all males there were fewer point samples with no neighbours at the larger (5-10 m) distance category than at 0-5 m. Among males of rank 3 to 7 (Nos. 14 to 18) at both distance categories there was a strong correlation of dominance rank with rank percentage time with no neighbours (0-5 m: $r_S = 0.70$, n = 5, NS; 5-10 m: $r_S = 0.90$, n = 5, NS) indicating that more subordinate males spent less time alone than more dominant males.

Pregnant female mandrills. Figure V.6 shows the percentage time with no neighbours in female mandrills when they were pregnant. Females spent markedly less time alone than did male mandrills. At 0-5 m females had half the time alone (36.7%) than did males (64.1%) and this sex difference was significant (t = 3.375, df = 10, $p < 0.01$). The same pattern was seen at 5-10 m with males spending nearly three times as much time with no neighbours (42.8%) than females (16.5%) (t = 3.369, df = 10, $p < 0.01$). As can be seen in Figure V.6 the alpha female, No. 2, was not consistently different from other females at either distance category. At 0-5 m she had no neighbours a third of the time (33.9%), slightly less than other females (mean = 37.2%) but this small difference was not significant (t = 0.713, df = 4, NS). At 5-10 m a similar pattern was evident, with Female 2 having slightly fewer samples with no

Figure V.6. Percentage time with no neighbours in pregnant female mandrills



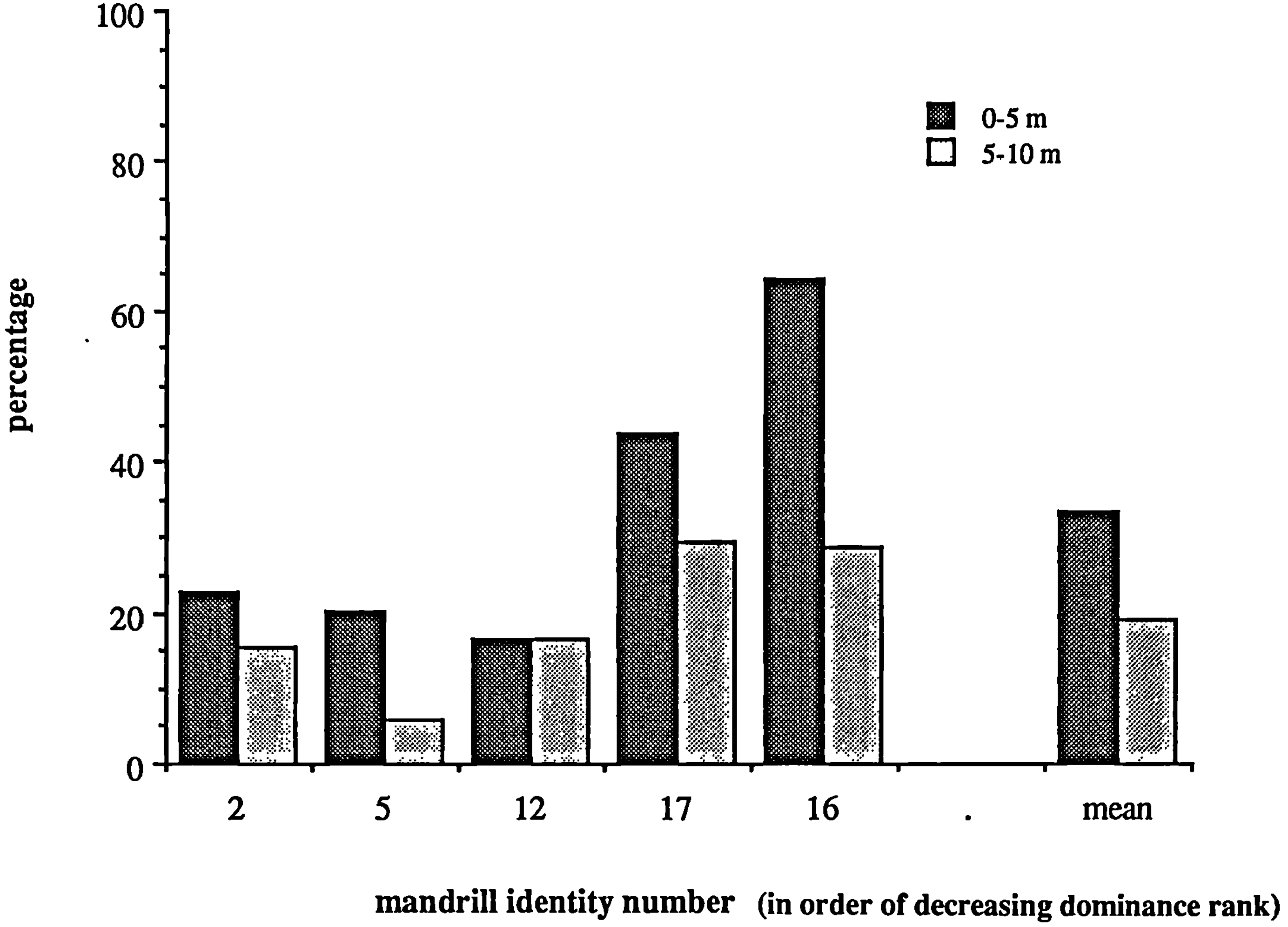
neighbours (10.3%) than other females (mean = 17.8%) though not significantly fewer (t = 2.351, df = 4, NS). There was no relationship betwen dominance rank and time spent without neighbours in pregnant females (range at both distance categories and including and excluding the alpha female r_S = 0.00 to -0.43, NS).

Lactating female mandrills. Figure V.7 depicts the percentage of time that lactating female mandrills had no neighbours. These females were alone significantly less often than males, at both distance categories (0-5 m: females vs. males, 33.6% vs. 64.1%, t = 2.681, df = 9, $p < 0.05$; 5-10 m 19.2% vs. 42.8%, t = 2.781, df = 9, $p < 0.05$). The alpha female spent less time with no neighbours than the other females at both distance categories, but in neither case were these differences significant (0-5 m: Female 2 vs. mean of others 22.7% vs. 36.3%, t = 0.230, df = 3, NS; 5-10 m: 15.6% vs. 20.1%, t = 0.809, df = 3, NS). For the four females (Nos. 2, 5, 12, and 17) for whom data in both reproductive states were available, each spent less time with no neighbours at the 0-5 m distance category when lactating than when pregnant (compare Figure V.6 and V.7). There was no such consistency at the 5-10 m category. Three females spent more time alone when lactating than when pregnant and one (No. 5) spent less time. There was a strong negative correlation betweeen dominance rank and rank time without neighbours at both distance categories (r_S = -0.80, n = 4). This was maintained for the 5-10 m category when the alpha female's data were included (r_S = -0.80, n = 5, NS) but not at 0-5 m (r_S = 0.37, n = 5, NS).

Summary

Overall females spent a third (35%) of their time with no other founders within 5 m of them. On average there were no differences between pregnant and lactating females at either distance category. In comparison males spent 71% of their time without the company of founders at less than 5 m, with the exception of the alpha male. Like females, he spent only a third (31%) of his time with no one within 5 m of him. Data presented above indicated that during the 70% of the time when another founder

Figure V.7. Percentage time with no neighbours in lactating female mandrills



was within 5 m of the alpha male, the founder was likely to be an adult female. Females spent only a fifth (18%) of their time with no founder neighbours at 5-10 m. For males nearly half their time (48%) no other founder was at 5-10 m of them. Again the alpha male was an exception among males - he spent only 15% of the time without neighbours at this distance.

Conclusion

The male mandrills at CIRMF, with the exception of the alpha male, spent most of their time with no other founders in close proximity, and with company at 5-10 m for only half the time. The alpha male had neighbours within 5 m most of the time, and there was nearly always another founder mandrill within 10 m of him. These founders were mainly females, who also spent most of their time near him and near other females. On average both pregnant and lactating females had no neighbours at 0-5 m 35% of the time, and none at 5-10 m 18% of the time. The implications of these findings for social structure are discussed in Chapter VII.

GROOMING RELATIONSHIPS

The present section concentrates on describing affiliative relationships. In keeping with previous research in primatology (see brief review in Smuts, 1985, p.38) grooming was used as a measure of affinity. Since grooming relationships show considerable variation between different species, an investigation of grooming relationships in the CIRMF founder mandrills was expected to be a useful means by which to characterise mandrill social relations and compare them to those of other species, particularly in relation to hamadryas and gelada baboons which both form one-male units yet have very different grooming relations.

During the same focal samples, in Part II of the study, in which data about proximity were collected, the behaviour of the focal animal was also recorded in point samples every minute (see Chapter II). An analysis of grooming behaviour recorded by this method is presented below. Self-grooming was excluded from analysis, so the data below refer only to social grooming (allogrooming).

When the focal mandrill was engaged in grooming, the identity of its grooming partner and the groomer/groomee roles were recorded. The number of point samples in which grooming occurred was divided by the total number of point samples and converted to a percentage to give the percentage of time spent grooming.

In the same way as the data for proximity reported above, the grooming data for males were categorised into two sets. One set contained data from days in which a female was in oestrus, the other set data from days in which no female in the group was in oestrus. For females the grooming data were divided by reproductive state - pregnant, lactating, and oestrus. These data were analysed separately. Only the data relating to non-oestrous states are reported below. Data collected during periods of oestrus are analysed in Chapter VI. The number of focal samples and of point samples of behaviour in each category are given in Appendix V.1.

Planned comparison t-tests were used to test for differences between males and females. One-sample t-tests were used within sex to see if the alpha individual was different from the others. Spearman rank order correlations of rank grooming data and dominance rank were done to test whether grooming behaviour varied predictably with dominance rank. The Spearman statistic was not reported if there was more than one tie. Since the alpha individual was predicted to differ from others the Spearman correlations were done in two ways: (a) excluding the data of the alpha individual and (b) with this individual's data included. The solitary male No. 3 was excluded from all analyses as he was so rarely near anyone, and in fact he was never observed to groom anyone except himself. All probabilities were two-tailed and alpha was set at 0.05. In all figures mandrills are shown in order of decreasing dominance rank within sex.

Time spent grooming

The total percentage time (total percentage point samples) spent grooming by males on anoestrous days, and by pregnant and lactating females is described below.

The percentage time spent grooming by males is illustrated in Figure V.8. The mandrills are shown in order of decreasing dominance rank, as stated above, with the exception of the solitary second-ranking male (No. 3) who is the last male shown. Even excluding him, two (33%) of the six remaining males were never recorded grooming. The alpha male (No. 7) spent significantly more time grooming (7.4%) than other males (mean 0.8%, $t = 20.687$, $df = 4$, $p < 0.001$). There was no correlation of rank time grooming with dominance rank among the other males ($r_S = -0.13$, $n = 5$, NS).

For females, grooming with their own offspring was excluded from this analysis. This was done to reduce variance in grooming between females due to differing number, age, and sex of offspring. In addition, preliminary observations had shown that females groomed regularly with their offspring. Since in all cases their paternity was unknown, kinship of male founder mandrills was unknown. All further reference to offspring refers to a female's own offspring, i.e., her relatives. Grooming with offspring by females was excluded in an attempt to make male-female comparisons less biassed towards females. Grooming by females with offspring (i.e., their own offspring) is analysed later in this chapter.

Figure V.9 illustrates the percentage time spent grooming by pregnant ($n = 6$) and lactating ($n = 5$) females with individuals other than their offspring. Contrary to the pattern in males, all females were recorded in grooming relationships. Females spent more time grooming than males, both when pregnant (female mean = 5.5%, male mean = 1.9%) and lactating (9.1% vs. 1.9%), although the difference was only significant for lactating females (pregnant females vs. males: $t = 1.773$, $df = 10$, NS; lactating

Figure V.8. Percentage time spent grooming by male mandrills

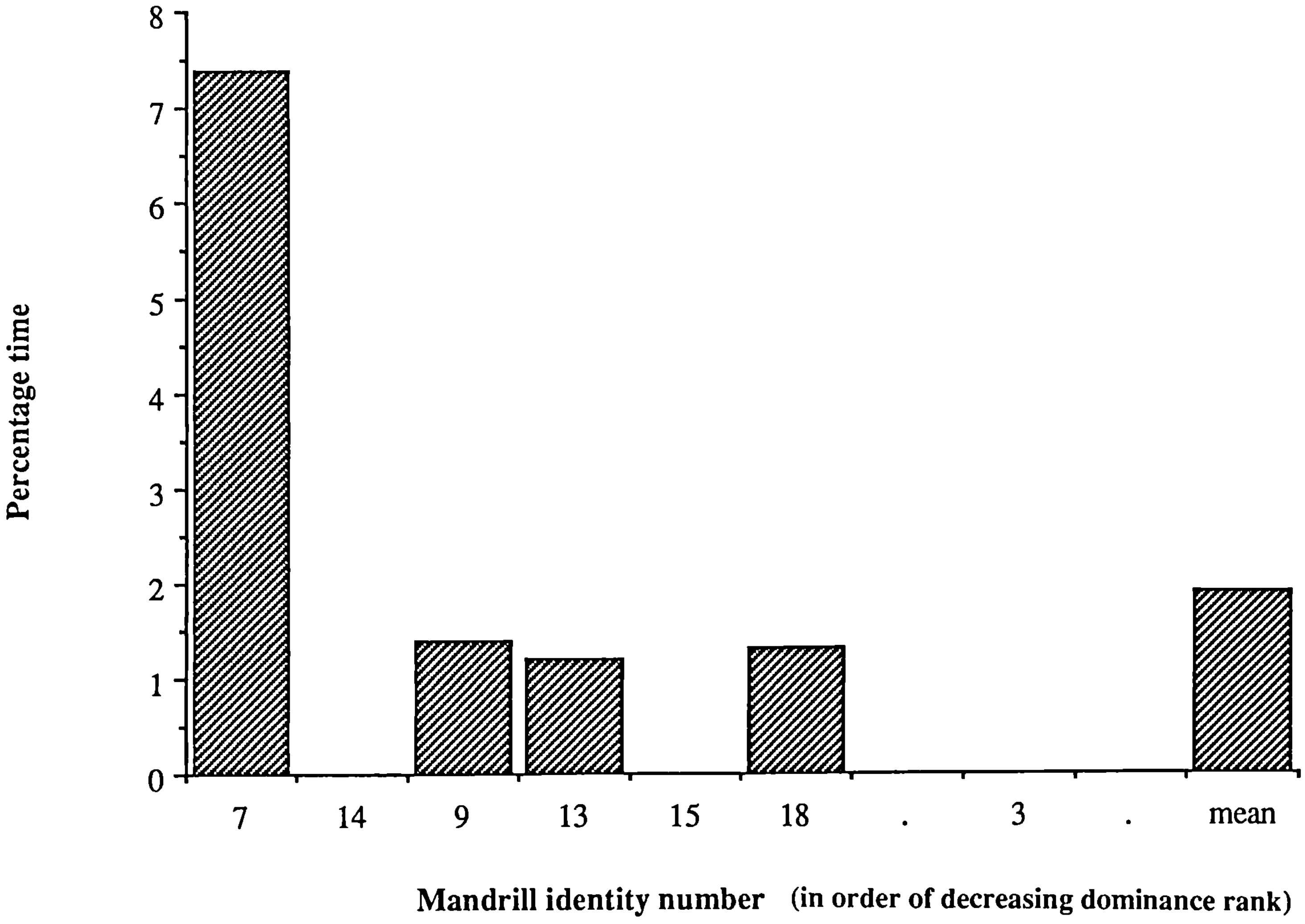
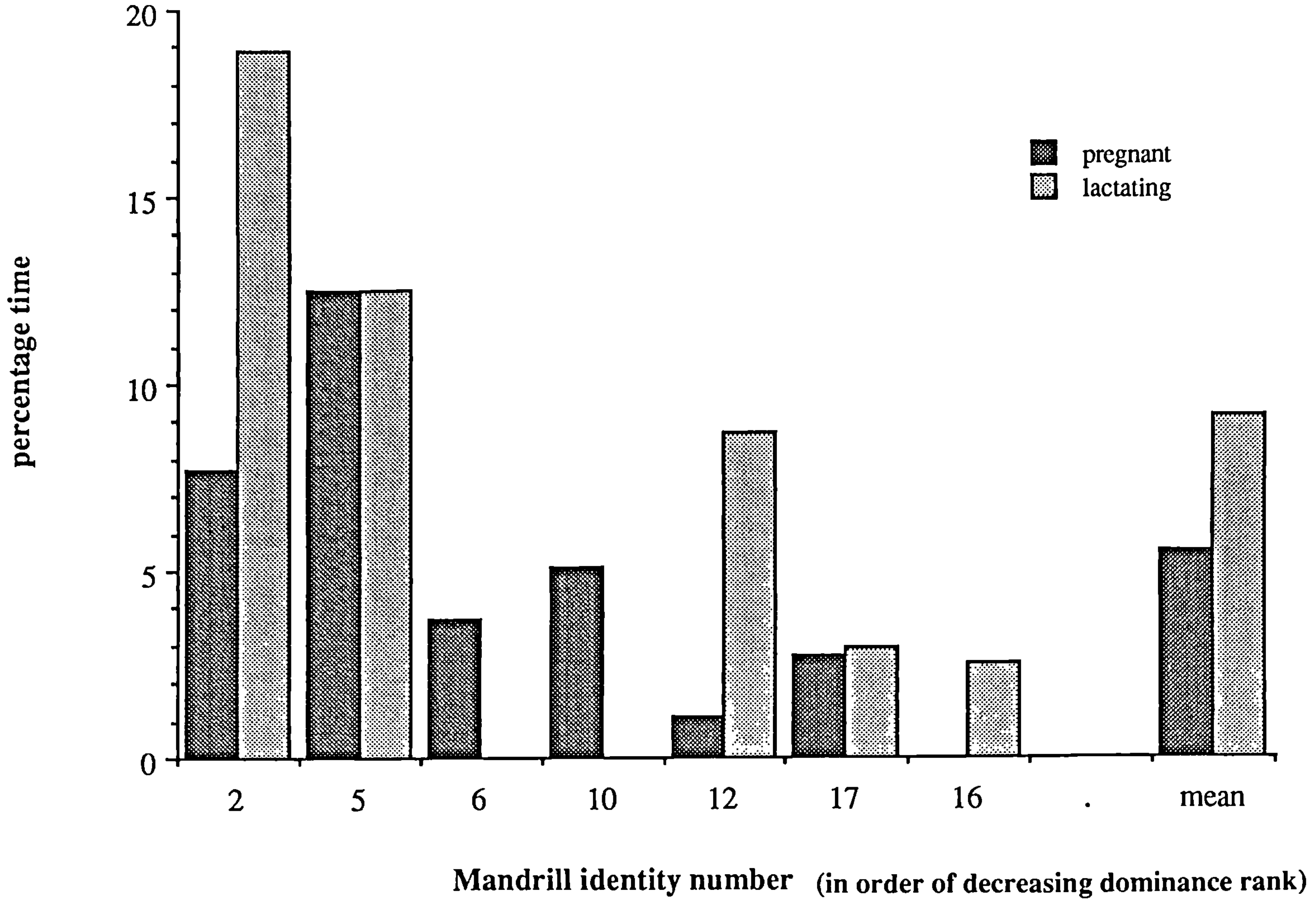


Figure V.9. Percentage time spent grooming by female mandrills



females vs. males: $t = 2.368$, $df = 9$, $p < 0.05$).

The alpha female (No. 2) spent more time grooming than other females in both reproductive states, but she groomed significantly more only when lactating (pregnant: alpha female vs. others, 7.7% vs. 5.0%, $t = 1.353$, $df = 4$, NS; lactating: 18.9% vs. 6.7%, $t = 5.083$, $df = 3$, $p < 0.02$). Grooming correlated positively with dominance rank with both pregnant ($r_S = 0.83$, $n = 6$, NS) and lactating ($r_S = 1.00$, $n = 5$, $p < 0.05$) dominant females spending more time grooming than more subordinate individuals. These relationships persisted when the alpha female was excluded from the analysis (pregnant: $r_S = 0.80$, $n = 5$, NS; lactating: $r_S = 1.00$, $n = 4$).

In order to examine grooming relationships in more detail, the data on grooming were split into give grooming (groomer) and receive grooming (groomee) scores. In males grooming was further subdivided by grooming partner, (a) with founder mandrills (i.e., subadults and adults) and (b) with all other age-sex classes. For females, in addition to these two categories, a third (c) grooming with own offspring, was distinguished.

Males

As can be seen in Figure V.8 only four (Nos. 7, 9, 13, and 18) of the six group males were recorded in grooming interactions. They groomed exclusively with adolescent and adult females. They never were seen to groom other males, even youngsters (although some males, particularly Nos. 9 and 18, played with juvenile males). Although all four males groomed exclusively with females, the category of female partner was not the same for all males. The alpha male (No. 7) and Male 13 did all their grooming with adult (founder) females, but Males 9 and 18 did less than half their grooming (27% and 40% respectively) with founder females, and the rest with CIRMF-born adolescent females. Division of roles when grooming with adult females was highly skewed. In three of the four males, over 94% of the grooming was given to them by females. However, the most subordinate male (No. 18) was the groomer 100% of the time.

Females

The data for pregnant and lactating females are presented in three sections: total grooming, giving grooming, and being groomed.

Total grooming. Founder females groomed with individuals of all age-sex classes. Figure V.10 shows the proportion of total grooming pregnant females did with their own offspring and with founder individuals. There was considerable variation between females in the distribution of their grooming.* Correlations between dominance rank and rank proportion of grooming with offspring and founders indicated that there was a tendency for subordinate females to groom with their offspring more than did dominant females ($r_s = -0.66$, $n = 6$, NS) and for more dominant founder females to groom more with other founders than subordinate pregnant females ($r_s = 0.66$, $n = 6$, NS). These coefficients were reduced by exclusion of the alpha female (offspring: $r_s = -0.60$, $n = 5$, NS; founders: $r_s = 0.30$, $n = 5$, NS). The alpha female was not extreme, and in fact she, Female 5, and Female 17 all groomed about 40% with their own offspring and 60% with founders. For most females (83%), members of these two groups were their only grooming partners. However, Female 6 did over 60% of her grooming with other individuals. This may partly have been due to her having only a single offspring, a three-and-a-half year old son, whereas other females had multiple and/or younger and/or female offspring. In addition to her son - No. 6A, and founders Female 6 groomed with two adolescent females and three young juvenile males.

Figure V.11 shows the proportion of grooming with offspring and founders by lactating females. There was considerable variation between individuals. There was no correlation of dominance with proportion of grooming with offspring ($r_s = 0.00$, $n = 5$,

Figure V.10. Percent of total grooming of pregnant females with offspring and founders

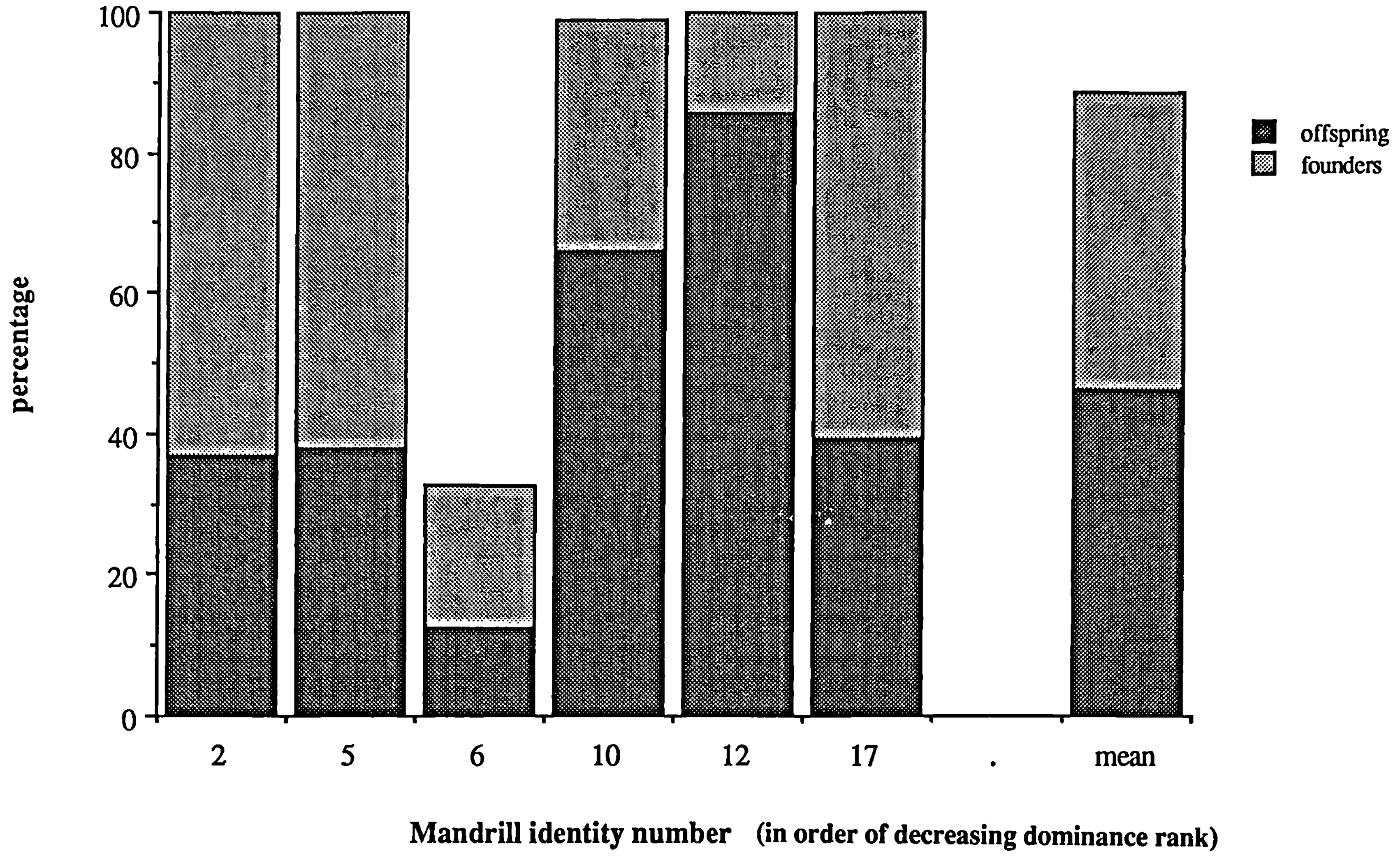
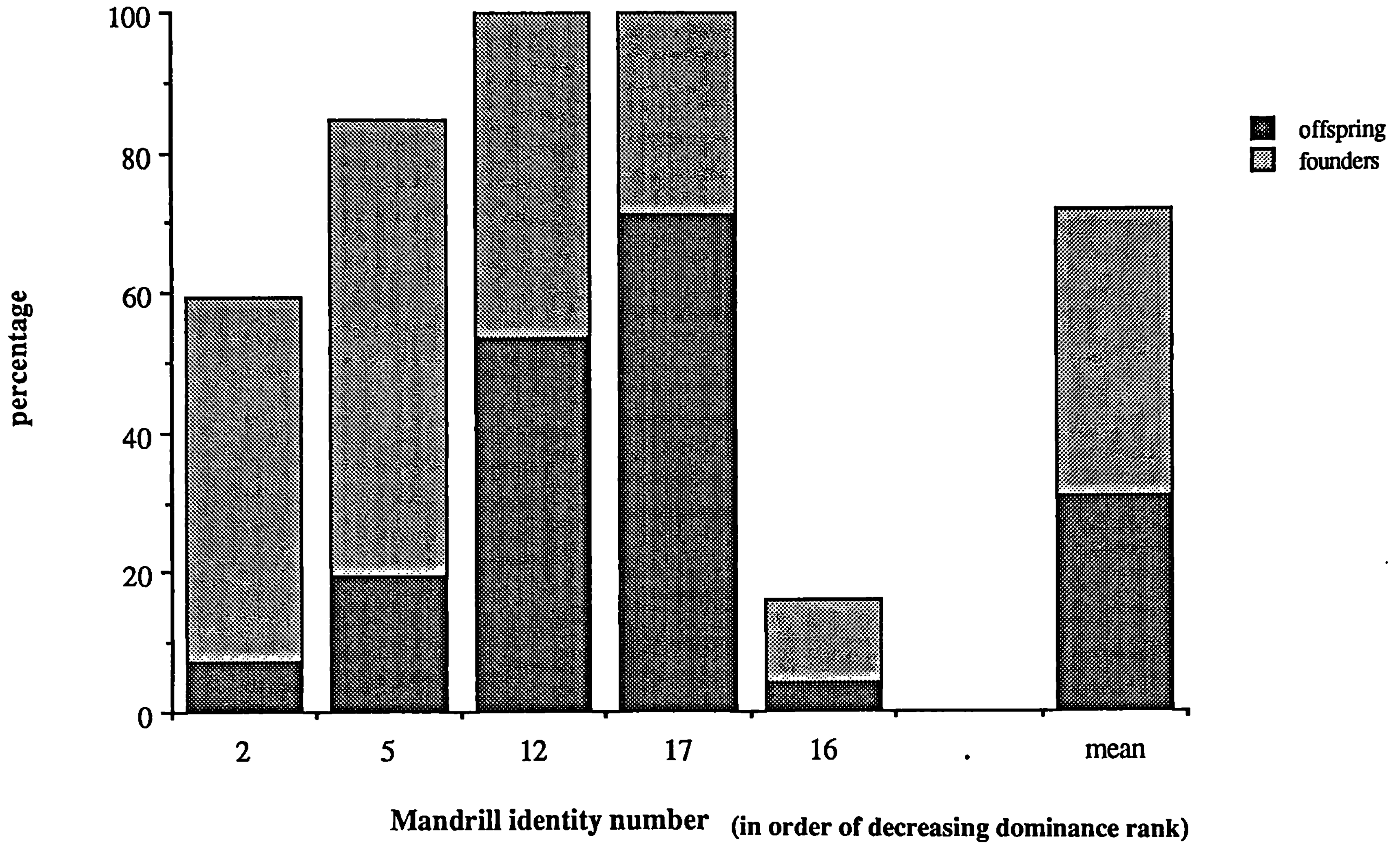


Figure V.11. Percent of total grooming of lactating females with offspring and founders



NS) yet the proportion of grooming with founders correlated strongly with dominance ($r_S = 0.90$, $n = 5$, NS), with dominant females grooming more with other adult and subadult founders than did subordinates, which was a similar pattern to that seen in pregnant females. Exclusion of the alpha female did not alter substantially the correlations (offspring: $r_S = 0.20$, $n = 4$; founders: $r_S = 1.00$, $n = 4$). Comparison of Figures V.10 and V.11 emphasizes the overall difference between pregnant and lactating females and also the differences within the four individuals (Nos. 2, 5, 12, and 17) for whom data were available in both reproductive states. For only two of the five lactating females (40%) did the categories offspring and founders account for all their grooming, whereas 83% of pregnant females groomed only with offspring and founders. Thus lactating females groomed with a wider range of grooming partners than did pregnant females. In the two most dominant females, Nos. 2 and 5, the additional grooming was accounted for by grooming with adolescent females, who were strongly attracted to young infants. The most subordinate female (No. 16) groomed mostly (64%) with juveniles.

Giving grooming. Groomer/groomee roles of pregnant female mandrills are shown in Figure V.12. All females groomed others at least as much as they were groomed and on average they were the groomer 70% of the time. Figure V.13 shows the proportion of grooming given to offspring and founders by pregnant females. In all females except Female No. 6, grooming was given only to offspring and founders. On average 58% of grooming was given to offspring (Figure V.13).

Groomer/groomee roles of lactating female mandrills are shown in Figure V.14. The proportions of grooming in each role varied considerably from those during pregnancy (as seen by a comparison of Figures V.12 and V.14). When females had very young infants they gave grooming only 50% of the time on average, 20% less than during pregnancy. Although total grooming with lactating females was not

Figure V.12. Groomer/groomee roles in pregnant female mandrills

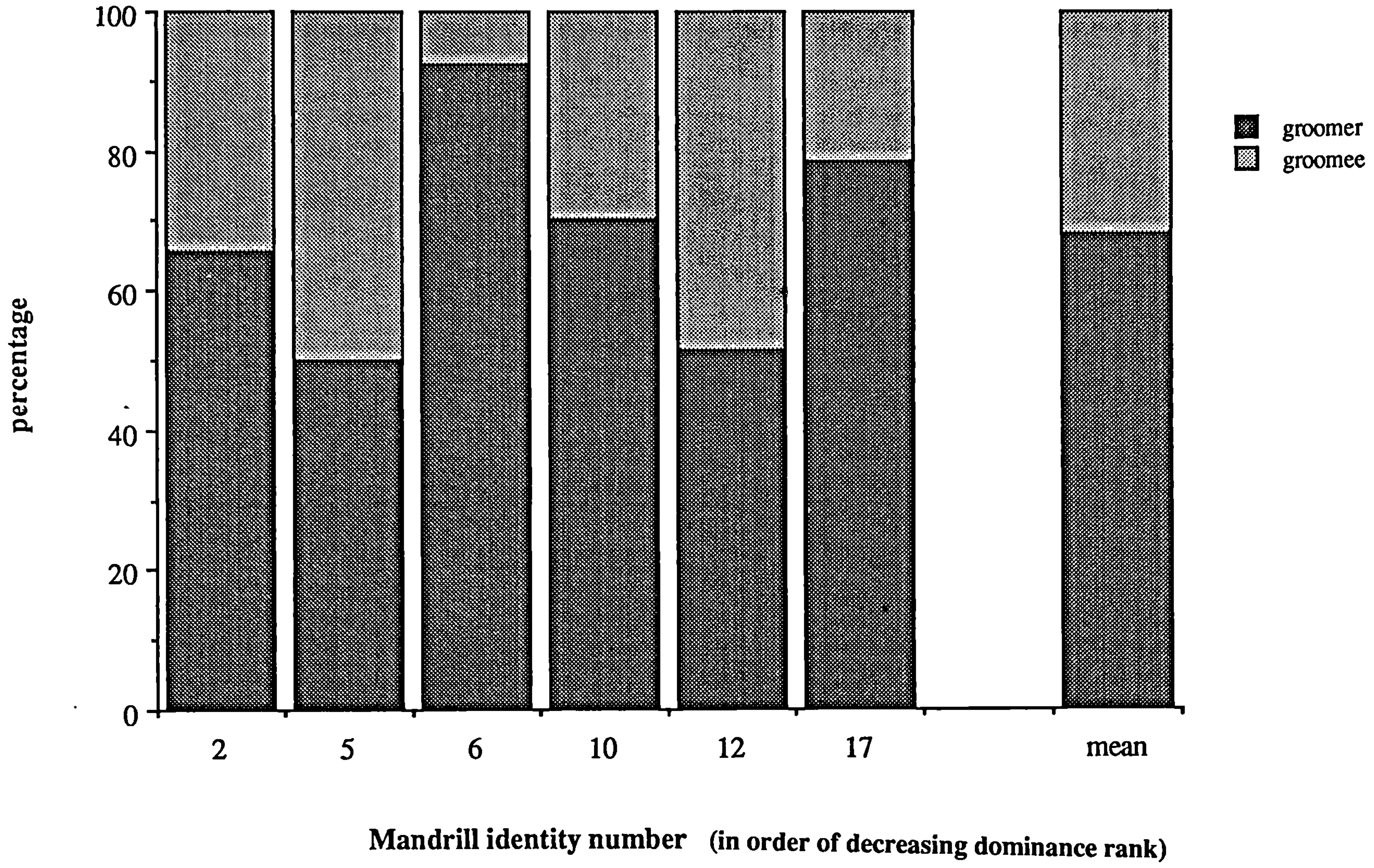


Figure V.13. Percent of grooming given to offspring and founders by pregnant females

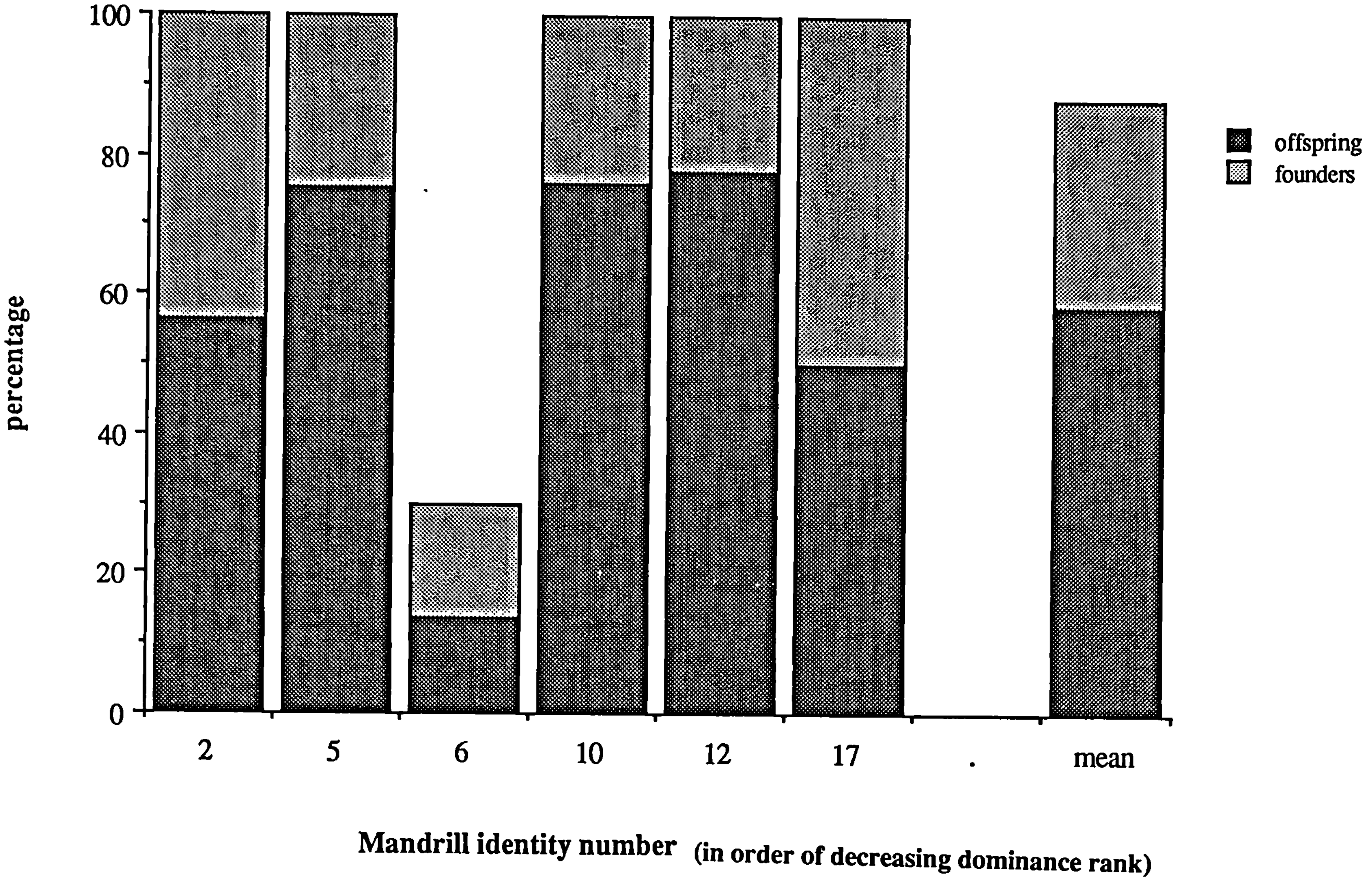
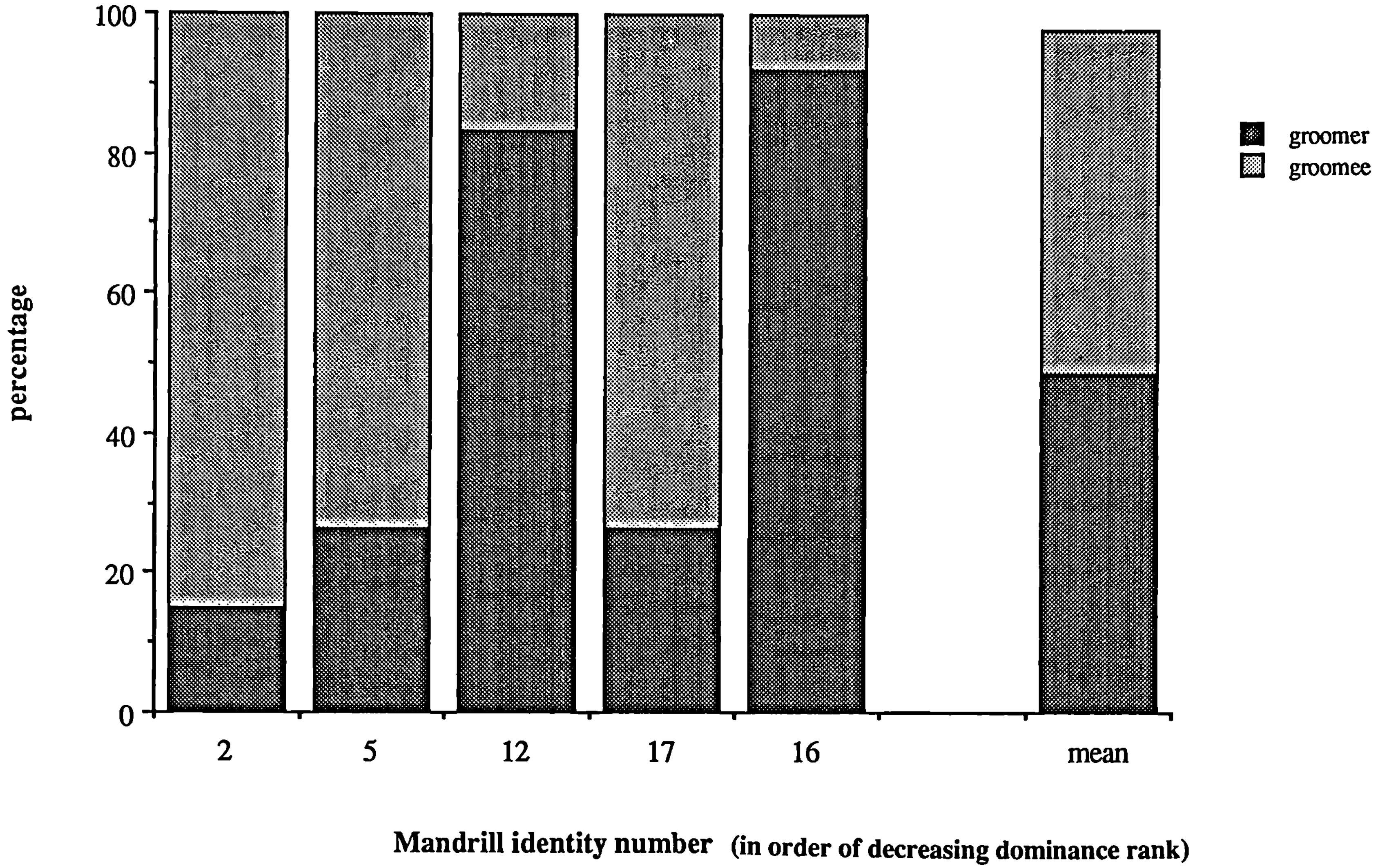


Figure V.14. Groomer/groomee roles in lactating female mandrills



accounted for wholly by grooming with founders and offspring (as was illustrated in Figure V.11) in terms of grooming *given* by lactating females, they were only recorded as grooming their own offspring and founders (Figure V.15) as was also the case in most (83%) pregnant females. On average the proportion of grooming given to offspring by lactating mothers (54%) was similar to when they were pregnant (58%). The most subordinate female was distinctive in giving no grooming to her nine-month old son and in grooming only rarely with other founder subadults and adults (see Figure V.15).

In both reproductive states percent time spent giving grooming correlated positively with dominance rank (r_S = +0.60, NS), with more dominant females spending more time giving grooming than did subordinates, although this was not statistically significant. Exclusion of the alpha female strengthened the correlation (pregnant: r_S = 0.70, n = 5, NS; lactating: r_S = 0.80, n = 4). This can partly be explained by the fact that overall dominant females groomed more than subordinates (see previous section). However, the proportion of grooming in which a pregnant female was the groomer did not correlate with dominance (r_S = 0.03, n = 6, NS; excluding alpha female: r_S = -0.30, n = 5, NS). When females were lactating more subordinate females took the groomer role more often than dominant females (r_S = -0.70, n = 5, NS; excl. alpha female: r_S = -0.40, n = 4).

Being groomed. The proportion of grooming which a pregnant female received from others is shown in Figure V.12. On average a female was groomed by another for a third of her grooming. Figure V.16 illustrates the proportion of grooming received by pregnant females which was given to them by their offspring and by founders. Three of the six females were groomed only by other founders, and these were mainly other adult females - on average 78% of grooming received from other founders was received from females. Age and sex of offspring appeared to be

Figure V.15. Percentage of grooming given to offspring and founders by lactating females

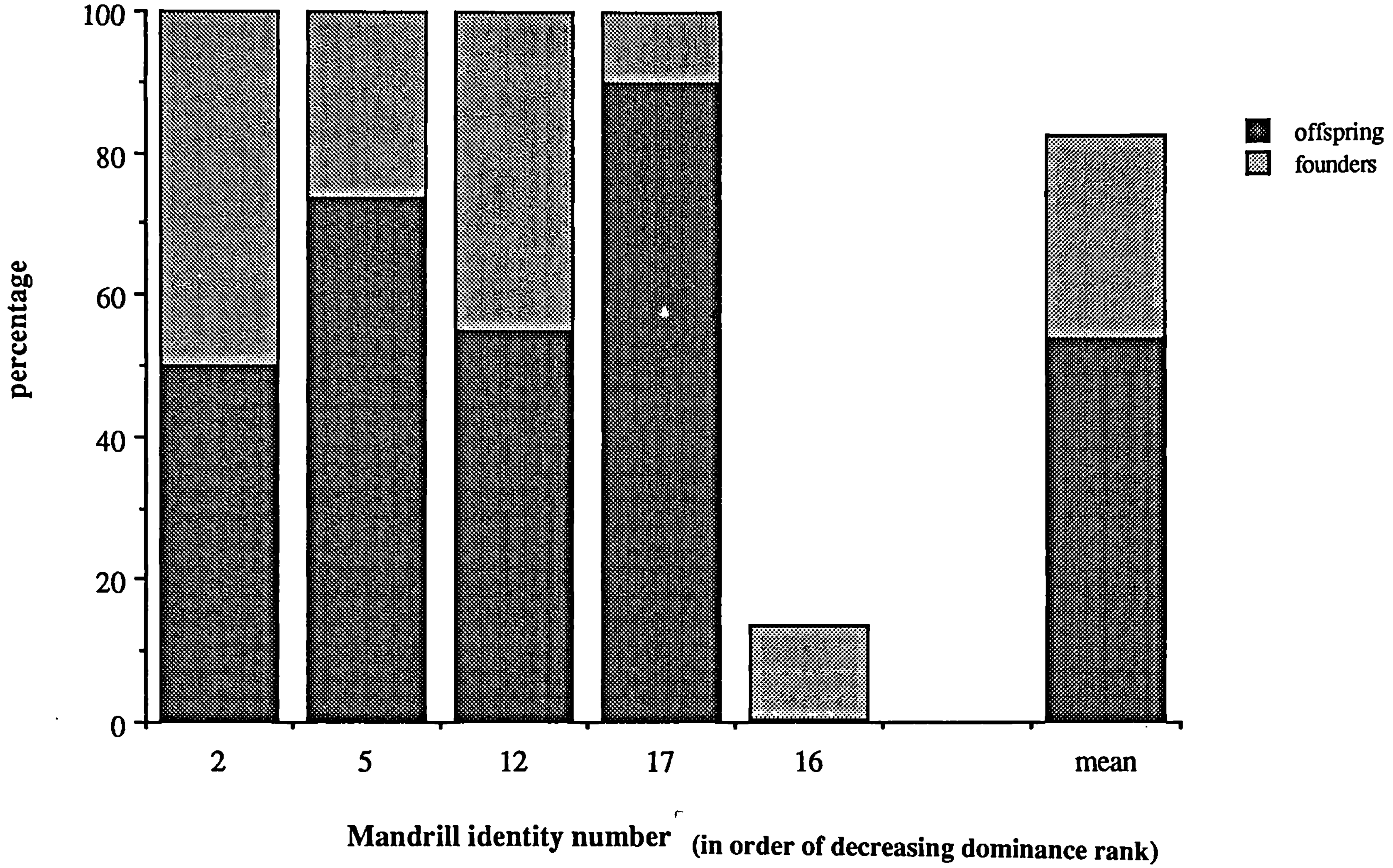
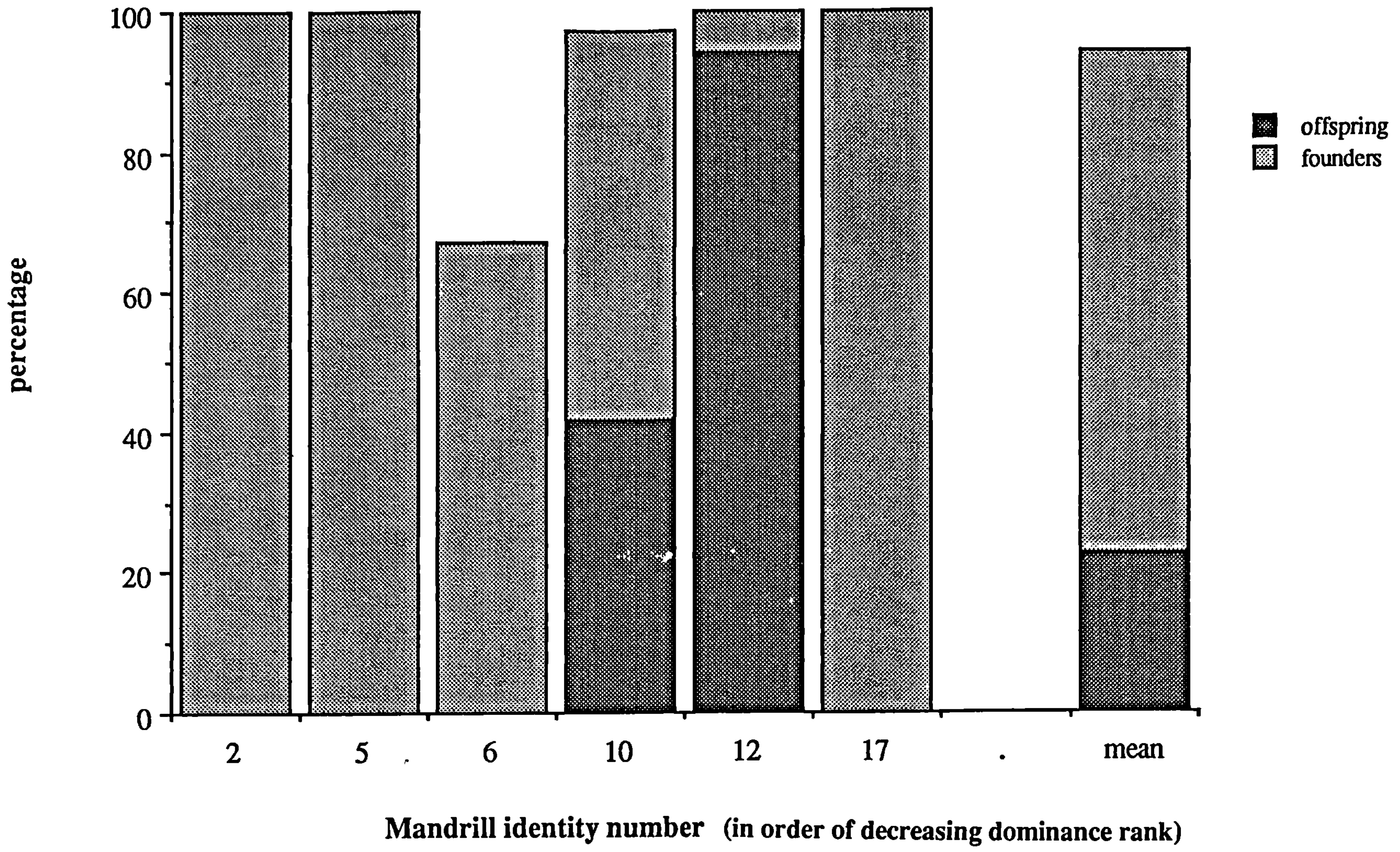


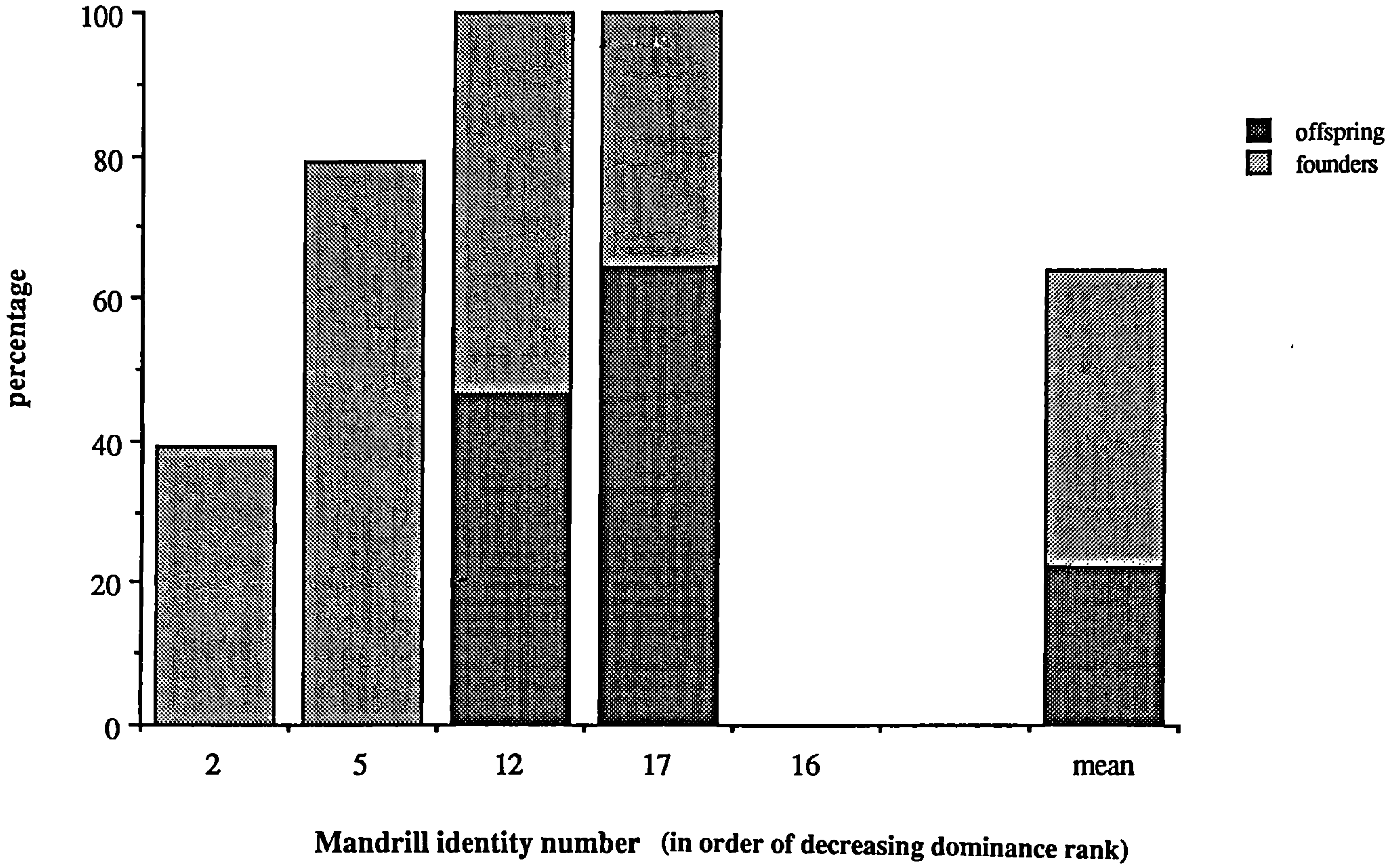
Figure V.16. Percent of grooming received by pregnant females from offspring and founders



important factors determining an adult female's grooming relationships. In only a third of the mandrills did the female receive any grooming from her offspring. The high proportions of grooming by offspring of Females 10 and 12 (Figure V.16) were due to their being groomed by their adolescent daughters 10A and 12A. Although Female 5 also had an adolescent daughter, 5A, mother and daughter never were recorded to groom together and in fact their relationship could be characterised as antagonistic (see the following section on agonistic relationships). There were no strong correlations of rank time being groomed ($r_S = 0.43$, $n = 6$, NS) or proportion of grooming being the groomee ($r_S = 0.31$, $n = 6$, NS) with dominance rank in pregnant females. Exclusion of the alpha female did not change these correlations ($r_S = 0.40$, $n = 5$, NS; $r_S = 0.30$, $n = 5$, NS).

On average lactating females received about half of their grooming from individuals other than their own offspring and other founders (Figure V.14). This was a greater proportion than when they were pregnant. However, the mean proportion received from offspring (22%) was the same in both reproductive states (as shown by a comparison of the darkly shaded part of the 'mean' column in Figures V.16 and V.17). The latter figure also illustrates the striking differences between individual females in the proportion of grooming they received from different classes of individuals. Females 2 and 5 received no grooming from their offspring and 20% to 60% of their grooming was received from individuals other than founders. These two lactating females were groomed by adolescent females; Female 2 by 5A and 12A, and Female 5 by 10A and 12A. Female 16 was groomed by others for only 8% of her total grooming interactions and this grooming was received from a juvenile male (No. 6A). A comparison of Figures V.15 and V.17 shows the difference in distribution of grooming given by lactating females (Figure V.15) and received by them (Figure V.17). More dominant lactating females spent more time being groomed than did more subordinate females ($r_S = +0.90$, $n = 5$, NS; excluding the alpha female: $r_S = 0.80$, $n = 5$, NS). However, the

Figure V.17. Percentage of grooming received by lactating females from offspring and founders



proportion of all grooming which was received grooming did not correlate strongly with dominance (r_S = +0.50, n = 5, NS; excluding the alpha female: r_S = 0.00, n = 4).

Summary

Grooming relationships in the CIRMF mandrills can be summarised as follows:

(1) Subadult and adult male mandrills very rarely groomed. A third of the males never was observed grooming, and on average males spent only 2% of the time for which they were observed in social grooming, although the alpha male groomed significantly more (about seven times more) than other males. Males groomed exclusively with adult and adolescent females. Most males received nearly all their grooming when grooming with female founders. However, the youngest and most subordinate male groomed others.

(2) Adult females spent about 12% of the time for which they were observed grooming, and about 40% of this was with other founders, most of whom were females. During pregnancy they groomed with their offspring about half the time, more if they had an affiliative bond with an adolescent daughter, and when lactating, grooming with offspring dropped to about a third.

(3) In both reproductive states most females gave grooming only to founders and their own offspring. However, a greater diversity of individuals groomed lactating females than gave grooming to pregnant females. In both states females received about 22% of grooming from their own offspring. Pregnant females were groomed by non-relatives for about 30% of their total grooming and lactating females received more, about 50%, of their grooming from non-relatives

AGONISTIC RELATIONSHIPS

In the following section agonistic behaviour between founder mandrills is described and presented in terms of male-male, female-female, and male-female interactions.

Dominance rank was determined on the basis of wins and losses in dyadic agonistic interactions. Winner and loser were determined as described by Hausfater (1975, p.25). An animal who directed one or more submissive behaviours and no aggressive behaviours towards a second animal in response to aggressive behaviour (or other nonsubmissive behaviour) was classed as a loser. The individual giving only aggressive and/or nonsubmissive behaviour was the winner. In addition an individual spontaneously giving submissive behaviour towards another (i.e., not in response to aggressive/other behaviour) was classed as a loser, and the individual to whom the submissive behaviour was directed as the winner. Dominance rank was obtained from the formula DR = n-r, where n = number of individuals under consideration and r = the number of individuals consistently dominated (Hausfater, 1975, p.29). Thus if a female was consistently dominant to four of the seven females in the group she was assigned rank three. The ranks reported below are based on dyadic interactions with clear winner-loser outcomes scored during the period March 1986 to May 1987 from focal sampling, behaviour sampling and *ad lib.* sampling combined. Some examples of clear dyadic interactions between individuals of the same sex are given below:

17 April 1986
0859: Female 10 threat grunts and head-bobs at Female 12. Female
12 presents to Female 10.

20 May 1986
0920: Female 5 approaches Female 10 who is foraging. Female 10 moves away and Female 5 takes over her foraging site.

4 June 1986
1703: Female 6 presents to Female 2.

30 April 1986
1549: Male 9 head-bobs at Male 15. Male 15 moves away.

6 August 1986
0946: Male 13 presents to Male 7.

The interaction between Female 10 and 12 and between Male 9 and 15 illustrate submissive behaviour in response to threat. A simple displacement, with the loser walking away, as in the interaction between Female 10 and 5, illustrates the situation where an individual (the loser) moves in response to non-agonistic behaviour - a simple approach - on the part of the another (the winner). The interaction of the 4th June and 6th August exemplify a mandrill (the loser) spontaneously giving submissive behaviour to another (the winner) in the absence of an overt stimulus from the other animal.

Several interactions were undecided in terms of clear winner-loser categories, for example due to the non-response from an animal receiving aggression. Some examples are given below:

6 May 1986
0940: Female 6 head-bobs Female 10 three times. Female 10 ignores her.

23 December 1986
1023: Male 3 head-bobs Male 9 who does not respond.

Male dominance relationships

Table V.7 shows the matrix of outcomes of interactions between founder males. The male hierarchy was strictly linear with no reversals in 314 cases and no cases of non-transitive dominance. The hierarchy was stable over the main study and remained so during the whole study (i.e., to June 1988). There were no clear dominance interactions, as defined above, between the two fully adult males in the enclosure, Nos. 7 and 3 (of rank positions one and two respectively). They seemed generally to be ambivalent towards each other and to avoid direct confrontation.

> 14 February 1987
> 1103: Male 3 is in the feeding site, and Females 6 and 12 are there too. Male 7 arrives and climbs into a bush outside. Male 3 marches out of the feeding site and 7 avoids eye-contact completely.
> 1104: 7 enters the feeding site.

It is interesting to note that Male 7 did not enter the feeding site on arrival, but stayed outside. He did not direct any behaviour at Male 3 either. However, it was clear from other observations that Male 7 was dominant to Male 3, despite the latter being over twice the size of Male 7. The former was the leader of the group and copulated with oestrous females, whereas Male 3 was largely solitary. In one observed fight between the two (see description in Chapter VI), Male 3 received the worse injuries and he was the one who left the site of the conflict. However at no time did he give submissive signals to Male 7.

During Part 2 of the study the relative dominance status of Males 3 and 14 (rank positions two and three respectively) also seemed unclear. The description below, taken from focal samples on Male 3 and from *ad lib.* field notes, is a detailed account of an interaction between the two males. During the 56-minute interaction neither male gave

Table V.7. Male dominance hierarchy

		Loser							
		7	**3**	**14**	**9**	**13**	**15**	**18**	
Winner	**7**			7	18	25	14	29	**93**
	3			1	7	3	6		**17**
	14				11	14	34	15	**74**
	9					23	23	13	**59**
	13						16	11	**27**
	15							44	**44**
	18								

n = 314

clear aggressive or submissive signals and both gave appeasement gestures. This detailed account also provides an illustration of the occurrence and possible function of other behaviour such as scent-making, tension/display yawn, etc..

10 February 1987
0717: I locate Male 3, who is sitting in one of his habitual sleeping trees at the periphery of the enclosure. The group are at a different sleeping site in the middle of the enclosure.
0745: Male 14 turns up, walking along by the fence.
0751: He goes into the undergrowth below 3's tree.
0752: 3 Tension/Display yawns (TY) and self-grooms.
0753: 3 licks the trunk of the tree, TY twice, and scratches himself.
0754: 14 climbs to 5 m height and is at <5 m from 3.
0755: 3 self-grooms and TY.
0756: 14 sniffs the trunk; 3 masturbates briefly.
0757: 3 TY, 14 climbs and is directly below 3.
0758: 14 sniffs trunk and then climbs towards 3. 3 stands and 14 sits 2 m from him.
0759: 14 acts very busy, 'foraging' on the bark and self-grooming.
0800: 3 watches 14, then moves to a fork in the tree, standing at 1 m from 14.
0801: 3 self-grooms.
0802: 3 looks at 14 and leans against the trunk. He looks relaxed.
0803: 14 self-grooms and TY; 3 lolls
0804: 3 TY
0805: 3 scratches
0808: 3 sits, 14 continues to be very busy.
0809: 3 stands and scratches
0810: 3 moves slightly higher in the tree so 14 is now at 2 m. 3 TY
0811: 3 returns to the fork (so 14 at 1 m) and scratches twice.
0813: 3 TY and scratches
0815: 3 looks repeatedly south over the enclosure (in the direction of the group) and scratches. He seems very unsettled and repeatedly stands then sits.

0816: 3 scratches; 14 TY (14 may TY more frequently, he's partly hidden by foliage), 3 sits.
0817: 3 stands, leans and fiddles with the trunk.
0819: 14 fiddles with bark, 3 scratches
0820: 3 sits, stands, 14 stands and 'grabs' towards 3 then sits. 3 sniffs trunk 1.5 m above 14 and licks it.
0821: 3 scratches, 14 moves up a fraction (i.e., towards 3) and 3 smiles at 14 and backs off a bit. 14's crest is raised
0824: 3 stands, scratches
0825: 3 TY, sits
0826: 14 face north, 3 faces south (i.e. they are sitting parallel to each other). 3 stands, 14 smiles repeatedly and self-grooms
0827: 14 stands, 3 stands then sits
0828: 14 sits, 3 self-grooms and scratches
0829: 3 relaxes stretching his legs out. 14 stands, 3 stands, 14 jumps down 3 m, and 3 immediately descends to 14's place
0830: They both forage
0831: 14 climbs, 3 stands, 14 moves to 5 m from 3, 3 sits facing north (or facing 14).
0832: 14 turns to face 3, looks at him and smiles. 3 licks the trunk. 14 descends and displays (branch shakes), 3 descends and displays similarly
0833: 14 is now terrestrial, 15-18 m from 3
0834: 3 climbs and scent marks
0836: 3 finishes scent marking (having done a total of 14 sternal rubs)
0841: 3 descends to the ground, 14 moves off and I lose him.
0858: 3 goes into undergrowth,
0900: and is lost from view.

Both mandrills were clearly tense throughout most of the interaction. This was shown by their frequent yawning, scratching, and the intense 'self-focus' with which they self-groomed and displacement foraged. Male 3's scratching scores illustrate the effect of the close proximity of another, possibly rival, male.

(1) Before 14 climbs to < 5 m (0733-0754), 3 bouts in 21 mins, i.e., 1:7

(2) During the time 14 is < 2 m (0758-0831), 11 bouts in 33 mins,
i.e., 1:3

(3) After 14 descends > 5 m (0831-0900), 0 bouts in 29 mins

This example also gives an indication of the use of scent-marking. Male No. 3 frequently sniffed the trunk, chinned, and licked it and then he scent-marked vigorously after Male 14 left.

Prior to and subsequent to this episode both males were seen with canine slashes, and it is my interpretation that their dominance status was unstable at this time. (In fact Male 3 was seen licking and grooming his right shoulder the evening before the above interaction with 14, although the slash itself wasn't clearly seen until over a week later). As the two were very rarely seen together after this it was difficult to assess their relative status.

Strong aggression was extremely rare between males. As stated above only a single fight was witnessed and indirect evidence of fights, e.g., the presence of wounds such as canine slashes and punctures, were rarely seen. For the most part, especially for subadult Males 9, 13, and 15, who seemed to get on well and occasionally played together, relationships were fairly amicable. These three males sometimes left the group and went off together, one following the other, but they did not associate consistently to form an all-male band.

Female dominance relationships

Table V.8 shows the matrix of outcomes of 988 dyadic interactions in which both individuals were female and there were clear winner-loser outcomes. Three adolescent females (5A, 10A, and 12A) are also included but their dominance interactions are excluded from further analyses. The female hierarchy was strictly

Table V.8. Female dominance hierarchy

Loser

Winner

	2	5A	5	6	10	10A	12	12A	17	16	
2		45	84	57	26	5	38	10	44	19	**328**
5A			35	17	14	7	16	15	15	5	**124**
5				24	22	6	52	16	52	27	**199**
6		1			7	1	17	5	26	27	**84**
10							14	2	21	5	**42**
10A							13	7	8	5	**33**
12				1	1			3	61	20	**86**
12A									23	11	**34**
17										58	**58**
16											n = 988

linear, with only three (0.3%) reversals, and was without cases of non-transitive dominance. It remained stable throughout the whole study (i.e., to June 1988).

In general offspring took the rank immediately below their mother and thus whole matrilines could be ranked on the basis of rank of matriarch. The exception was adolescent female 5A who was dominant to her mother, Female 5. When the alpha female No. 2 threatened Female 5, 5A joined in and supported Female 2 against her mother. By consistently allying herself with the alpha female, 5A was able to dominate her mother.

> 22 May 1986
> 1406: Female 5 and her adolescent daughter 5A are squabbling. 5A grabs at 5 who then presents to her. 5A approaches Female 2 and then 2 threatens 5. Female 5A looks at the alpha male (Male 7) and then threatens her mother again.
>
> 1703: Female 2 threat grunts and head-bobs repeatedly at Female 5. Adolescent 5A then runs up, puts her hands on Female 2's flank and starts to groom her.

The relationship between mother and daughter was characterised by an almost complete absence of grooming and by ambivalence in the usual kin support system.

> 12 February 1987
> 1523: Adolescent female 5A approaches Female 5 and grooms her very briefly before Female 5 walks away from her.
> 22 May 1986
> 1443: Adolescent female 5A and juvenile male 2A are engaged in vigorous rough play. 5A squeals and her mother, Female 5, ignores her.

18 October 1986
0824: Male 14 plays with Adolescent 5A.
0826: 5A squeaks at 14 and runs after him. Her mother, Female 5, comes rushing up and chases 14, but the chase is low-key, and lacks the yell vocalisations.

The interaction of the 12th February would be very unusual between any other pair of individuals since it was extremely rare for any mandrill to refuse a chance to be groomed. This was the only grooming interaction I observed between 5 and 5A and I interpreted Female 5A as only interested in grooming her mother as a way of getting close to 5's recently born infant 5D, in whom 5A, who was herself pregnant, was extremely interested. She had not attempted to groom Female 5 prior to this. The second interaction was also unusual by 'normal' mandrill standards since a squeal usually elicited supportive action from a mother instantly (as described in Chapter IV).

Data on dominance interactions were also collected at the feeding site. The resultant dominance ranks were identical to those illustrated in Table V.7 and Table V.8 and there were no reversals in either sex. The hierarchies from feeding-site interactions are presented in Appendix V.2 for males and Appendix V.3 for females.

Male - Female dominance relationships

Of agonistic interactions between males and females a total of 506 had clear winner-loser outcomes. Table V.9 shows the interactions when males were winners and females losers. No interactions were scored in two of the 49 dyads (marked by a cross in Tables V.9 and V.10). Of the remaining 47 dyads, males won over females in 51.1%. Some examples of clear interactions of male winners over female losers are given below:

Table V.9. Male - Female dominance hierarchy

Female Losers

Male Winners

	2	5	6	10	12	17	16	
7	47	22	23	21	13	19	9	**154**
3	3	☒	2	1	1	2	1	**10**
14	3	3	1	1	9	13	5	**35**
9	13		2	6	7	6	7	**41**
13	42	3	2	☒	11	4	6	**68**
15	11	4		2	23	16	21	**77**
18	2	1	1		1	11	9	**25**

n = 410

2 June 1986
1530: Male 3 head-bobs Female 12. She presents to him.

29 May 1986
1511: Female 10 presents to Male 9.

5 December 1986
1531: Male 15 displaces Female 16 from her foraging site.

The alpha male had the extreme position in having the greatest number of wins (Table V.9). Most of Male 7's wins were from females presenting to him without prior threat rather than as responses to aggressive behaviour on his part. This corroborated data presented in Chapter IV which indicated that Male 7 did not show the highest frequency of threat behaviour among males. There was no other correlation within the male hierarchy of male rank and wins over females. The alpha female was also extreme in having the greatest number of losses.

Table V.10 shows the interactions when females were winners and males losers. Six of the seven founder females had at least one win over a founder male, the exception being the most subordinate female, No. 16, and in 3 (6.4%) of the 47 dyads females had only wins. Some examples of females winning over males are given below:

14 January 1987
1007: Female 5 displaces Male 18 from his foraging site.

17 February 1987
1014: Female 12 screams, yells and chases Male 15. He flees.

2 April 1987
0826: Male 18 presents to Female 10

Table V.10. Female - Male dominance hierarchy

Male Losers

Female Winners

	7	3	14	9	13	15	18	
2	1		1		1	1	5	**9**
5	2	X	1	1	5	3	16	**28**
6			1	1	1	5	18	**26**
10					X		3	**3**
12			1			2	6	**9**
17			1			2	18	**21**
16								

n = 96

The alpha female was not extreme in frequency of wins, nor was the alpha male in terms of losses. However, excluding the alpha male and the solitary male there was a strong correlation between dominance rank and number of losses ($r_S = 0.90$, $n = 5$, NS) such that more subordinate males lost more to females than more dominant males.

Unlike the intra-sex hierarchies the interactions between males and females were characterised by a high proportion of reversals. In 42.5% of dyads there were reversals in winner-loser outcome with 19% of interactions being won by females.

The alpha female (No. 2) who had high loser scores in relation to males interacted more with Males 7 and 13 than other females. This was particularly true for Male 13 with whom, during the earlier part of the study, she seemed to have a special relationship resembling friendship (Smuts, 1985). When she approached Male 13 she often presented to him before grooming him; she also presented to him if he interacted with her offspring as illustrated below. This corroborates data presented in Chapter IV which indicated than Female 2 did not present significantly less than other more subordinate females. It appeared that a female presented to a male in order to approach him closely.

> 21 April 1986
> 1423: Female 2 presents to Male 13. Then infant female 2C (2's daughter) climbs on Male 13.

Many agonistic interactions were followed by further occurrences of agonism involving other mandrills ('chain reactions') including examples of 'redirected aggression', illustrated below:

> 21 November 1986
> 0909: Female 12 displaces Female 17 then Female 17 goes and displaces Male 18.

4 December 1986
1613: Female 2 head-bobs adolescent Female 5A. 5A responds by presenting to Male 7. Male 7 head-bobs and threat rushes Female 5A. Then Female 5A threat-rushes Female 17.
1616: Female 17 threat-rushes Female 16, and Female 5 joins in by directing head-bobs and threat grunts at Female 16.

11 December 1986
1031: Female 5 presents to Male 7. Female 2 displaces Female 5 from her proximity to Male 7 and Female 5 then immediately threatens Female 12 who presents to her.

Sometimes a female incite screamed at a male who ran away before her screaming provoked a response from the alpha male. The majority of female wins over males involved females lunging out at males and vigorously chasing them, emitting the characteristic female yell (see Chapter IV), rather than simple displacements. An example is given below:

24 May 1986
0752: Male 13 displaces Female 2 who then screams, turns, and chases him. He runs away.

In some cases males moved away in 'expectation' of attack from mothers of threatened youngsters or from the alpha male.

25 March 1986
1556: Male 3 head-bobs Female 6 who presents to him. Then she turns and screams at Male 3 who ignores her. When Male 7 appears she incite-screams and then Male 3 moves away. Male 7 does not threaten Male 3.

13 April 1986
0931: Male 14 head-bobs Juvenile Male 6A. Female 6 (6A's mother) does nothing until Male 7 appears and then
0932: she threat-grunts and head-bobs at Male 14 who runs off.

6 May 1986
1015: Juvenile Male 2A presents to Male 9. Then 2A yells at Male 9 who moves away.

9 December 1986
0947: Juvenile 2B screams at Male 15. Female 2 (2B's mother) runs at Male 15 yelling, and he climbs away from her.

The alpha male (No. 7) played a policing role, frequently interfering on the side of the threatened individual regardless of sex or dominance rank. Some examples are given below:

28 March 1986
1532: Female 2 repeatedly head-bobs Female 17. Female 17 avoids her and sticks close to Male 7, dodging from Female 2. Male 7 head-bobs then chases Female 2.

7 April 1986
0815: Female 2 threat grunts, head-bobs and then threat rushes Female 10. Female 5 joins in by threat grunting and head-bobbing Female 10.
0817: Male 7 head-bobs and then chases Female 2 who then presents to him.

9 April 1986
0945: Female 5 threat-rushes Female 17 who moves then backs towards Male 7. He then chases Female 5.

23 April 1986
1130: Male 15 threatens Female 16 who runs away screaming. Male 7 threatens and chases Male 15 who runs away.

31 May 1986
1040: Juvenile Male 2A attacks Female 16 who screams. Male 7 chases 2A.

In sum, male-female agonistic relationships were complex. In general, females were subordinate to males though they could dominate males on occasion. When this happened female motivation/arousal was usually very high. In addition there was the possibility of support from the alpha male.

The fact that these mandrills had been together for many years, and from an early age and thus knew each other very well, may have influenced their relationships. In this respect they may differ somewhat from wild mandrill groups in which there are likely to be fewer non-natal males than there were in the CIRMF group. In the wild, the males with a group are likely to be the mature alpha male and young subadult natal males.

Although mandrills have a reputation as being very aggressive, the rate of agonistic encounters between founder individuals was remarkably low. If all agonistic interactions between founders during focal samples on non-oestrous days are divided by the number of minutes of focal sampling, the rate of agonistic interactions was 2.6/hr. Per individual this was only 0.18/hr. This compares with 4.89 agonistic bouts/hr between male *Papio cynocephalus* (Hausfater, 1975) and 8.9/hr for male rhesus macaques (*Macaca mulatta*) (Feistner, 1983). This is discussed in relation to Popp's (1983) hypotheses in Chapter VII.

CHAPTER VI.

RELATIONSHIPS DURING OESTRUS

In the previous chapter, relationships between the founder mandrills were described during periods when females were not sexually receptive, either they were pregnant or lactating. In this chapter these same relationships - spatial, grooming, and agonistic relationships - are examined during periods when females had maximally swollen perineal swellings - i.e., when females were in oestrus. Relationships during these limited periods are compared to those during anoestrus. In addition, information on sexual relationships is presented.

SPATIAL RELATIONSHIPS

Data about proximity were collected during focal samples during Part 2 of the study in exactly the same manner as described in the previous chapter. The data presented below on males are from focal samples done on days on which a female was in oestrus. These days will be termed oestrous days. The proximity measures for males are based on analyses of 1,532 point samples. Data were collected on three females (Nos. 2, 6, and 10) during oestrus and the proximity measures are based on analyses of 1,222 point samples. Data on the same three females were also collected during their pregnancies (whereas of the three females, only for Female 2 were data available during lactation) so oestrus scores could be compared with pregnancy scores within females. The number of focal samples for each individual are given in Appendix V.1. In all figures and tables mandrills are presented in order of decreasing dominance rank within sex.

Planned comparison t-tests were used to test for differences between males and females. One-sample t-tests were used within sex to see if the alpha individual was different from the others. This was only done for males since there were so few females. Paired t-tests were used to test for differences between reproductive states within individuals. Spearman rank order correlations were used to test whether rank sociability, proximity, etc. correlated with dominance rank within sex. The Spearman statistic was not reported if there was more than one tie. Alpha was set at 0.05 and all probabilities were two-tailed. The limitations of small sample sizes, discussed in Chapter V, apply also to the data presented in this chapter.

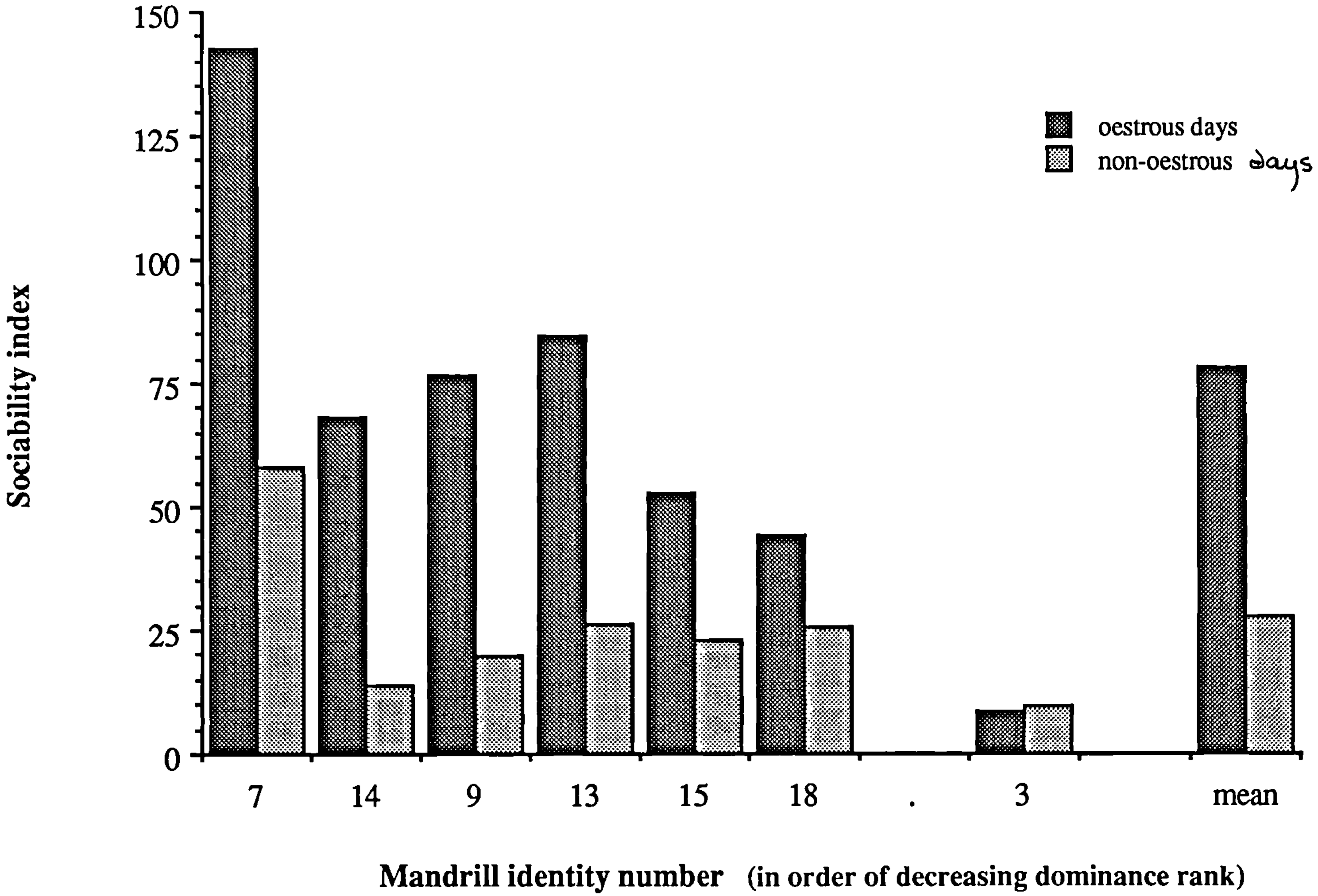
General sociability

As described in Chapter V, for each focal individual the composite scores of the 13 other founder mandrills were summed to produce a sociability index. The higher the index, the more 'sociable' the individual.

Figure VI.1 illustrates the sociability indices for males on oestrous days; indices for non-oestrus are also included for comparison. The mandrills are shown in order of decreasing dominance rank, as stated above, with the exception of Male No. 3. He held the second dominance position but is shown at the end because of his solitary status; no other founder mandrill was present in 85% of the point samples at 0-5 m or in 83% of point samples at 5-10 m.

It is clearly seen in Figure VI.1 that, as was the case during non-oestrus, the alpha male, No. 7, had the highest index. He was significantly more sociable than the other males (142.4 vs. mean = 65.2, $t = 10.293$, $df = 4$, $p < 0.001$) and their indices averaged only 46% of his index. Excluding Males 3 and 7 there was a nonsignificant positive correlation of rank sociability with dominance rank ($r_S = 0.60$, $n = 5$, NS) with dominant males having higher indices, indicating that they were more sociable than more subordinate males. When the data for Male 7 were included the correlation increased ($r_S = 0.77$, $n = 6$, NS). The relationship between rank sociability and dominance rank on oestrous days was in the opposite direction to that during non-oestrus, when more subordinate males had higher sociability indices. All the males

Figure VI.1. Sociability indices of male mandrills



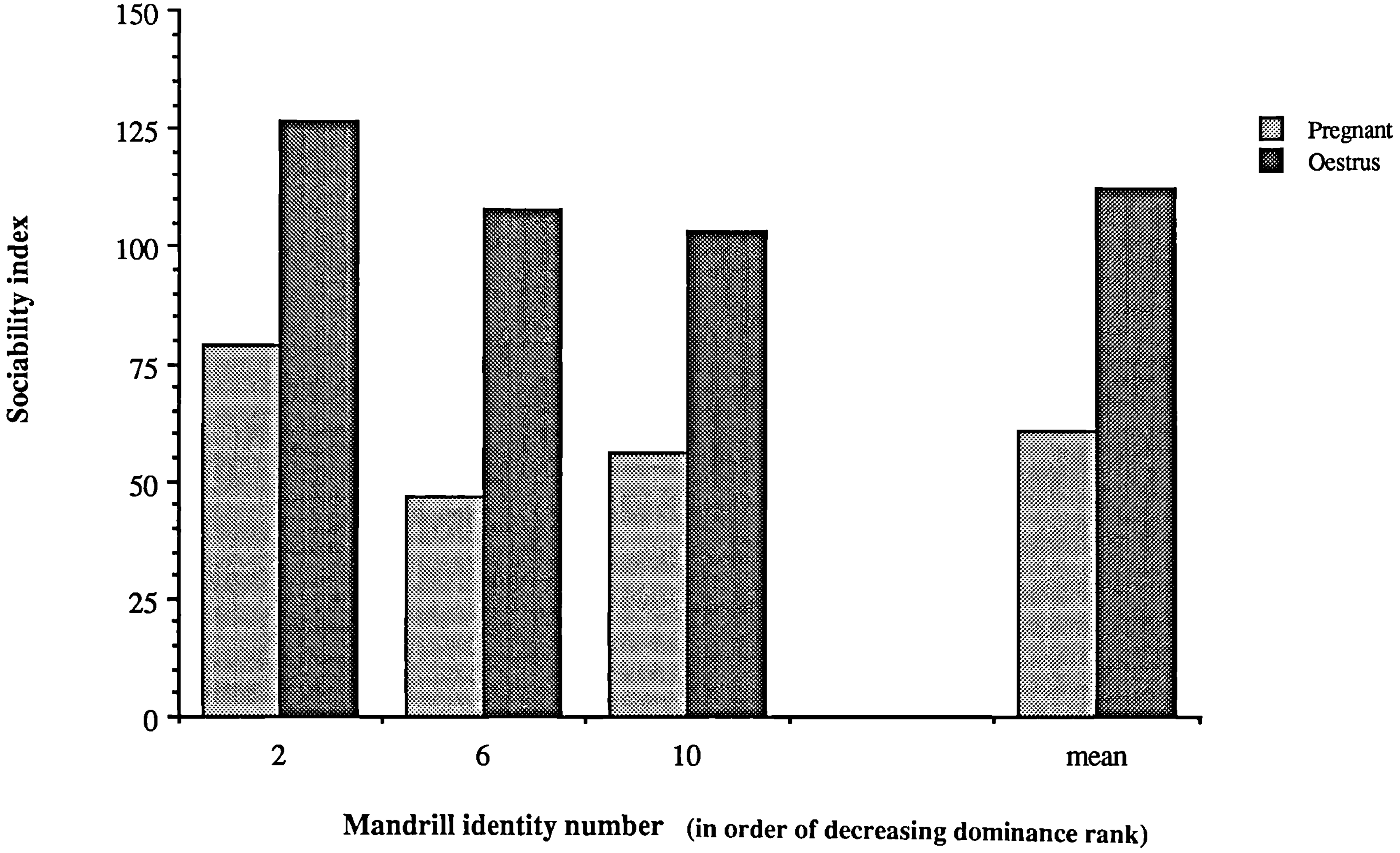
(with the exception of Male 3) had significantly higher indices on oestrous days than non-oestrous days ($t = 5.267$, $df = 5$, $p < 0.01$). The increase in sociability index from non-oestrus to oestrus was larger for the alpha male than for the other males (Male 7 = 84, Males 14, 9, and 13 = approx. 56, Male 15 = 30, Male 18 = 18) and there was a strong correlation between dominance rank and increase in sociability ($r_S = 0.77$, $n = 6$, NS) with more dominant males having a greater increase in sociability index than more subordinate males.

The female sociability indices for oestrus are shown in Figure VI.2 and the indices for these females when they were pregnant are included for comparison. In all three females oestrus sociability indices were significantly higher than those in pregnancy ($t = 10.953$, $df = 2$, $p < 0.01$). In contrast to pregnant and lactating females, who were significantly more sociable than males on non-oestrous days, females in oestrus did not have sociability indices that were significantly different from males on oestrous days ($t = 1.610$, $df = 7$, NS) although the mean index of females was greater than that of males (112.5 vs. 78.1). During oestrus sociability indices of females paralleled dominance rank, with the alpha female (No. 2) having the greatest index and thus being the most sociable female. This contrasted to her relative position during pregnancy when she was not extreme in comparison to all other pregnant females, and dominance did not correlate with sociability (see Chapter V).

In order to examine in more detail the spatial relationships between individuals during periods of female sexual receptivity, the 0-5 m distance categories were examined separately. The analyses reported below used the unweighted percentage scores.

As explained in Chapter V, some individuals were never recorded within a specific distance category in relation to a focal individual and thus their score was 0% of the time. These 0% scores were termed 'empty slots' and the mean percentage of empty slots was calculated as described in Chapter V, Table V.3.

Figure VI.2. Sociability indices of female mandrills during pregnancy and oestrus



One-sample t-tests were used to test for difference between the alpha male and other males. To assess whether dominance rank correlated with proximity, Spearman rank correlations of rank proximity score (percentage time) and dominance rank were done for distance categories where on average < 33% of slots were empty. Since the alpha individual was predicted to differ from others the Spearman correlations were done in two ways: (a) excluding the data of the alpha individual and (b) with this individual's data included. The Spearman statistic was not reported if there was more than one tie. Alpha was set at 0.05 and all probabilities were two-tailed.

Spatial relationships of females in oestrus

The data from 62 focal samples of three females (Nos. 2, 6, and 10) in oestrus are reported below.

A) Oestrous Female - Male Proximity

In examing the proximity data for females in oestrus the following questions were considered:

> In relation to females in oestrus, is the alpha male extreme
> among males in his proximity?
> Does the dominance rank of males predict their spatial proximity
> to oestrous females?

a) At 0-1 m on average 50% of the slots for males were empty (Table VI.1), indicating that on average half the males were never within a metre of an oestrous female. As shown in Table VI.1 the alpha female (No. 2) had the smallest percentage of empty slots, so more males spent some time close to her than did to the other two females. The average number of empty male slots was fewer for these females when they were in oestrus than when they were pregnant (Table VI.1) suggesting that more males were in proximity to oestrous females than to pregnant females, and hence that female reproductive state affected spatial relationships. Being within arms' length of an oestrous females was monopolised by the alpha male (No. 7). Table VI.2 shows the

Table VI.1. Mean percentage empty slots in relation to focal females

	0-1 m	1-2 m	2-5 m
Oestrous female - male			
No. 2	33	17	0
No. 6	67	50	0
No. 10	50	22	0
Mean	50	22	0
Pregnant female - male			
No. 2	50	50	0
No. 6	83	50	0
No. 10	50	33	0
Mean	61	44	0
Oestrous female - female			
No. 2	67	17	0
No. 6	50	50	0
No. 10	17	0	0
Mean	45	22	0
Pregnant female - female			
No. 2	17	17	0
No. 6	17	0	0
No. 10	0	0	0
Mean	11	6	0

percentage time that Male 7, in comparison to the average of the other five males, spent in proximity to the three oestrous females at various distance categories. The results of t-tests showed that he was significantly different to other males in all cases, and spent more time close to females in oestrus than did other males (Table VI.2). At 0-1 m, Male 7 had the highest score, in terms of time spent in proximity, in relation to all three females. While other males spent less than 1% of the time <1 m from oestrous females, Male No. 7 spent from 12% to 15% of the time at this distance category.

b) At 1-2 m an average of 22% of the slots were empty, half as many as when the females were pregnant (Table VI.1). The alpha female (No. 2) had the smallest percentage of empty slots. The alpha male (No. 7) spent the most time (2% to 13%) at this distance category for all three oestrous females, significantly more than other males, who averaged less than 1% (Table VI.2). There were no strong correlations between rank proximity and dominance rank among the other males, but all correlations increased when the data of the alpha male were included (Table VI.3). The alpha male also spent the most time near these females during their pregnancies, though no male spent more than 3% (Table VI.2).

c) There were no empty slots at 2-5 m (Table VI.1) so all males were recorded between 2 and 5 m of a female in oestrus. The alpha male (No. 7) spent the most time at this distance from all three females. His significantly greater scores were three to five times higher than those of other males and averaged 30% of the time in proximity to their mean value of 9% (calculated from Table VI.2). There were no consistent correlations of rank proximity scores with dominace rank among the other males (Table VI.3). Inclusion of Male 7's data increased the correlations (Table VI.3).

Summary

More males spent time near oestrous females than they did near these females during their pregnancies. In addition, all males spent more time close to females in oestrus than they did close to these females when they were pregnant. However, most males spent less than 1% of the time within 2 m of an oestrous female. The clear

Table VI.2. Percentage time that males were in proximity to focal females in oestrus and to focal pregnant females; the alpha male (No. 7) vs. other males (n = 5)

Distance category	Female identity	Oestrus		Pregnant	
		Male 7	Other males	Male 7	Other males
	No. 2	12.1	1.1 ***	7.3	0.2 ***
0-1 m	No. 6	15.4	0.1 ***	0.0	0.0
	No. 10	12.9	0.4 ***	3.7	0.2 ***
	No. 2	12.5	1.3 ***	3.1	0.2 ***
1-2 m	No. 6	2.4	0.5 **	1.6	0.1 **
	No. 10	6.9	0.6 ***	1.7	0.1 ***
	No. 2	46.2	9.6 ***	11.4	3.9 ***
2-5 m	No. 6	25.5	9.8 *	7.6	3.0 **
	No. 10	21.6	7.2 **	16.5	2.3 ***
	No. 2	70.8	12.0 ***	21.8	4.3 ***
Total	No. 6	43.3	10.4 **	9.2	3.1 ***
	No. 10	41.3	8.3 ***	21.9	2.6 ***

One-sample t-test, Male 7 vs. other males, df = 4,
* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table VI.3. Spearman rank correlations between rank percentage time in proximity and dominance rank among mandrills during periods of oestrus

Distance	0-1 m		1-2 m		2-5 m	
Alpha	Excl.	Incl.	Excl.	Incl.	Excl.	Incl.
	n = 5	n = 6	n = 5	n = 6	n = 5	n = 6
Oestrous female - male						
No. 2	-0.13Δ	0.36	0.30Δ	0.60	-0.50Δ	0.14
No. 6	-Δ	-	-Δ	0.53	0.00Δ	0.43
No. 10	-Δ	-	0.57Δ	**0.76**	0.57Δ	**0.76**
Oestrous female - female						
No. 2	-	-	-	-	0.44	0.44
No. 6	-	-	-	-	0.65Δ	**0.83**
No. 10	0.40	0.47	0.20	-0.10	**0.80**	**0.83**
Oestrous# male - female (n = 6, n = 7)						
No. 7	-	-	-Δ	-	**0.89***	**0.85***
No. 14	-	-	-	-	-0.60	-0.32
No. 9	-	-	-	-	0.31	0.29
No. 13	-	-	-	-	0.53	0.42
No. 15	-	-	-	-	-0.66	-0.68
No. 18	-	-	-	-	**-0.70**	-0.63
Oestrous male - male (n = 4, n = 5)						
No. 7	-	-	-	-	-0.30	-0.30
No. 14	-	-	-	-	-0.60	-0.60
No. 9	-	-	-	-	-0.65	-0.53
No. 13	-	-	-	-	**0.80**	**0.90***
No. 15	-	-	-	-	0.40	0.60
No. 18	-	-	-	-	-	-

No r_S reported when > 33% empty slots or > 1 tie * $p < 0.05$
Δ alpha individual extreme
data for males from oestrous days
Coefficients in bold type are those accounting for at least 50% of the variance
(see Chapter V) Mandrills presented in order of decreasing dominance rank within sex

exception was the alpha male (No. 7) who was less than a metre from an oestrous female 13% of the time, and from 1-2 m 7% of the time. Summing over all three distance categories and averaging over the three females, Male No. 7 was within five metres of an oestrous female in 50% of point samples; other males averaged only 10% (Table VI.2).

B) Oestrous Female - Female Proximity

Similar questions were asked about relationships between females.

Is the alpha female extreme in her proximity to oestrous females?

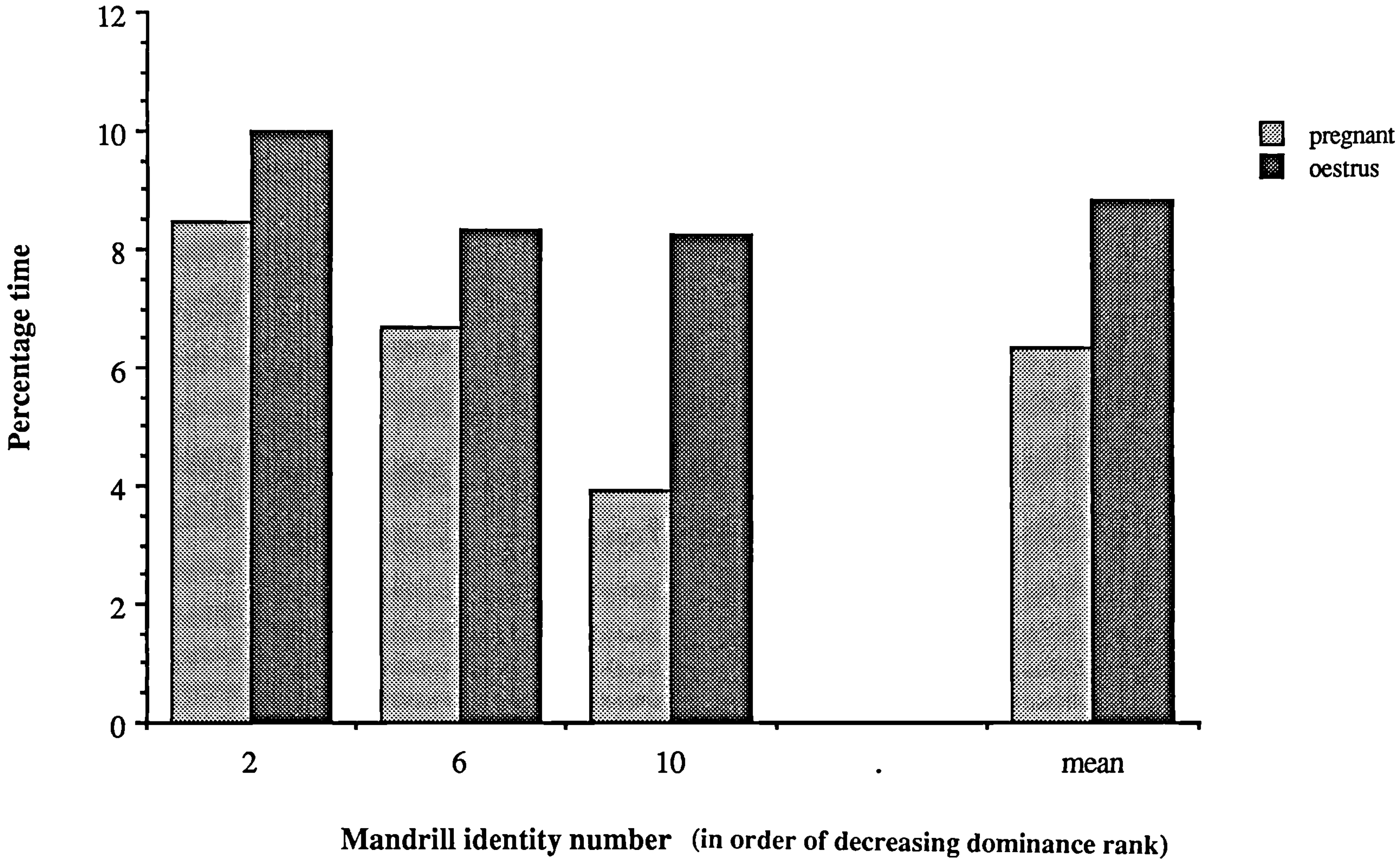
Does dominance rank predict spatial proximity of females to female in oestrus?

a) At <1 m on average 45% of the slots were empty, indicating that nearly half of the females were never recorded within arm's length of a female in oestrus (Table VI.1). This was an absence of four times as many females as was the case when the same three focal females were pregnant (Table VI.1). Thus fewer females spent any time in close proximity to females in oestrus than they did to pregnant females.

b) Although four-fifths of the females were recorded 1-2 m from an oestrous female, on average they spent less than 1% of the time at that distance. As with the previous distance category, far fewer females were close to oestrous females than were close to pregnant individuals (Table VI.1).

c) All females spent some time 2-5 m from an oestrous female, as was also the case when the focal females were pregnant (Table VI.1). In two of the three females there was a strong correlation of time in proximity and dominance rank when the data of the alpha female were included ($r_S = 0.83$, $n = 6$, NS) with more dominant individuals spending more time close to oestrous females than more subordinate females. On average females spent more time 2-5 m from oestrous females than they did from pregnant females. This is illustrated in Figure VI.3.

Figure VI.3. Percentage time in proximity at 2-5 m of females to oestrous females



Summary

In general, when females were in oestrus fewer other females spent any time close to them than they did when these same females were pregnant. However, those females who did spend time near oestrous females spent more time with them during their oestrus than during pregnancy. The increased proximity of males, and in particular the alpha male, to females in oestrus may influence the spatial relations between females. Some females may be prevented from being in proximity to oestrous females by the presence of the alpha male.

Relationships of Males

The data reported below come from focal samples (n = 69) on males which were taken on days in which a female was in oestrus.

A) Male - Male proximity

Similar questions about the effects of dominance on spatial proximity of individuals to focal males were examined.

> Is the alpha male extreme in his proximity to males on oestrous days?
>
> Does dominance rank predict spatial proximity between males?

a) Most males were never within a metre of another male, as indicated by an average of 87% empty slots (Table VI.4). Information about empty slots during non-oestrus are included in Table VI.4 for comparison and there was a slightly smaller percentage of empty slots (80%) during non-oestrus than during oestrous days.

b) At 1-2 m an average of 60% of slots was empty indicating that nearly two-thirds of the males never were in close proximity to another male (Table VI.4). This was fewer males than during non-oestrus (73%). The most dominant (No. 7) and most subordinate (No. 18) males had very high percentages of empty slots - 100%; no

Table VI.4. Mean percentage empty slots in relation to focal males

Identity	0-1 m	1-2 m	2-5 m
Oestrous* males - females			
No. 7	29	14	0
No. 14	86	43	0
No. 9	29	43	0
No. 13	43	29	0
No. 15	100	57	0
No. 18	71	73	17
Mean	60	38	3
Non-oestrousΔ males - females			
No. 7	29	29	0
No. 14	86	43	0
No. 9	43	29	0
No. 13	71	57	0
No. 15	86	57	0
No. 18	71	29	0
Mean	64	41	0
Oestrous males - males			
No. 7	80	100	0
No. 14	100	60	0
No. 9	100	40	0
No. 13	80	20	0
No. 15	80	40	0
No. 18	80	100	40
Mean	87	60	7
Non-oestrous males - males			
No. 7	80	60	0
No. 14	100	100	0
No. 9	80	80	0
No. 13	40	40	0
No. 15	100	60	0
No. 18	80	100	0
Mean	80	73	0

* Data from days on which a female was in oestrus
Δ Data from days on which females were anoestrus

Mandrills presented in order of decreasing dominance rank other males were ever recorded at this distance from them.

c) For five of the six males all other males spent some time 2-5 m from them (Table VI.4). There were no consistent correlations of time in proximity with dominance rank (Table VI.3). For the three most dominant mandrills these correlations were negative, but nonsignificant. They were not substantially altered by inclusion of the alpha individual. The negative correlations indicated a tendency for dominant individuals rarely to be close to each other. However, in comparison to non-oestrous days, all males spent more time in proximity to other males; in some cases this increase was dramatic. The mean percentage time other males spent 2-5 m from the focal male during oestrus and non-oestrus are shown in Figure VI.4. There was a strong positive correlation ($r_S = 0.90$, $n = 6$, $P < 0.05$) between dominance rank and the rank increase in the percentage time, such that more dominant males spent more time in proximity to each other on days when a female was in oestrus than they did on anoestrous days. On average time spent in proximity increased from 2% during non-oestrus to 7% during oestrus (Figure VI.4). Given that time spent by males in spatial proximity to females increased during oestrus, particularly by the alpha male, any male who spent more time near oestrous females would likely also be near another male. This may account for the unexpected increase in time spent in spatial proximity to each other by males

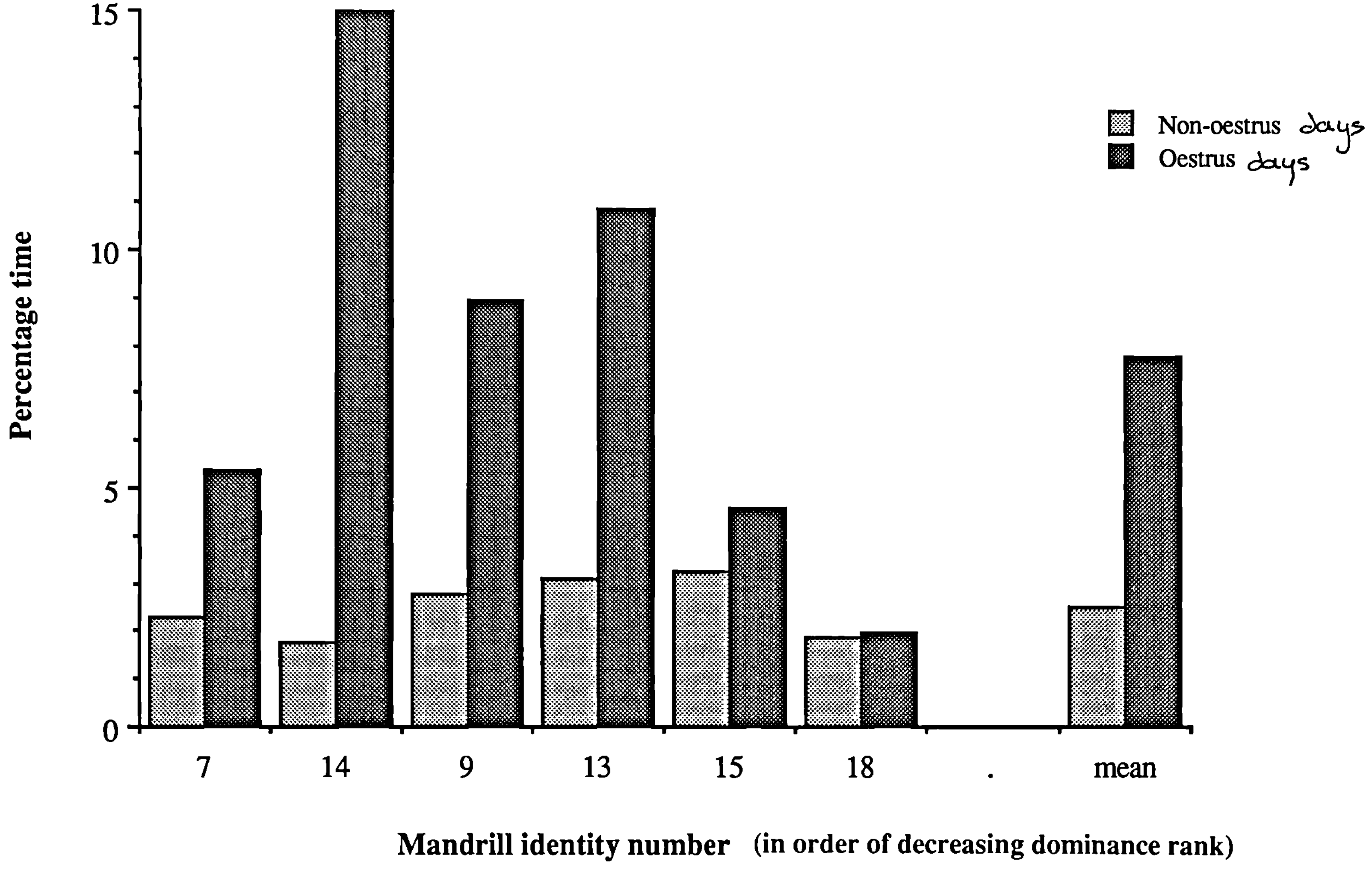
B) Male - Female proximity

Proximity between males on oestrous days and females was examined as follows:

Is the alpha female extreme among females in her proximity to males on oestrous days?

Does female dominance rank predict spatial proximity between females and males on oestrous days?

Figure VI.4. Male - male proximity at 2-5 m

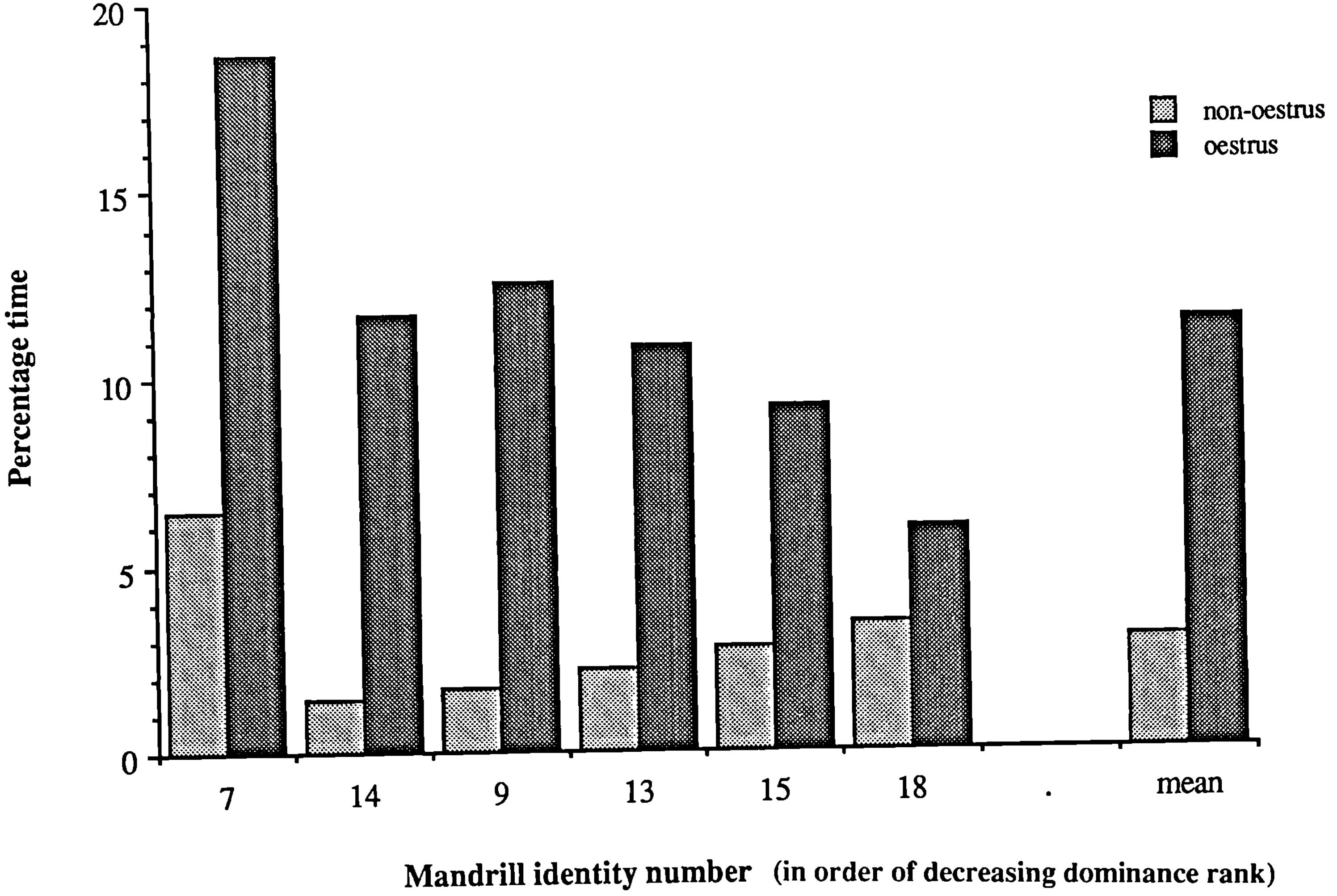


a) On average 60% of the females never were observed at 0-1 m of a male, which was very similar to that for non-oestrus (64%). However, for the alpha male and one other male (No. 9) 30% of females were never recorded close to them (Table VI.4).

b) At 1-2 m 38% of females never were recorded near males, which resembled the proportion for pregnancy. The alpha male (No. 7) had the extreme low score, with only 14% of females never recorded at this distance from him.

c) On average most females were recorded as spending some time 2-5 m from a male on oestrous days. Males and females spent more time near each other, in comparison to non-oestrus days. Figure VI.5 shows the mean percentage time females spent 2-5 m from the focal male during on oestrous and non-oestrous days. Although all males spent more time in proximity to females during oestrous days than non-oestrous days, the pattern in relation to male dominance rank was very different. In both conditions the alpha male had the extreme high score, spending more time in proximity to females than any other male (Figure VI.5). Among the other five males, during non-oestrus there was a perfect negative correlation (r_S = -1.00, n = 5, $p <$ 0.05) between dominance rank and rank time spent in proximity, with subordinate males spending more time near anoestrous females than males of higher rank. This is clearly illustrated in Figure VI.5. However, on days in which a female was in oestrus, there was a strong positive correlation (r_S = +0.90, n = 5, NS) between dominance rank and time spent in proximity, with more dominant males spending more time near females than subordinates. In addition, the increase from non-oestrus to oestrus in percentage time spent in proximity also correlated positively with dominance (r_S = 0.90, n = 6, $p < 0.05$) such that the difference was greater for dominant males than it was for subordinates, indicating that male-female proximity increased more for dominants than for subordinates on days on which there was a female in oestrus in the group.

Figure VI.5. Female proximity at 2-5 m in relation to focal males

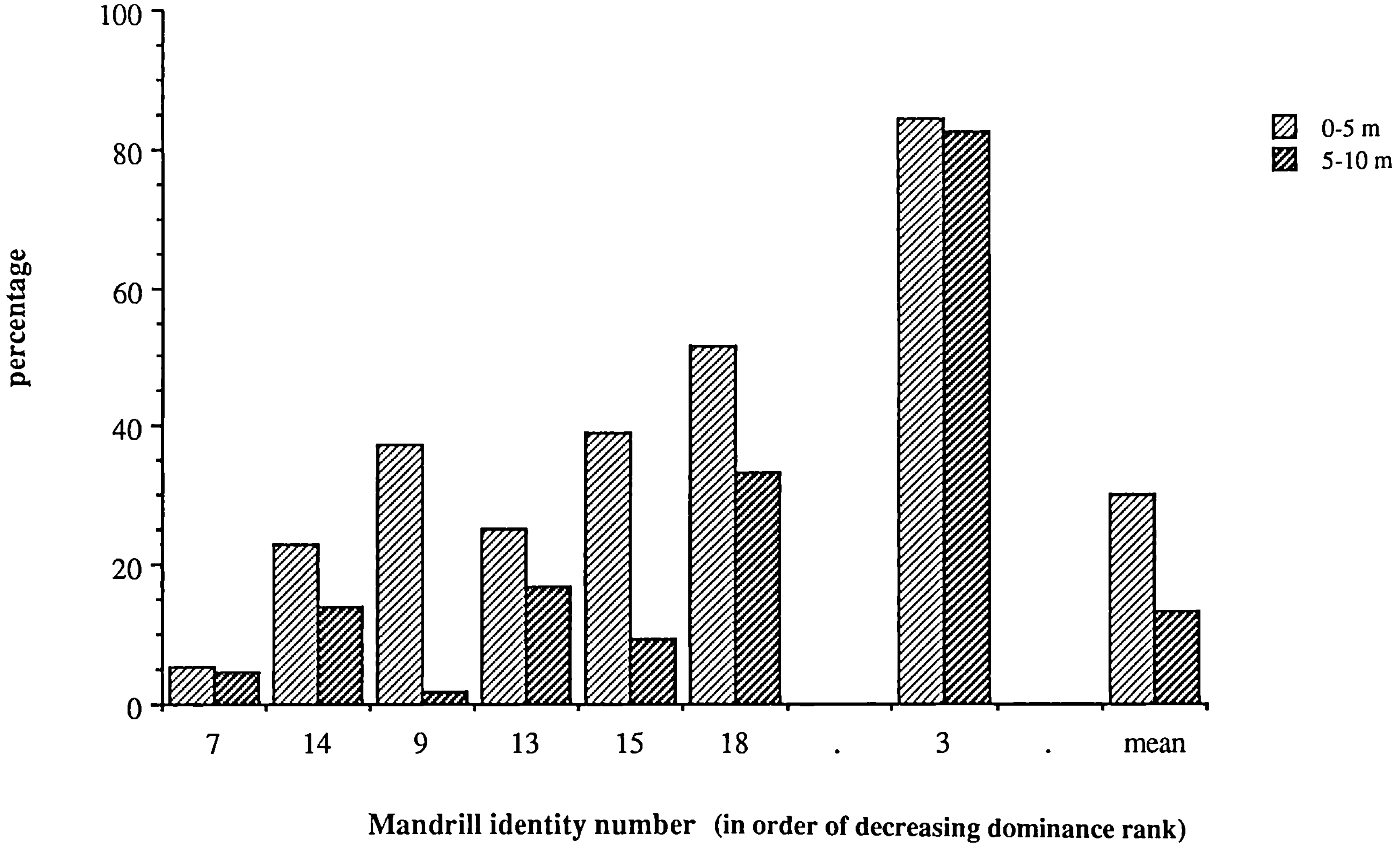


As in the previous chapter, measures of absence were analysed in order to obtain a more general picture of dispersion. The point samples in which no other founder mandrill was recorded in proximity were summed and divided by the total number of point samples to give the percentage time a focal individual had no founder neighbours at 0-5 m and at 5-10 m.

Planned comparison t-tests were used to test for differences between males and females. One-sample t-tests were used within males to see if the alpha individual was different from the others. Spearman rank order correlations were used to test whether the rank percentage time with no neighbours correlated with dominance rank within males. The Spearman statistic was not reported if there was more than one tie. Since the alpha individual was predicted to differ from others the Spearman correlations were done in two ways: (a) excluding the data of the alpha male and (b) with this alpha male's data included. All probabilities were two-tailed and alpha was set at 0.05. In all figures mandrills are shown in order of decreasing dominance rank within sex. Male No. 3 was excluded from analysis.

Male mandrills. Figure VI.6 shows the percentage time males spent with with no founder neighbours on days on which a female was in oestrus. The second ranking male, No. 3, is shown at the end. It is clear that the alpha male, No. 7, had the lowest percentage at the 0-5 m distance category, indicating that he was without neighbours on significantly fewer occasions than other males (Male 7 vs. others, 5.3% vs. mean = 35.2%, $t = 5.783$, $df = 4$, $p < 0.01$). This difference was not significant at 5-10 m ($t = 1.969$, $df = 4$, NS) although Male 7 spent less time with no neighbours (4.7%) than other males (mean = 15.0%). At both distance categories there was a negative correlation of dominance rank with rank percentage time with no neighbours (0-5 m: $r_S = -0.90$, $n = 5$, NS; 5-10 m: $r_S = -0.50$, $n = 5$, NS) indicating that subordinate males spent more time alone than more dominant males. Both the relationships were strengthened by inclusion of the alpha male (0-5 m: $r_S = -0.94$, n =

Figure VI.6. Percentage time with no neighbours in male mandrills on oestrous days



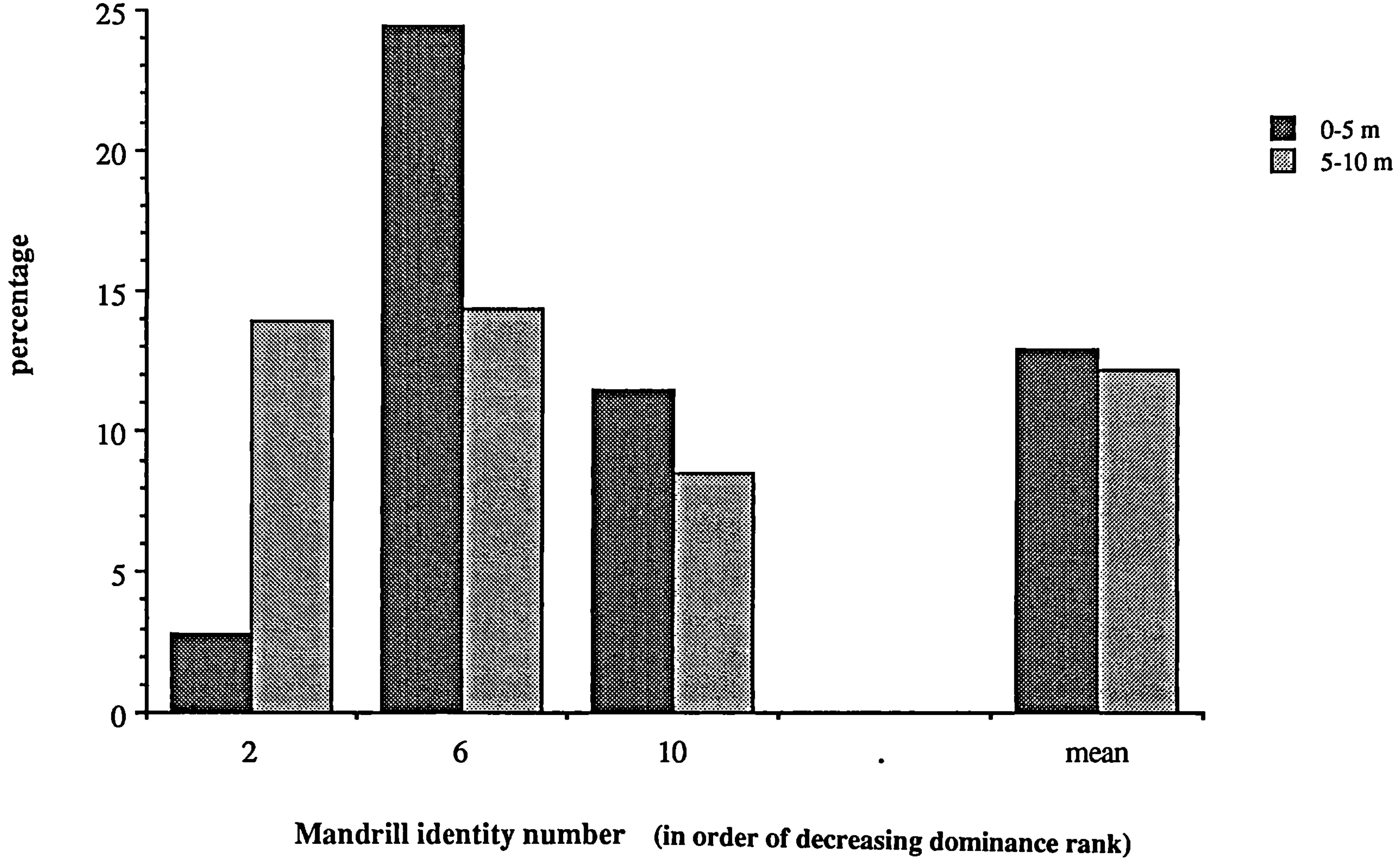
6, $p < 0.05$; 5-10 m: $r_s = -0.60$, $n = 6$, NS). This trend was the reverse of that found on non-oestrous days (Chapter V), when more subordinate males spent less time alone than dominants. All male mandrills spent less time alone on oestrous days than they did on non-oestrous days and the difference was significant at both distance categories (0-5 m: $t = 5.372$, $df = 5$, $p < 0.01$; 5-10 m: $t = 3.902$, $df = 5$, $p < 0.02$).

Female mandrills. Figure VI.7 shows the percentage time female mandrills in oestrus spent with no founder neighbours. Females in oestrus did not spend significantly less time alone than males on oestrous days, (0-5 m: females vs. males, 13.2% vs. 30.2%, $t = 1.617$, $df = 7$, NS; 5-10 m: 12.2% vs. 13.3%, $t = 0.161$, $df = 7$, NS) contrary to the situation when females were pregnant (Chapter V) when at both distance categories they spent significantly less time alone than males. The three females spent significantly less time alone when in oestrus than when pregnant at 0-5 m (12.9% vs. 40.7%, $t = 8.602$, $df = 2$, $p < 0.02$) but not at 5-10 m (12.2% vs. 17.5%, $t = 2.428$, $df = 2$, NS).

Summary

The absence measures on oestrous days were markedly different from those reported in the previous chapter, collected during periods of anoestrus, in both males and females. Individuals of both sexes spent significantly less time alone during periods when females were sexually receptive than when they were not. On average oestrous females spent 13% of the time with no other founders within 5 m of them, whereas when they were pregnant these same females were alone 41% of the time. In males the time they spent without founder neighbours at less than 5 m on oestrous days (35%) was halved from that on non-oestrous days (71%). The alpha male was exceptional among males in that he spent the least time (5%) alone at this distance. Among other males, more dominant individuals spent less time alone than did subordinates. This was the reverse of the situation on non-oestrous days. At the 5-10 m distance category, males had no founder neighbours 15% of the time, a third of the time

Figure VI.7. Percentage time with no neighbours of female mandrills in oestrus



with no neighbours on non-oestrous days (48%). In females the differences were much less marked. In both reproductive states, pregnancy and oestrus, females spent about 15% of the time with no other founders at 5-10 m. The implications of these findings for social structure are discussed in Chapter VII.

Overall comparisons of spatial relationships between males and females in relation to different reproductive states can be made by examining the pattern of empty slots. As mentioned in Chapter V empty slots is a powerful measure in that the percentage of empty slots indicates the proportion of individuals (of a specified sex) which were never recorded at a particular distance from a focal mandrill. So what follows is an overall description based on *absence* of proximity.

Comparisons in relation to focal males and then focal females are summarised below and presented graphically in Figures VI.8 and VI.9.

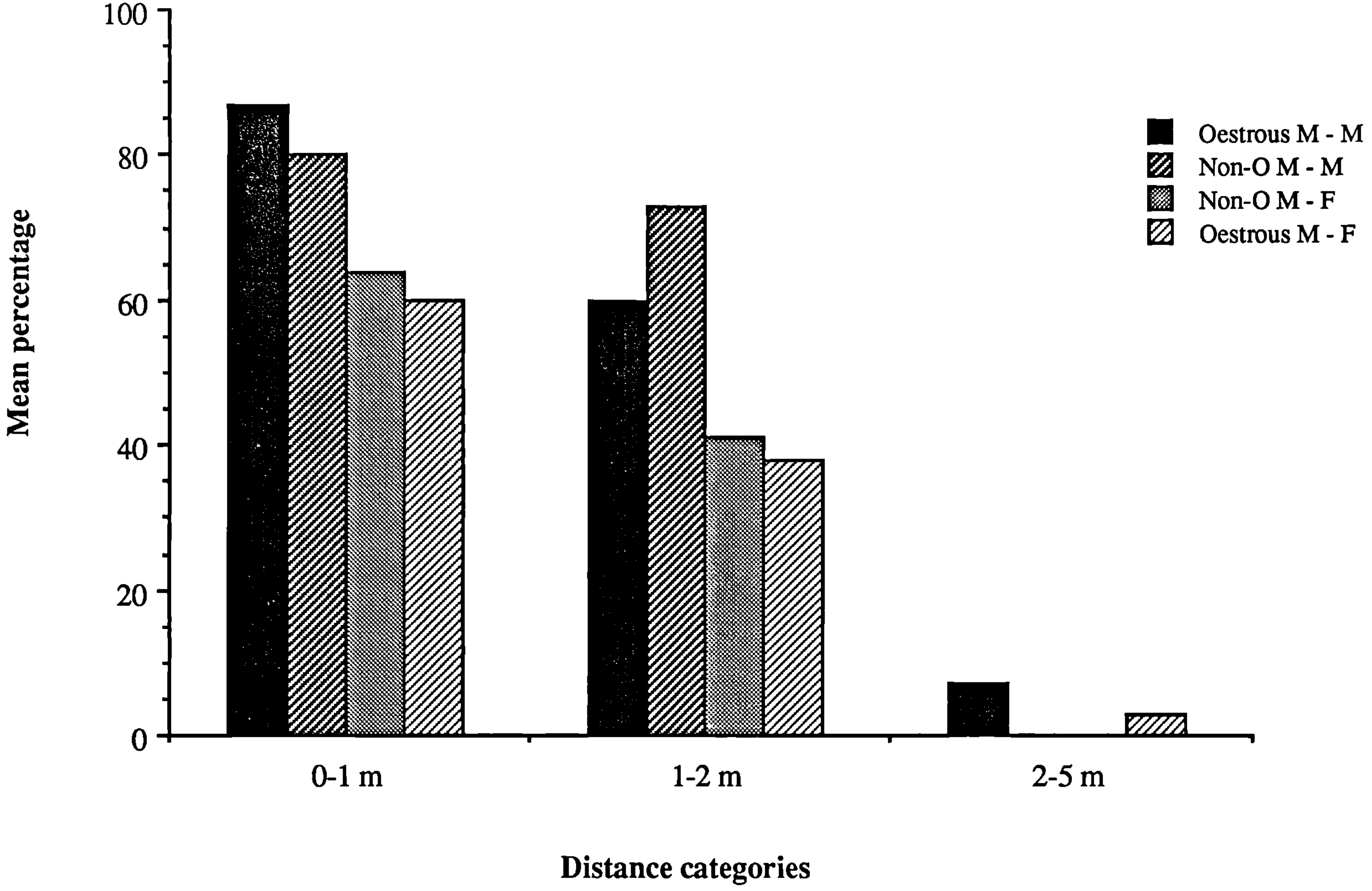
Focal males

The mean percentages of empty slots in relation to focal males (n = 6) are illustrated in Figure VI.8.

a) 0-1 m. Individuals who were least often together were male mandrills on days when a female was in oestrus (black column in Figure VI.8). Nearly 90% of males were never within arm's length of another male. The individuals with the next highest percentage of empty slots were males on days when females were anoestrous - again 80% of males were never within a metre of another male (dark striped column in Figure VI.8). About 62% of anoestrous females were never within arm's length of a male. Even on days when an oestrous female/s was present in the group 60% of females never were observed close to a male.

b) 1-2 m. At this distance males were the least likely to be close to each other on an anoestrous day - about 75% of males were never recorded within this distance of a focal male. On oestrous days 60% of males were never near each other. For females the pattern at 1-2 m was similar to that at 0-1 m, although more females were recorded near

Figure VI.8. Mean percentage empty slots for focal males



males i.e., there was a lower percentage of empty slots. About 40% of females, whether oestrous or anoestrous, were never 1-2 m of a male.

c) 2-5 m. During oestrous days about 10% of males and 5% of females were never recorded 2-5 m of a focal male.

In summary, males were very rarely in proximity (<2 m) to other males and the proportion of females in proximity to males increased at 1-2 m over 0-1 m but was similarly low on oestrous and non-oestrous days.

Focal Females

The mean percentage of empty slots in relation to the three focal females are illustrated in Figure VI.9.

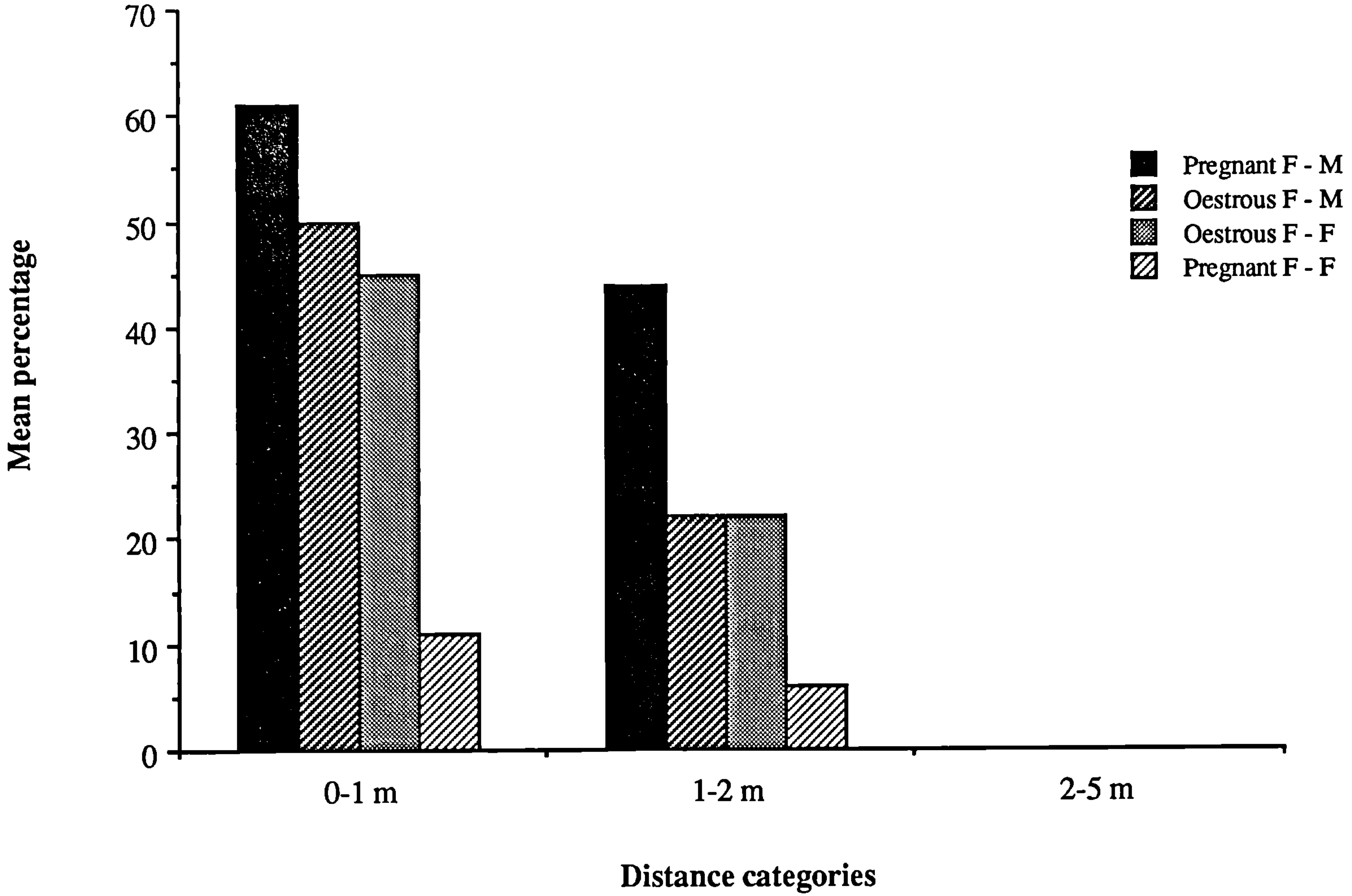
a) 0-1 m. Sixty percent of males never were recorded at this distance from a pregnant female, and half the males were never recorded so close to oestrous females. Even between females, 45% of females never were recorded within arm's length of an oestrous female. However, when females were pregnant 90% of other females spent some time very close to them (pale striped column in Figure VI.9).

b) 1-2 m. The least association between individuals at this distance category was between males and pregnant females, with 45% of males never recorded at this distance. A fifth of both males and females were never near an oestrous female. However, in relation to pregnant females 95% of females spent some time near them.

c) 2-5 m. All individuals spent some time 2-5 m from a female, whether she was pregnant or in oestrus.

In summary, both males and females were rarely in close proximity (<2 m) to focal females. However, females associated more with each other than they did with males, particularly during pregnancy.

Figure VI.9. Mean percentage empty slots for oestrous and pregnant focal females



GROOMING RELATIONSHIPS

This section describes the grooming interactions of the founder mandrills at CIRMF during periods when females were in oestrus. The data on grooming were collected during focal samples exactly as described in the previous chapter. As before, Male 3's data were excluded from analysis. Data were collected on three females (Nos. 2, 6, and 10) during oestrus. Focal sample data were also collected on these same three females during their pregnancies so oestrus scores could be compared with pregnancy scores within females. For males the grooming data were from days on which a female was in oestrus - termed oestrous days. The number of oestrus focal samples are given in Appendix V.1.

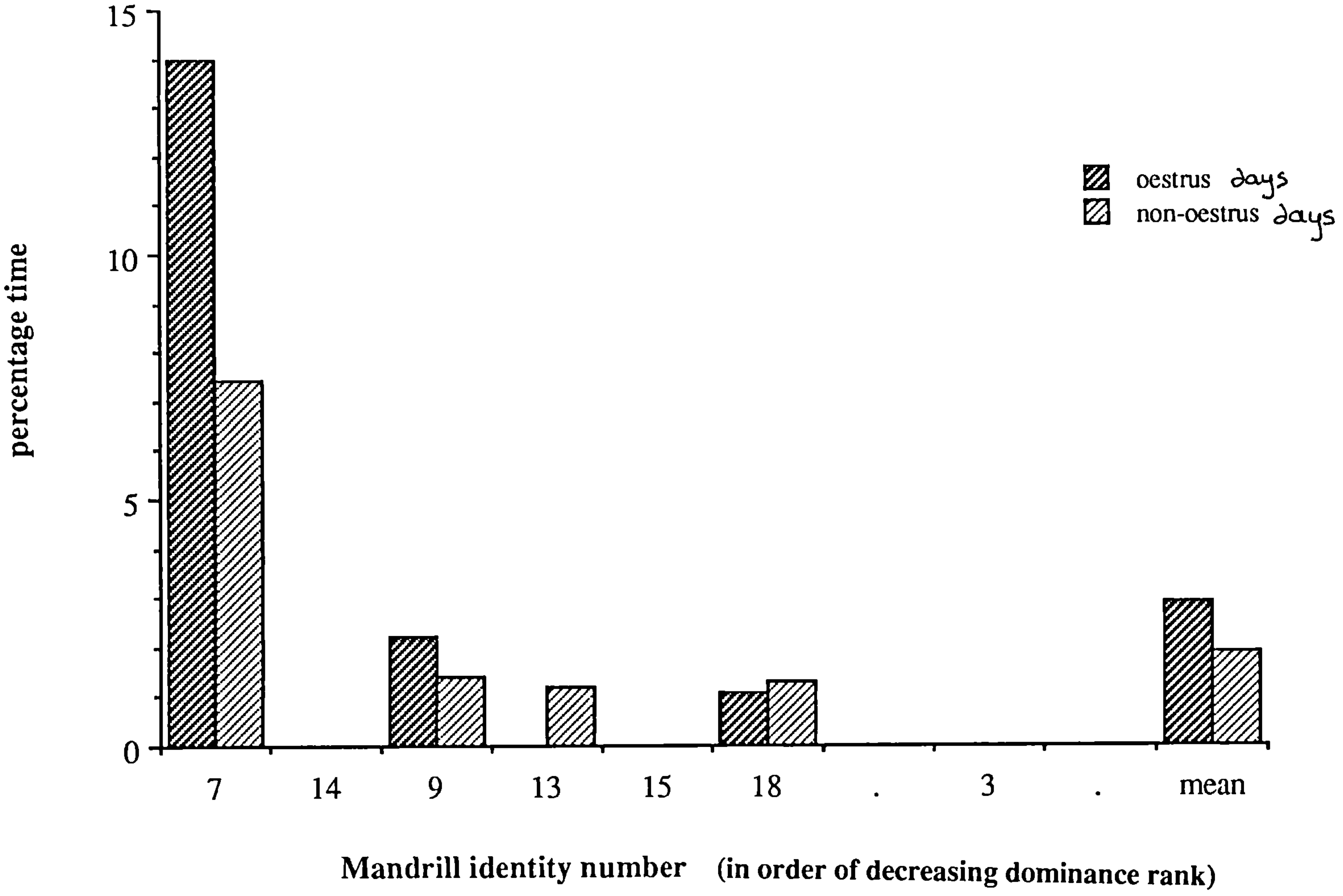
Planned comparison t-tests were used to test for differences between males and females. One-sample t-tests were used within males to see if the alpha individual was different from the others. Paired t-tests were used to test for differences between reproductive states between individuals. Tests for correlations between dominance rank and rank grooming data were not done due to the small number of individuals and large number of ties. All probabilities were two-tailed and alpha was set at 0.05. In all figures mandrills are shown in order of decreasing dominance rank within sex. Male No. 3 was excluded from analysis.

Time spent grooming

The total percentage time spent grooming by males on oestrous days and by oestrous females are described below.

The percentage time spent grooming by males on oestrous days is shown in dark hatching in Figure VI.10. Half the males were never recorded grooming. The alpha male (No. 7) had the extreme high score, spending significantly more time grooming (13.9%, about twenty times more) than the other males (0.7%, $t = 30.091$, $df = 4$, $p < 0.001$). On average males groomed more on oestrous days (2.9%) than during non-oestrus (1.9%) (light hatching in Figure VI.10) but this difference was not

Figure VI.10. Percentage time spent grooming by male mandrills



significant ($t = 1.601$, $df = 5$, NS) and was largely due to the increase in grooming of the alpha male who spent twice as much time grooming on oestrous days (13.9%) than he did on non-oestrous days (7.4%).

For females grooming with kin was excluded from this analysis to reduce variance between females and reduce bias in male-female comparisons, as explained in Chapter V. Grooming by oestrous females with their own offspring is analysed later in this chapter.

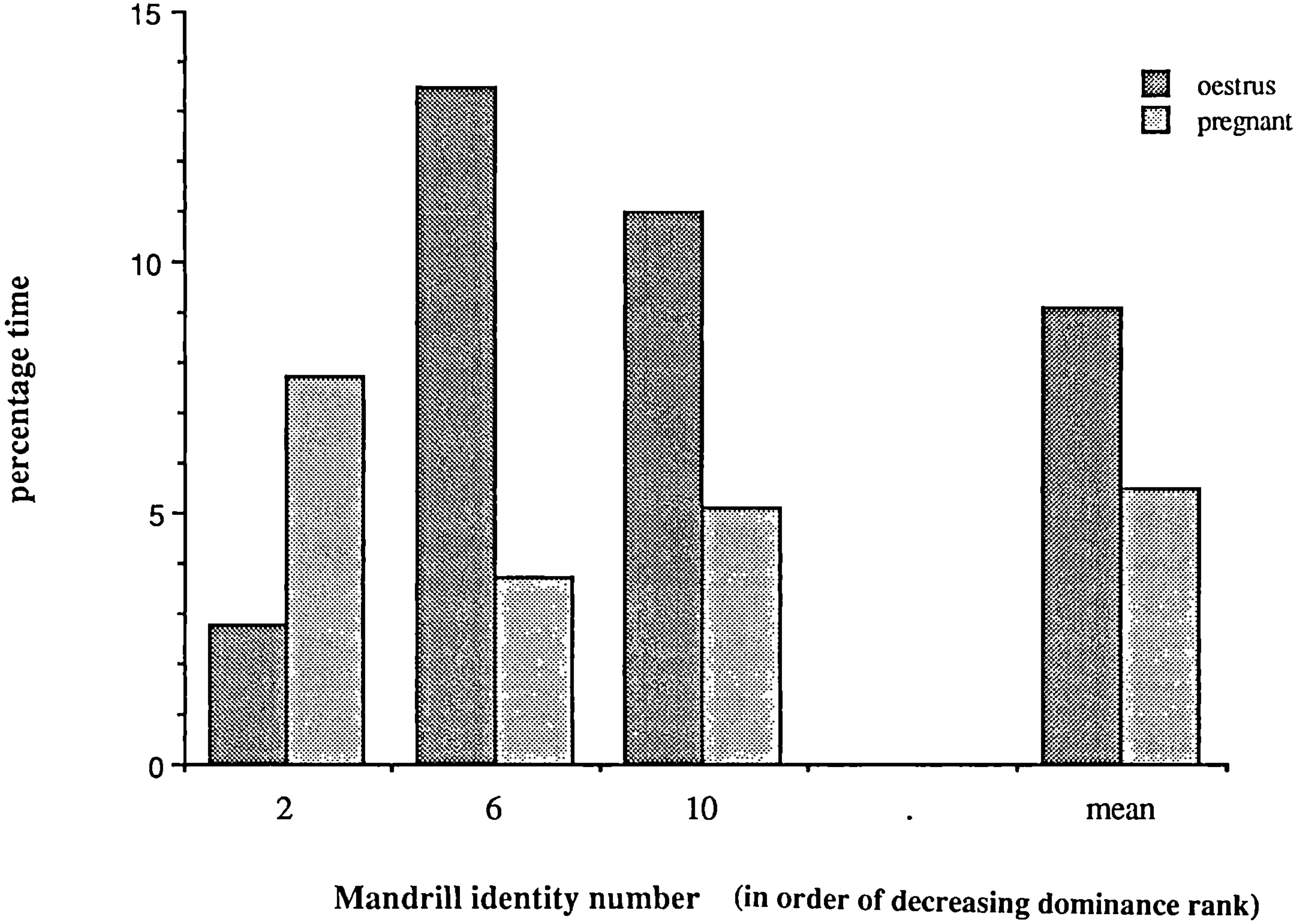
Figure VI.11 illustrates the total percentage time spent grooming with individuals other than offspring by oestrous females. Data from the same three females when they were pregnant are included in the figure for comparison. Females groomed significantly more during oestrus than when pregnant ($t = 4.929$, $df = 2$, $p < 0.05$).

To examine grooming interactions in more detail the data were divided by groomer/groomee role and by age-sex class of partner as described in Chapter V. For males, partners were categorised into (a) founders and (b) all other age-sex classes; for females, a third category, (c) own offspring, was distinguished.

Males

As can be seen in Figure VI.10 only three of the six males (Nos. 7, 9, and 18) were recorded in grooming interactions and they groomed exclusively with adult females. The two more dominant individuals (No. 7 and 9) received more grooming (mean = 74%) than they gave (mean = 26%) but gave more grooming on oestrous days than on non-oestrous days (mean = 3%). The most subordinate male (No. 18) was the groomer 100% of the time, as he was on non-oestrous days.

Figure VI.11. Percentage time spent grooming by female mandrills during oestrus and pregnancy



Females

The data for females are presented in three sections: total grooming, giving grooming, and being groomed.

Total grooming. Females in oestrus groomed only with their own offspring and with founders, and the diversity of age-sex classes of grooming-partners seen during pregnancy for these three females was not observed during oestrus [Female No. 6 had the highest diversity of grooming partners during pregnancy, see Chapter V.] On average oestrous females did 72% of their grooming with founders, much more than they did when pregnant (39%). In addition, during oestrus all females did a greater proportion of this grooming with males than they did during pregnancy. This is illustrated in Figure VI.12. During oestrus, 67% of grooming with founders was with males, twice as much as the proportion of grooming done with males founders during pregnancy (33%), as shown in Figure VI.13.

Giving grooming. During oestrus two of the three females gave less grooming to others than they did when pregnant (as shown in Figure VI.14) and all gave less to offspring during oestrus than during pregnancy. During oestrus on average females were the groomer during two-thirds of grooming, in comparison to three-quarters when pregnant (Figure VI.14). Pregnant females gave half their grooming to offspring during pregnancy but this dropped to a third when they were in oestrus. The other two-third of grooming was given to founders. Males received most (96%) of the grooming given to founders and this was over twice as much as they had received from these same females during their pregnancies (40%).

Receiving grooming: On average females received more grooming when in oestrus (33%) than when pregnant (24%). This is illustrated in Figure VI.15. Only one of the three females (No. 10) received any grooming from offspring in either reproductive state and she received about the same (40%) from her adolescent daughter

Figure VI.12. Proportion of grooming done with founders during oestrus and pregnancy

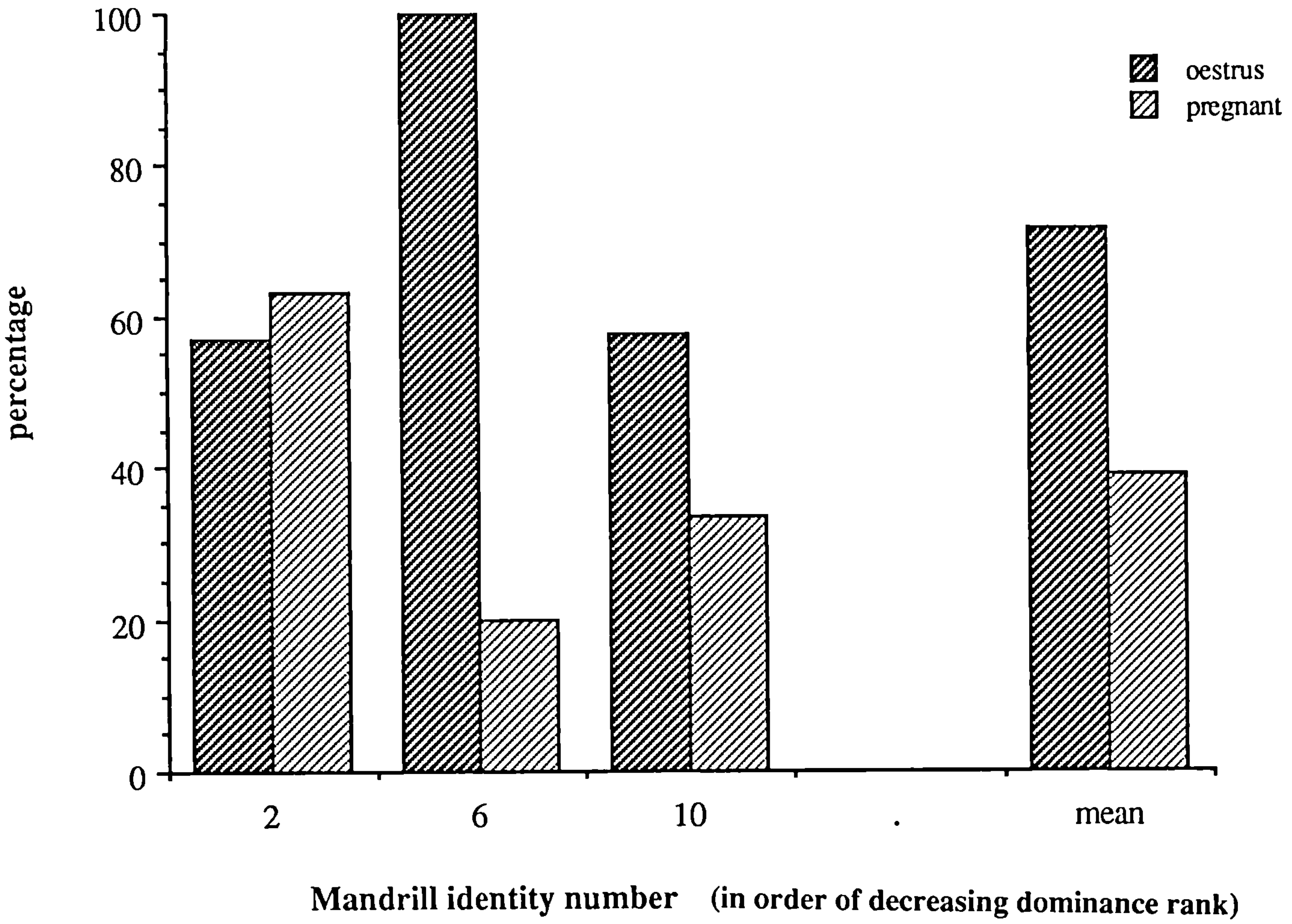


Figure VI.13. Grooming with founders by focal females: proportion done with males

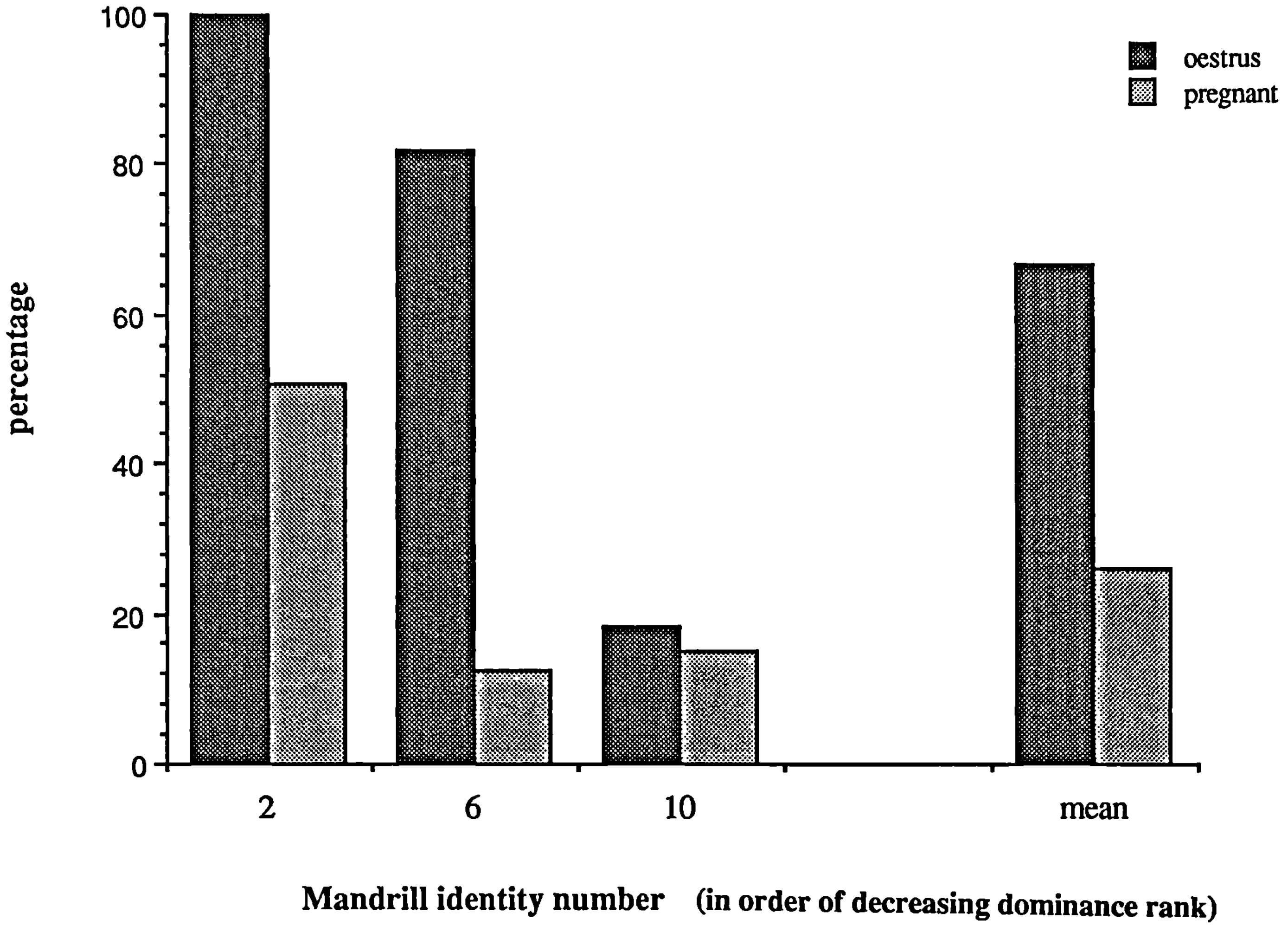


Figure VI.14. Proportion of grooming in which females groomed others

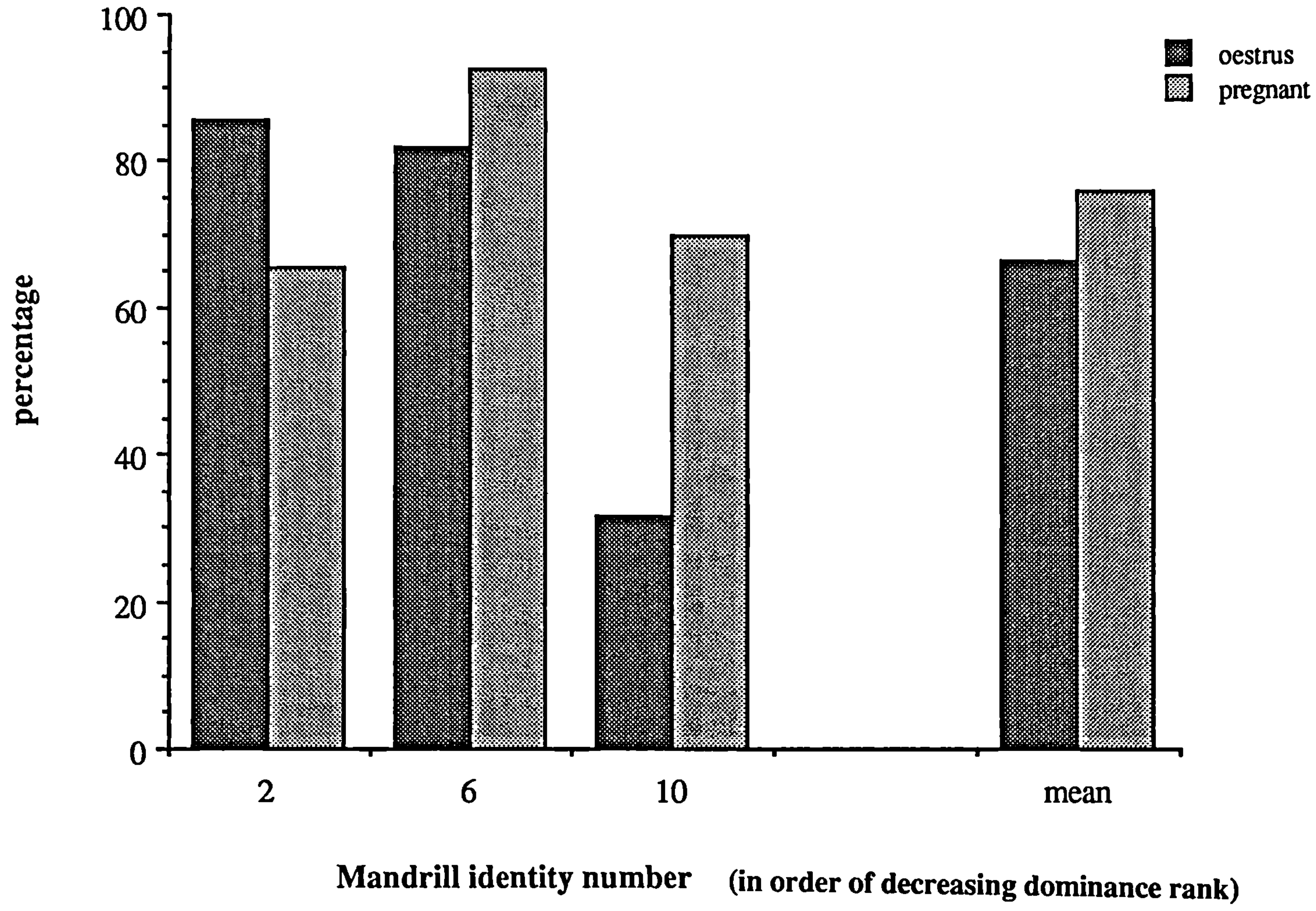
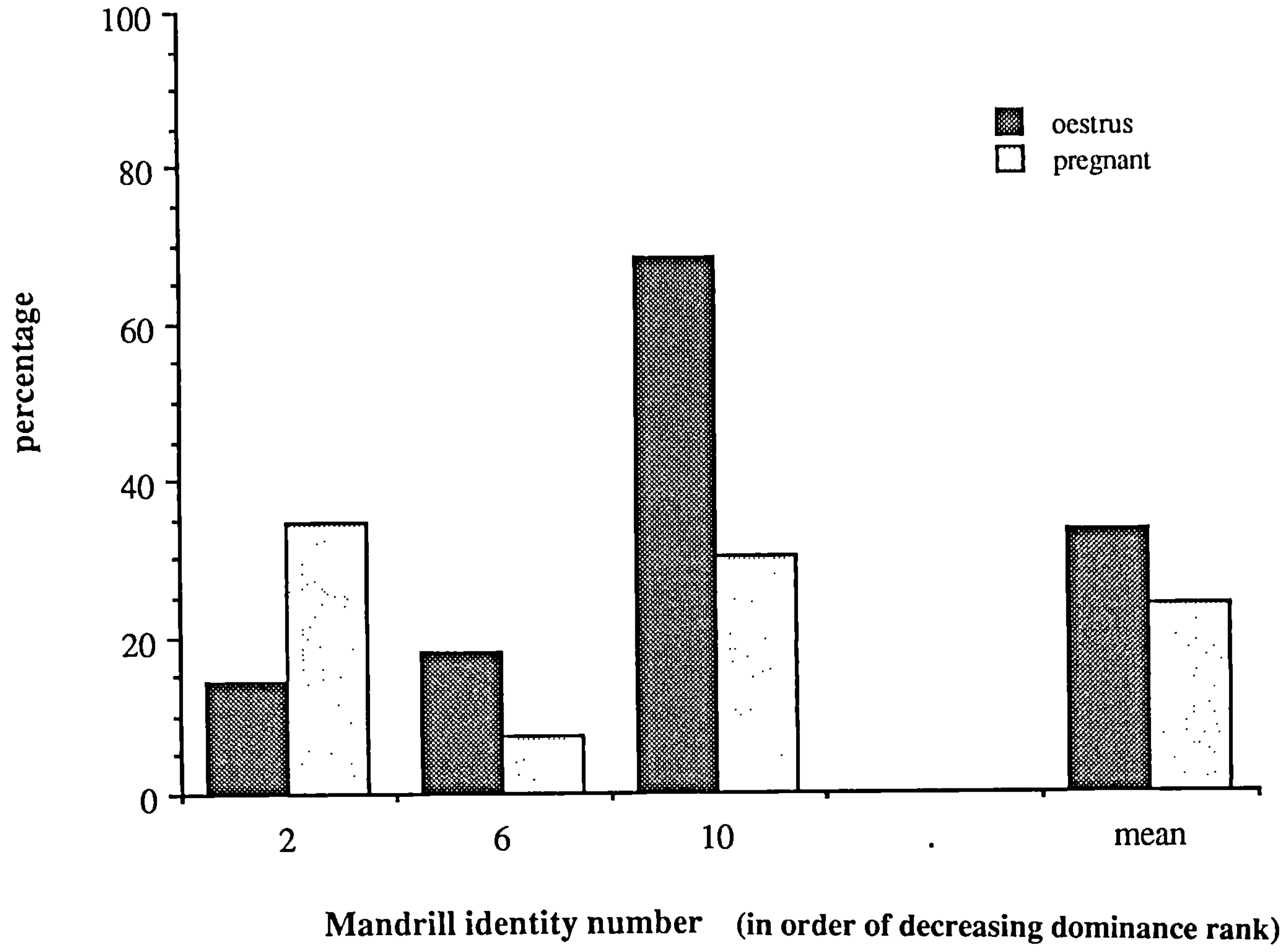


Figure VI.15. Proportion of grooming in which females were groomed by others



(10A) in both.

The two more dominant individuals (Nos. 2 and 6) received all their grooming from founders when they were in oestrus. On average 62% of this was received from males, however individually the amount an oestrous female was groomed by males related to her dominance. The alpha female, No. 2, received 100% of her grooming from males, Female 6 received 60%, and Female 10 received 25%. When pregnant, on average only 12% of grooming received from founders was given to females by males.

Summary

Grooming relationships in the CIRMF female mandrills during their periods of oestrus in comparison to during pregnancy can be summarised as follows:

(1) Females spent more time grooming when they were in oestrus than when pregnant.

(2) Females groomed with fewer age-sex classes during oestrus than when pregnant, and groomed only with their offspring and founders.

(3) During oestrus most (72%) of their grooming was with founders, whereas during pregnancy less than half was (39%).

(4) Males received nearly all the grooming given to founders by oestrous females, whereas pregnant females gave three-quarters of grooming to female founders.

(5) Females in oestrus received more grooming than pregnant females; they received more from founders and 62% of it was from founder males. During pregnancy females received less grooming from others; they were groomed less by founders and 94% was from other adult females.

Grooming relationships in the CIRMF male mandrills on days in which a female was in oestrus in comparison to non-oestrous days (in which females were pregnant and/or lactating) can be summarised as follows:

(1) Subadult and adult males groomed more on oestrous days than non-oestrous days. The alpha male groomed twenty times more frequently than other males on oestrous days and he groomed twice as much when females were in oestrus than when non-oestrus. Half the males were never observed grooming other individuals on oestrous days.

(2) Males groomed exclusively with adult females on oestrous days, but with other age and sex classes during non-oestrous.

(3) Males gave nine times as much grooming on oestrous days than they did when no females were in oestrus.

AGONISTIC RELATIONSHIPS

Agonistic relationships during periods of oestrus were examined in order to see if female reproductive state changed the agonistic components of inter-individual relationships.

As stated in the previous chapter intra-sex dominance hierarchies were stable throughout the duration of the study so relative dominance did not change during periods of oestrus.

Days on which founder females were in oestrus accounted for 23% of days on which agonistic interactions were recorded. Thus if agonistic interactions between same-sex individuals were distributed irrespective of female reproductive state, one would expect about 23% of agonistic interactions to occur on these oestrous days. Table VI.5 shows the observed percentage of dyadic interactions between males which occurred on oestrous days. The most salient dyad is Male 7 and Male14, in which 86% of interactions occurred on oestrous days. In addition, Male 14's interactions with both Male 9 and Male 15 were also over twice the expected percentage. A possible explanation for this observed distribution of agonism is given below. Three dyads had interactions at least 25% below the expected percentage, Males 7 and 13, Males 13 and 18, and Males 15 and 18. None of Male 3's interactions with Males 14, 9, and 13

Table VI.5. Male - male interactions on oestrous days as a percentage of all days

Loser

Winner

	7	3	14	9	13	15	18
7		☒	86	17	12	21	24
3			0	0	0	33	☒
14				55	29	47	33
9					26	22	23
13						25	9
15							14
18							

Expected proportion = 23%

occurred during oestrus, however, a total of only 11 clear dyadic interactions between Male 3 and these males was scored during the study (Table V.7) and his dyads were excluded from further analyses. Of the 15 remaining dyads, 53% had a greater than expected proportion of agonism during oestrus.

The only fight observed during the entire study occurred in the presence of an oestrous female, and seemed to be precipitated by an attempt to copulate with her. Male 7 was mate-guarding Female 10 when Male 3 (the large, solitary male) approached and the two males fought. The interaction is described in detail below.

> 10 November 1986
> 0753: Most of the mandrills, including Male 3, are at sleeping site 2. Male 7, Female 10 who is in oestrus and whom he is mate-guarding, and adolescent Female 5A are in close proximity to each other.
> 0754: 5A presents to 7, who inspects her perineum exaggeratedly. Female 10 sits more-or-less in contact with Male 7. He grooms her.
>
> 0800: 7 is 1m from 10, Male 3 is 5 m from 10. All are arboreal. 7 smiles at 3.
> 0801: 5A presents to Male 3 who smiles at her. 5A presents to 7 who inspects her thoroughly and smiles.
> 0802: All is quiet.
> 0803: Female 10 climbs and 7 follows, passing 3 at 2 m. 7 stops and sits 2 m from 3.
> 0804: 10 climbs further and is now more than 5 m from 7.
> 7 follows her and is 7 m from 3.
> 0805: 10 climbs away again. 7 remains and 3 moves so the two males are 2 m from each other.
> 0806: 10 climbs back towards 7 to avoid 'hassle' from juvenile Male 2A.
> 0807: 7 and 10 are 6 m apart. 3 and 10 are 8 m apart.
> 0808: 3 head-bobs juvenile 2A. 7 smiles at 10.
> 0809: 7 smiles at 10's son, 10B.
> 0810: 3 faces 7. Male 7 smiles at 3.

> 0811: 7 approaches 10 to 3 m. As 7 moves towards 10, 3 moves too. 7 approaches 10 and tries to mount her. She refuses him and climbs away, 7 follows, 3 does too. 7 approaches 10 again, mounts, and they copulate. 7 has thrust 26 times when
> 0812: 3 suddenly approaches 7 and they fight. Other mandrills yell. 3 ends suspended below a branch, gains the top of the bough and stands 3-4 m from 7. Both are bleeding.
> 0813: 3 descends and leaves going south on Transect 2, leaving a trail of blood. His right hand is split open between the second and third digits. 7 has a 5 cm slash on the side of his muzzle.
> 0814: Male 18, who is terrestrial, licks 3's blood off a leaf. 7 approaches 10 to 1 m and licks the blood dripping into the side of his mouth.
> 0815: same
> 0816: 10 avoids 7 and descends. 7 descends the tree fast after her. She goes south on transect 2, after 3. She sniffs the bloody leaves. 7 follows her at 2 m. Adolescent Females12A and 5A, and Female 12 follow. 7 takes the lead on transect 2, i.e., he is between 10, the other females, and Male 3.
>
> I leave the group behind and follow the trail of blood.
> 0835: Find 3 west of transect 23 standing in the stream.

Male 7 was the winner of the interaction in that he suffered a lesser injury and his alpha position and ability to mate-guard females did not change. As described in the previous chapter Male 3's position relative to the third-ranking male, No. 14, also appeared to be in a 'state of flux'.

As shown in Figure III.14 in Chapter III, Male 7 had relatively low blood testosterone levels in October 1986 (a month before the incident described above). The previous year he had 12.8ng/ml and Male 3 had only 4.1ng/ml. However, in October 1986 their blood testosterone was 6.6 and 5.6 ng/ml respectively. In both years blood testosterone level correlated significantly with dominance rank, and it is possible that their relative similarity in hormone level may have had behavioural consequences. This idea is discussed further in Chapter VII.

Agonistic interactions between females on oestrous days can be examined in a similar manner to those of males, reported above. As before, 23% of agonistic interactions could be expected to occur on oestrous days. Table VI.6 shows the percentage of interactions of each dyad which occurred on oestrous days. In only 14% of dyads was there a higher than expected proportion of interactions during oestrus. In general females interacted agonistically less than expected. This may have been due to the influence of male-female relationships during oestrus. Proximity between males and females increased on oestrous days and oestrous females received a certain degree of protection from the alpha male, particularly when he was mate-guarding them - see below. This may have 'deterred' females from threatening a female in close association with the alpha male.

If the frequency of all agonistic interactions between founders during focal samples on oestrous days are divided by the number of minutes of focal sampling on those days, the rate of agonistic interactions could be calculated. It was 3.9/hr, which was equivalent to 0.28/hr per individual. This was more than 1.5 times the rate on non-oestrous days (see previous chapter), but was still very low compared to rates in other primates, e.g., Hausfater (1975) reported a rate of 4.5 agonistic bouts/hr between male *Papio cynocephalus*. Rates of agonistic interaction in the CIRMF mandrills are further discussed in Chapter VII.

Table VI.6. Female - female interactions on oestrous days as a percentage of all days

Loser

Winner

	2	5	6	10	12	17	16
2		11	23	39	16	16	11
5			4	14	15	15	22
6				14	12	19	11
10					0	5	20
12						28	30
17							12
16							

Expected proportion = 23%

SEXUAL RELATIONSHIPS

In the following section sexual relationships are described and in particular mate-guarding and the occurrence of this behaviour in relation to female sexual cycle.

Mate-guarding

During the mating season a behaviour which I termed 'mate-guarding' was observed. It consisted of a male deliberately maintaining proximity to a female in oestrus, by following her, sitting near her, etc. Other males were 'discouraged' from interacting with her by the mere presence of the mate-guarding male. An example of this is given below, in which a male avoids an approach by a female in oestrus. Usually males did not move away in response to approaches by females. Vocalisations (see Chapter IV) by the mate-guarding male - warning grunts - were sufficient in some cases to deter an approaching male, i.e., a male could mate-guard from a distance such as 10-15 m by voice alone. Sometimes threat grunts were also given. Mate-guarding was passive in that the male simply followed the female and did not try to influence her movements, e.g., no instances of behaviour resembling herding were seen.

In hamadryas baboons herding of females by males occurs frequently when units are travelling. Leader males look back at their females and threaten them if they lag behind. The mildest threat is a stare. A more intense reaction is a bite on the nape of the neck or back, which immediately causes a female to follow the male (Kummer, 1968, p.36-37). In the CIRMF mandrills, stares and head-bobs never resulted in an increase in spatial proximity between individuals. A threat rush sometimes resulted in the threatened animal approaching to present but then it immediately increased its distance from the individual who had behaved aggressively. The descriptions of mate-guarding given below emphasize the 'follower' role of the alpha male. The data presented below are from the 1986 mating season unless stated otherwise.

5 August 1986
Male 7 is mate-guarding Female 6
0840: Male 7 and Female 6 are arboreal, together with most of the group, at Site 2.
0845: Female 6 climbs and 7 follows her immediately.
0848: Male 7 follows as she moves again and then sits 'blocking ' her exit from (or another's entrance to) the tree.
0850: Female 6 descends past Male 7 and he immediately climbs down after her, following at 4 m.
0851: Other females appear.
0854: Male 7 maintains his position at less than 4 m from 6.
0857: Females 2, 5A, 5 and Male 7 are all < 4 m of 6.
0859: Male 7 is the only mandrill within 5 m of Female 6.

19 August 1986
Male 7 is mate-guarding adolescent Female 5A.
1525: At the feeding site are Female 16, Male 15, and Male 14; the other females have left.
Then Male 18 appears followed by adolescent Female 5A. Suddenly Male 7 arrives at a run.
1532: At the feeding site now are: Females 5A and 16, and Males 7, 14, 15, and 18.
1533: 5A leaves clutching a piece of bread. 10 secs later Male 7 follows.
1534: 5A climbs into a *Musanga* tree behind the chow-bin. Male 7 waits at the chow.
1536: 5A descends and leaves. 10 secs later Male 7 departs after her at a run.
1539: The mandrills are down one of the transects and 5A is 4 m up a tree. Male 7 sits at the base of the tree.
1549: 5A climbs out of the tree and retrieves some bread Male 14 has left and moves away. 5 secs later Male 7 moves towards her.

The above description shows the alpha male maintaining close proximity to the oestrous female. His behaviour seemed to follow hers, in that he moved within 10 seconds of her leaving or changing position. At the feeding site were four other males, yet none of them made any attempt to interact with the fully-swollen adolescent.

Various aspects of mate-guarding were investigated.

Who mate-guards?

When does mate-guarding occur -

a) in relation to the menstrual cycle?

b) within the period of maximum swelling?

Who mate-guards?

Mate-guarding by males in relation to their dominance rank is shown in Table VI.7, which shows the number of days spent mate-guarding by males of different dominance rank. The alpha male (No. 7) was, with one exception, the only male who showed this behaviour and he was able to monopolize sexual access to females by mate-guarding them. Other males frequently avoided the approach of oestrous females who were being mate-guarded by him.

2 August 1986
Male 7 is mate-guarding Female 6
1100: Female 6 appears at the fence, closely followed by Male 7. Male 9 is the only other mandrill in view. She slowly approaches 9, keeping an eye on Male 7 who is by the wall.
1101: Male 9 turns away from her and moves a few steps. He tension yawns.
1102: Both Male 9 and Female 6 watch Male 7, who has approached to 5 m of 6, who is herself only 1.5 m from Male 9. Male 9 has developed an erection.
1103: 7 closes the gap between himself and Female 6 to 4 m. Male 9 moves off a little way and displacement forages.
1104: Male 9 masturbates, but the angle of his thigh hides this from 7.

Table VI.7. Mate-guarding and male dominance rank

Male Rank	Total days spent mate-guarding	Total females guarded*
1	45	6
2	0	0
3	2	2
4	0	0
5	0	0
6	0	0
7	0	0

* Data are from 1986 and refer to 7 sexually-active females and 13 episodes of cyclical sex skin changes

1105: Male 7 tension yawns. 9 smiles at Female 6. She walks past him and 9 is now between 6 and 7, who are 5 m to either side of him.
1106: 7 grooms his leg and 9 forages idly.
1107: Male 9 approaches 7 and smiles, half presents to 7, and moves away into the undergrowth. 7 approaches 6.

5 August 1986
Male 7 is mate-guarding Female 6
0956: Female 6 climbs into a large tree at Site 2 south. Male 13 is also arboreal, about 10 m from her.
0957: Male 7 starts climbing a tree and 13, who was climbing towards 6, does a detour which takes him away from 6 and sits.
0959: Female 6 climbs along the valley (moving north) and 7 climbs higher and keeps between 6 and 13.
1000: Female 6 seems restless and continues climbing. Male 7 follows at 6 m. He is the closest to her, being the only other mandrill within 15 m except for juvenile male No. 2A.

The only other male observed mate-guarding was Male 14, who was the third-ranking male. The second-ranking male, No. 3, was solitary and rarely was seen in proximity with the group. On the day on which No. 14 mate-guarded a female, No. 7 was mate-guarding another female of higher rank.

Mate-guarding and the menstrual cycle

All mate-guarding occurred during the part of the cycle when the female's perineal sex skin was maximally swollen, i.e., during oestrus.

Mate-guarding during oestrus

As described in Chapter III, in baboons conception is likely to occur three days before detumescence (D-day) of the sexual swelling (i.e., on day D-3). Any male mating on this day would have a chance of fathering offspring. I looked at the pattern of mate-guarding of oestrous femles in relation to the period around the day of likely conception - from D-6 to D-day. Of 45 days Male 7 spent mate-guarding females, 73% were in the period D-6 to D-1. Table VI.8 shows the distribution of mate-guarding by the dominant male in relation to this seven day span encompassing the day on which a male would have the greatest probability of fertilizing an ovum. In many cases mate-guarding occurred on D-3 and adjacent days, and Male 7 was thus the most likely or probable father of the six offspring conceived during the cycles shown in Table VI.8, although Male No. 14 could be considered a possible father of Female No. 6's infant (Table VI.8). Mate-guarding occurred on 83% of observed D-4 to D-2 days i.e., the days immediately before and after the day of most likely conception (Table VI.8). The lines on Table VI.8 link females who were mate-guarded on consecutive days. The alpha male seemed to be able to discriminate the peri-ovulatory period and change females accordingly. In all cases of swopping females on consecutive days, shown in Table VI.8, he changed to females of higher rank. Probably olfactory cues were important in detecting the peri-ovulatory period, for males were observed sniffing the perineum of oestrous females, as described below. The possible lack of concealment of ovulation is further discussed in Chapter VII.

> 8 August 1986
> 1501: Male 13 approaches Female 17. She presents to him and he sniffs her perineum and walks on.
> 1531: Female 17 presents to Male 7.
> He grooms her perineum very briefly and inspects her swelling.
>
> 22 August 1986
> 1536: Female 2 presents to Male 7. He inspects her perineum, gently parts her labia and sniffs.
>
> 24 September 1986
> 1652: Male 7 approaches Female 10 and sniffs her swelling. She moves. He follows, lip-smacking and smiling and shaking
> 1653: He mounts her and thrusts to ejaculation.

Table VI.8. Mate-guarding by the alpha male in relation to female reproductive cycle

Female ID	D-6	D-5	D-4	D-3	D-2	D-1	D	Oestrus
No. 6	*	*	✱			✱	*	D-1 to D-5
No. 12©			✱	✱	✱	*	*	D-1 to D-21
No. 5A	*	*	*	✱	*	*		D-1 to D-4
No. 17	✱	✱	*	*	✱	✱		D-1 to D-23
No. 6©				✱	Δ	*		D-1 to D-10
No. 2					✱	✱		D-1 to D-2
No. 10		*	✱	✱	✱	*		D-1 to D-16
No. 5A©	✱	*		✱	*	*	*	D-1 to D-10
No. 2©	*	✱	✱	✱	✱	*		D-1 to D-6
No. 10		✱	✱	✱				D-1 to D-5
No. 10©			✱	✱	✱	✱	*	D-1 to D-14
No. 6©			✱	✱	✱	✱		D-1 to D-14

* observation days; D = day of detumescence; oestrus = duration of maximum swelling
© cycles in which conception occurred
✱ mate-guarding by the alpha male, No. 7
Δ mate-guarding by No.14, the rank 3 male
lines link females mate-guarded on consecutive days

Figure VI.16 shows the proportion of observation days of D-6 to D-day on which mate-guarding occurred. The proportion is highest on day D-3, with mate-guarding occurring on 90% of the observed days.

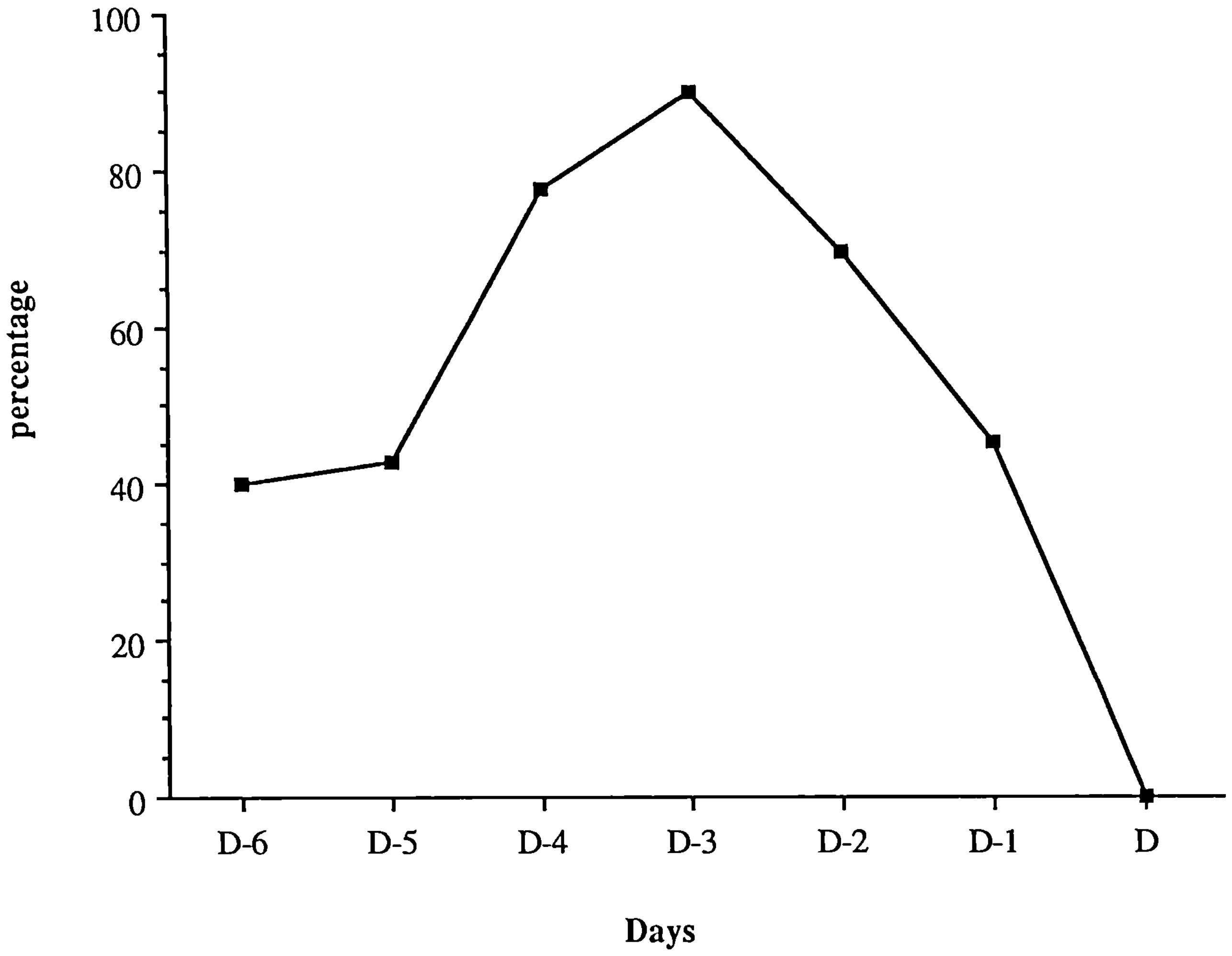
Most of the copulations by the alpha male occurred in the context of mate-guarding. Of 65 observed copulations by Male 7, 85% were with the female he was mate-guarding, and 80% of mate-guarded copulations resulted in ejaculation.

Ostentatious copulation

Some (34%) of Male 7's copulations seemed to be motivated by factors other than purely sexual attraction to the oestrous female. Copulations which were described as ostentatious (21%) seemed to be a direct response to the close presence or arrival of another male. Prior to what was subsequently described as an ostentatious copulation, Male 7 was relaxed and not showing pre-copulatory behaviour; on the arrival or increased proximity of another male, he abruptly initiated sexual interaction with 'his' oestrous female. These copulations (n = 14) occurred only in the context of mate-guarding when he had exclusive access to the female. Ostentatious copulation is illustrated by the descriptions given below:

> 6 August 1986
> Male 7 is mate-guarding Female 12
> 1613: 12 goes to the chow bin.
> 7 follows immediately and sits quietly 5 m from her.
> 1619: Male 9 descends a *Musanga* tree near the chow bin and approaches to 2m of 12 and follows her. 7 suddenly stands up and follows rapidly behind 12 and starts smiling and shaking and lip-smacking.
> 1620: 7 mounts 12 and thrusts but does not ejaculate. The copulation is ostentatious and occurs right infront of Male 9, who is standing at 3 m.

Figure VI.16. Proportion of observation days on which mate-guarding by the alpha male occurred



1630: Male 9 moves away along the wall and down one of the transects.
1634: Females 6, 12, and 17 are in the feeding site. Male 7 moves and sits in the doorway.
1635: Male 14 turns up.
1636: Male 7 approaches 12 and copulates ostentatiously with her to ejaculation, right in front of 14 who is standing 3 m away from them.

7 October 1986
Male 7 is mate-guarding Female 2
1626: Female 2 climbs a tree. Male 7, giving threat-grunts, climbs too. Male 18 is in the neighbouring tree.
1628: Female 2 is right at the top of the tree.
1630: 2 sits on a bough nearest 18's tree, then she jumps into it near 18. 7 rapidly descends the tree and runs to the base of the tree that 2 and 18 are in, giving threat grunts.
1632: 2 approaches 18 to 5m - she seems to be ignoring 7. Then she descends and walks off. 7 follows her.
1633: With Male 7 7 m behind her, Female 2 approaches Male 13 to 1m. 7 catches up and approaches 2 to 2m and 13 moves away a little. 2 also moves and 7 follows her lip-smacking and smiling and shaking. He copulates to ejaculation with her ostentatiously. Both Male 18 and Male 13 are less than 5 m away.

In the above example it is almost as though Male 7 was aroused by the presence of the other males, but instead of aggressively driving them away (which he had sufficient status to do) he copulated with the oestrous female right in front of them.

Other copulations seemed to be a direct consequence of arousal following aggression. Eight (12%) of Male 7's copulations occurred immediately post-aggression. An example is given below:

> 6 August 1986
> Male 7 is mate-guarding Female 12
> 1606: There is much aggression involving several females and Male 7, who has been threat-rushing various individuals.
> 1608: After the aggression 12 is in the corner of the enclosure standing on the wall ledge. 7 returns directly to 12 and jumps up on the wall behind 12 and she presents to him. He pushes her off the wall and then copulates with her to ejaculation.

It was not uncommon for males to get erections when they were 'tense' or aroused. It seems possible that this arousal, which usually gradually disappeared as the individual 'relaxed', or was dissipated by masturbation, could, during the mating season, be released by attempting to copulate with an oestrous female. Although most (87.5%) post-aggression copulations resulted in ejaculation, only half occurred in the context of mate-guarding.

Mate-guarding behaviour, the possible discrimination of ovulation by males, and the effect of reproductive synchrony among females in relation to mating system and social organisation are discussed in the following chapter, Chapter VII.

CHAPTER VII. DISCUSSION

Introduction

The aim of this discussion is to integrate the biological and behavioural data on mandrills presented in this study and ecological information from studies of wild mandrills in an attempt to provide a more complete understanding of this forest primate.

First, the CIRMF study is placed in context with other studies. Various aspects of mandrill biology and behaviour are discussed in the context of their ecology as a large-bodied, frugivorous, semi-terrestrial tropical-forest dwelling primate. Diet and inter-specific competion for food are considered. Features of mandrills such as colouration, scent-marking, and vocalisations are interpreted as adaptations to the ecological constraints tropical forest. The lack of consensus as to mandrill social organisation, i.e., whether the basic social grouping of mandrills is a single- or multi-male group is discussed and data from this thesis are applied to Dunbar's (1988) model relating to this. Spatial, grooming, and agonistic relationships of mandrills are discussed and briefly compared with those of hamadryas and gelada baboons. The results of this study are used to assess Popp's (1983) predictions relating to ecological determinism in baboons. Similarities of mandrills and an Asian ecological analogue of mandrills, the pig-tailed macaque are explored.

Previous studies

All studies of captive mandrills to date have been of groups numbering less than six individuals and maintained in the confined and often impoverished conditions of zoo cages (e.g., approximately 132 m^3, Emory, 1975a, 1975b, 1976; 38 m^3 Kawata, 1980; 132 m^3, Mellen *et al.*, 1981). Reports of stereotyped behaviour (Chamove *et al.*, 1988), excessive aggressive behaviour (Markowitz *et al.*, 1981), and incompetent and inadequate maternal behaviour (Mellen *et al.*, 1981) are found in many of the captive studies. These factors limit our confidence in the relevance of the behaviour recorded in captivity to interpretations of the behaviour of wild mandrills. However, despite these limitations, mandrills in zoos can at least be directly studied and their behaviour observed and quantified. Unfortunately, this has not been achieved in most of the field studies, and reports of social behaviour are conspicuous by their absence from the limited literature on wild mandrills, reviewed in Chapter IV. The conditions in tropical forest - dense vegetation, low light levels, and the habits of the mandrills themselves - particularly their terrestrial travel over large areas - means that they are difficult to observe in a sustained way. Thus most studies have concentrated on analysis of indirect evidence of mandrill presence such as feeding traces and faeces (e.g., Hoshino, 1985; Lahm, 1986). None of the field studies achieved more than 90 hours observation of mandrills, with an average of only 3.6 contacts with mandrills per month of study.

The CIRMF study

The study presented in this thesis benefited from two major advantages, (1) a group of mandrills living in naturalistic conditions, (2) who were also observable. There were also some limitations. The study group lived in a 5.3 ha enclosure and received some provisioning on a daily basis, so various aspects of their behaviour may have been affected by this. There was only one group, initially formed from unrelated, mostly juvenile individuals, with equal numbers of males and females, and with no opportunities for emigration or immigration.

However, some of these drawbacks were attenuated as follows: for example, despite its relatively small size in comparison to the estimated home range of mandriils, the enclosure at CIRMF contained over 50 species of trees (of diameter at breast height greater than 13 cm) and was thus relatively diverse botanically (Norris, 1988). In addition, the enclosure contained trees known from field studies to be food sources of wild mandrills (Norris, *op. cit.*; pers. obs.) and was of natural relict gallery forest. Mandrills are known to use this type of forest in the wild (E.A. Williamson, pers. comm.). Since some aspects of the mandrills' ecology such as travel patterns and activity budgets were likely to be limited by their semifree-ranging and provisioned conditions, these aspects were not a focus of the current study. Despite the provisioning the mandrills spent 65% time foraging in the enclosure (Norris, 1988; this study). Although there was a sex ratio of 1:1 in the founder mandrills, at the time of the study only two males in the group were fully mature and one was the group 'leader' (Jouventin, 1975a), the other was a solitary male. This resembled group structure reported from the wild. Despite the lack of opportunity for immigration and emigration in the CIRMF mandrill facility, reproduction in the group led to a group size and proportion of immature individuals in the group which resembled that reported in feral mandrills. Any problems associated with provisioning such as increased rates of aggression (e.g., Wrangham, 1974) were offset by excluding from analysis data collected at the feeding site and round the chow bin. These factors increase the likelihood that the behaviour recorded in this group of mandrills will provide a relevant contribution to the study of the species. The current study of the mandrills at CIRMF presents the most comprehensive behavioural study yet reported.

Ecology

Mandrills can broadly be classified as large-bodied, frugivorous, semi-terrestrial, forest-dwelling primates. In order to survive they need to find food and avoid predators and in order to reproduce they need in addition to find members of the opposite sex. The tropical forest environment places various constraints on the ways in which this can be achieved, for example, food, in particular fruit, is often patchy and uneven in its spatial and temporal distribution, and there may be a large community of competitors for these scattered food resources. The dense foliage and poor light on the forest floor may limit the use of vision in locating and maintaining contact with conspecifics, and promote the use of other modalities such as audition and olfaction. The possible competitors for food of mandrills are discussed below and mandrill adaptations to the physical constraints of the forest environment are considered in later

Table VII.1. Monkeys and apes sympatric with mandrills in Gabon, Rio Muni, Equatorial Guinea, and Cameroon

Gabon [1]	Rio Muni [2]	Cameroon [3]	
Gorilla gorilla *	*G. gorilla*	*G. gorilla*	gorilla
Pan troglodytes *	*P. troglodytes*	*P. troglodytes*	chimpanzee
Lophocebus albigena	*L. albigena*	*L. albigena*	grey-cheeked mangabey
Cercocebus torquatus *	*C. torquatus*	*C. torquatus*	white-collared mangabey
Colobus satanas	*C. satanas*		black colobus
Cercopithecus nictitans	*C. nictitans*	*C. nictitans*	greater spot-nosed guenon
C. cephus	*C. cephus*	*C. cephus*	moustached guenon
C. pogonias	*C. pogonias*	*C. pogonias*	crowned guenon
C. neglectus *	*C. neglectus*	*C. neglectus*	de Brazza monkey
C. solatus *			sun-tailed guenon
Miopithecus talapoin *	*M. talapoin*	*M. talapoin*	talapoin monkey

* semi-terrestrial

Data taken from 1) Blom *et al.*, in prep.; 2) Sabater Pi and Jones, 1967;
3) Hoshino *et al.*, 1984

sections.

Diet

Mandrills have a very broad and eclectic diet (Chapter IV) but can best be described as frugivores (Hoshino,1985; Lahm, 1986). Their dentition supports this classification. Mandrills have broad, high-crowned incisors, with comparatively small cheek teeth which have low, rounded cusps (Jolly, 1970). This is consistent with a diet of forest fruits and tubers, which are often enclosed in a rind or husk. The outer covering needs to be removed before ingestion, and this is accomplished by incisal action. Once processed, the foods require little beyond crushing - and this can readily be done with blunt, rounded molar cusps (Jolly, 1970). The large temporal muscles are set obliquely and act to retract the mandible, as used in incisal nibbling, and resist forces displacing the mandible, as occurs when objects are held in the hands and stripped through the front teeth (Jolly, *op.cit.*). Mandrills could be characterised as 'strippers and pithers' as many food items including grass stems, roots, tubers, *Aframomum* stems, twigs, bark, and a variety of fruits and vegetables (both cultivated and wild), are prepared in this way (pers. obs.).

Competition for food

In the tropical forests of Africa, many frugivores are sympatric. For example, 82% of all primary consumers at M'Passa in north-east Gabon were frugivorous (Emmons *et al.*, 1983). In Gabon and Rio Muni, Equatorial Guinea mandrills are sympatric with nine species of monkey and two apes (Blom *et al.*, in prep.; Sabater Pi and Jones, 1967), and in Cameroon with at least seven monkeys and two apes (Hoshino *et al.*, 1984) (see Table VII.1). In particular, several of the other primates are semi-terrestrial (see Table VII.1) and may thus be in greater competition with mandrills than monkeys such as gray-cheeked mangabeys which are exclusively arboreal. For example, in Gabon, overlap in diet between gorillas, *Gorilla gorilla gorilla* (Williamson, 1988) and mandrills (Lahm, 1986) was 44%, and in Cameroon, between mandrills (Hoshino, 1985) and semi-terrestrial mangabeys, *Cercocebus torquatus*

torquatus (Mitani, 1989) was 46%. As well as other primates, bush-pigs (*Potamochoerus porcus*), various duikers (such as *Cephalophus monticolis* and *C. callipygus*), elephants (*Loxodonta africana*), and birds such as hornbills and turacos also eat fruit (Dubost, 1984; Emmons *et al.*, 1983; Williamson, 1988), so the potential for competition for fruit resources is high.

Although many primate frugivores may overlap broadly in distribution, specialisations for different habitat preferences may reduce inter-specific competition. For example, although the semi-terrestrial primates *Cercocebus torquatus*, the white-collared mangabey, and *Cercopithecus neglectus*, the de Brazza monkey, were reported to be broadly sympatric with mandrills in Rio Muni, when their distribution was examined in terms of habitat, they did not overlap with mandrills; the guenon and mangabey being confined to hygrophilic forest and littoral screen from which mandrills were absent (Sabater Pi and Jones, 1967, Table 1, p.107). Inter-specific competition may be reduced or avoided by 'escape in size'. Since metabolic requirements are very different for animals of different body size (Peters, 1983) primates that differ considerably in size from mandrills are unlikely to be major competitors with them for food resources. Thus avoidance or reduction in competition with mandrills by 'escape in size' is likely to occur with other semi-terrestrial primates such as the diminutive talapoin monkeys, *Cercopithecus (Miopithecus) talapoin*, and the relatively very large gorillas. However, even with these factors acting to decrease inter-specific competition, there can be little doubt that the large number of frugivores inhabiting the same forests as mandrills is likely to constitute a source of competition for resources such as ripe fruit.

Potential primate competitors of mandrills

It seems unlikely that talapoin monkeys, due to their small size (see above) and preference for riverine habitats (Gautier-Hion, 1971), are important competitors of mandrills, and so they will be excluded from the following discussion. De Brazza monkeys are unusual among guenons in being found in very small, apparently monogamous groups (at least this seems to be the case in Gabon, Gautier-Hion and Gautier, 1978; but see Leutenegger and Lubach, 1987). They are also found primarily associated with rivers. Relatively little is known about their socio-ecology (in comparison to sympatric arboreal guenons) and it seems unlikely that they are significant competitors of mandrills. Chimpanzees (*Pan troglodytes troglodytes*) and gorillas are considerably larger than mandrills, although, as mentioned above there is considerable overlap in diet between mandrills and gorillas and also between chimpanzees and gorillas - 60% of gorilla foods were recorded as food for chimpanzees (Tutin and Fernandez, 1985).

Of the semi-terrestrial primate species in Gabon sympatric with mandrills, listed in Table VII.1, the sun-tailed guenon *Cercopithecus solatus*, and the white-collared mangabey are potential competitors of mandrills. Little is yet known of the socio-ecology of the recently discovered sun-tailed guenon (Harrison, 1988). There is an indication that although its distribution to the west, north, and east is limited by physical barriers such as rivers (Harrison, 1988; Gautier *et al.*, in prep.), the southern limit of its range may be biologically determined by competition with mandrills. As the relative abundance of mandrills increases northwards from the south, the abundance of *C. solatus* decreases southwards (Gautier *et al.*, in prep.). The ecology and behaviour of the sun-tailed guenon is virtually unknown, although it seems likely that fruit and insects will form an important part of the diet (pers. obs. of captive guenons and of digestive tract contents). The ecological relationship between mandrills and sun-tailed guenons merits further study, particularly at the southern limit of the guenon species' range.

The white-collared mangabey has been little studied in Gabon. These mangabeys are generally reported to inhabit coastal, gallery, or swamp forest (Jones and Sabater Pi, 1968; Gartlan and Struhsaker, 1972), however, they have recently been studied in Campo Reserve, Cameroon (Mitani, 1989), in an area of evergreen forest where mandrills have also been studied (Hoshino *et al.*, 1984; Hoshino, 1985;

Kudo and Mitani, 1985; Kudo, 1987). Thus from Cameroon, an indication of the potentail for competition between the two species is available. A brief outline of the results of Mitani's (1989) 15-month study of *Cercocebus torquatus torquatus* is given below and compared with the socio-ecology of sympatric mandrills.

A number of similarities are apparent between white-collared mangabeys (Mitani, 1989) and mandrills (Hoshino *et al.*, 1984; Hoshino, 1985), outlined below. Both species were reported in groups of about 25 individuals. Since a number of the mangabey troop members were adult males, Mitani inferred that mangabeys live in multi-male troops. Mandrills were observed in both single male and multi-male groups. The adult male to adult female sex ratio differed between the two species, being more balanced in the mangabeys - 1:1.25, supporting the suggestion of a multi-male group composition, than in the mandrills (adult male:individuals, 1:13.9). Both species were reported to split into subgroups for foraging, and in both species these subgroups were reported as numbering about 20 individuals - which seems to be indistinguishable from group size. Solitary male mangabeys and mandrills were seen, but all-male bands were not observed in either species.

The mangabeys were mainly frugivorous, with fruit (60%) and seeds (20%) comprising about 80% of the diet as assessed from observation and feeding traces. This indicates considerable overlap in diet with mandrills which were also mainly frugivorous and which Hoshino (1985, p.265) classed as 'seed eaters' since 39% of fruit parts eaten were seeds and/or nuts. Monocotyledonous plants were also important food items for mangabeys, as they were for mandrills, who were reported as making 'substantial use of ... monocotyledonous plants' and Hoshino then reclassified mandrills as 'seed and monocotyledonous plant leaf eaters' (p.265). For both mangabeys and mandrills, members of the Marantaceae family were important herbaceous plant foods. However, mandrills ate mostly the leaves (Hoshino, 1985; although frequently only the leaf base is eaten, pers. obs.), whereas the mangabeys ate the shoots, especially the base. Interestingly, plants of the genus *Aframomum*, which are readily eaten by mandrills, chimpanzees, and gorillas (pers. obs; Hoshino, 1985; Tutin and Fernandez, 1985; Lahm, 1986; Williamson, 1988), were not observed to be eaten by the mangabeys despite being abundant in the study area (Mitani, 1989). The information presented above indicates considerable similarity between the two sympatric species. However, examination of the limited data on behaviour of the two species indicates several differences.

About 60% of observations of mangabeys during behaviour termed move and socio-rest (a composite of grooming and resting) were at less than than 5 m height, whereas about 40% of feeding sightings were at 20 to 30 m height. Thus it seems likely that a substantial part of the diet may be obtained from arboreal sources and that white-collared mangabeys may travel terrestrially between these arboreal fruit sources. By contrast, 67% of mandrill sightings were made exclusively at less than five metres height, and it was concluded that mandrills were basically terrestrial and tended to be ground eaters. This indicated a degree of resource partitioniong between the two species. Perhaps related to this difference in arboreal vs. terrestrial foraging, home range area differed substantially between the two species, and was much greater in the mandrills. The mangabey troop was estimated to range over approximately 250 ha over 15 months, divided into seasonal ranges of about 120 ha. This is equivalent to 2.5 km^2, which is considerably smaller than the ranges reported for the sympatric mandrills, which were estimated as 5 to 28 km^2 depending on group size. There was no indication of day range length for the mangabeys, but the mandrills were estimated to travel 2.5 to 4.5 km per day (Hoshino, 1985). The information on both species is yet too sparse to allow a more detailed analysis of the ecological separation of the white-collared mangabey and mandrill in Cameroon, but it appears that competition may be reduced by feeding at different levels in the canopy and when feeding on the ground by eating different parts of the same plant. Their very different ranging patterns suggest adaptation to different niches.

Ecological constraints - limited visibility in forest

In addition to competition for food, another problem encountered in tropical forest, particularly on the forest floor and in the understorey, and familiar to field workers trying to study the fauna of these zones, is limited visibility due to the dense foliage and poor light conditions. which may hinder visual monitoring, both for potential predators and for other conspecifics. Communication systems which rely on modalities other than exclusively visual signalling may be required to maintain social groupings. Various aspects of mandrill ecology and behaviour are discussed below in terms of these possible constraints.

Colour

Male mandrills are perhaps best known for, and are popular exhibits in zoos because of their exuberant colouring (see Frontispiece), particularly the striking juxtaposition of blue and red which is visible at both ends of their bodies (Hill, 1955). It is possible that the poor lighting conditions of their natural habitat may have influenced the development of colouration. This possibility and others are considered below, following a description of colour production in mandrills.

The blue of mandrills is produced by Tyndall scattering from melanin in the superficial layers of the dermis. On the muzzle the cobalt blue is also caused partly by the superficial collagen fibres of the dermis, which emit a brilliant blue fluorescence when viewed in reflected light (Hill, 1970). The red colour is caused by the haemoglobins of circulating blood, and colour thus varies with the richness of the capillary beds and can be influenced by vasomotor factors. The striking red of the mid-rib of the nose is produced by an arteriolar reticulum in the deep layer of the integument which is supplied by paired nasal arteries (Hill, 1969). Various explanations for the brilliant colouration of mandrills have been proposed and can broadly be divided into evolutionary, ecological, and behavioural explanations.

Evolutionary: The colours red and blue are widespread amongst the Old World monkeys (Wickler, 1967). This may be because these colours may be energetically and metabolically 'cheap' to produce and so the colours exhibited by mandrills are phylogenetically constrained. The similarity between the colours of face and rump may be an example of physiological economy in adapting localised areas of epidermis (Kingdon, 1988). Grubb (1973) hypothesised that the striking facial pattern of the mandrill, which distinguishes it from the black-faced drill, arose as part of an isolation mechanism, through divergent selection. This idea was echoed by Kingdon (1988) who asserted that the brightly coloured muzzle of mandrills is the single most species-specific signal.

Ecological explanations for the colourful rump of mandrills and drills have been linked to the poor visibility in the forest. Particular combinations of colour wavelengths travel well in low ambient light (Kingdon, 1988), in the same way that particular sound wavelengths also travel well in forest (see later section), so the colouring of mandrills may be adapted for maximum visibility given the constraints of the habitat. This possibility is supported by the observation that all semi-terrestrial guenons tend to have bright male genital colouring (Kingdon, 1980) which suggests that features of a terrestrial niche in forest may also have influenced the patterning of colour in mandrills.

Behavioural: Both the face and rump colour of mandrills have been interpreted as having social significance. Jouventin (1975b, p.456) proposed that the rump of the adult male mandrill was the optical complement of the two-phase grunt rallying vocalisation, and suggested that the luminous rear of the leader acted as a signal in the semi-obscurity of the undergrowth in response to which other animals would congregate. This idea can also be applied to the drill since it too has a similarly brightly coloured rear (albeit with a different pattern of colouring from the mandrill (Hill, 1955)), is also largely semi-terrestrial in tropical forest, and uses a two-phase grunt vocalisation as a rallying signal (Gartlan, 1970). It is supported by personal observation of feral and semifree-ranging mandrills, in whom the coloured rear of adult males, particularly the blue colour, is readily visible in the gloomy undergrowth. A similar phenomenon may account for the above-mentioned observation of bright genital colouring in semi-terrestrial guenons, since animals moving together on the forest floor may follow the circum-genital signals (which are also often blue in colour) of the individual in front, although this is entirely speculative since (to my knowledge) no data on terrestrial progression patterns are available for semi-terrestrial forest guenons.

Jouventin (1975b) asserted that the coloured penile region was used as a vivid signal in male-male dominance display, analogous to the red, white, and blue displays of some cercopithecines (Wickler, 1967). Jouventin stated that the exhibition of an erect penis was frequently observed and that it was associated with the threat yawn (p.457), although Wickler (*op. cit.*) did not observe this. My observations indicated that although males developed erections when aroused, and these may be temporally associated with wide display yawns which are an indication of tension, the males did not sit with a conspicuously erect penis in a way that indicated this to be a ritualised display. In connection with his dominance hypothesis about penile colouration, Jouventin presented mandrill models to a captive group of five mandrills which included one young adult male (Jouventin, 1975b). He interpreted the results, from four sets of trials with models whose face and penile regions were coloured green and yellow instead of red and blue, as showing that the genitals function in male dominance displays and that the colours red and blue are particularly 'attractive' to mandrills. If red and blue colouring is a species-identity label then the observation that mandrills paid attention to these colours more than they did to yellow and green is unsurprising.

Jouventin (1975b) outlined four alternatives as explanations for the facial colouring of mandrills. (1) The red and blue of the male mandrill's muzzle was aversive to predators. He dismissed this explanation since the leopard does not have colour vision. Another critisism of this explanation is provided by reports that males lead the flight from terrestrial predators rather than confront them (Tate, 1955; Jouventin, 1975a). (2) The face was a rallying signal like the rear. (3) The face was a copy of the rear (auto-mimicry) and face-presentation was the same as genital presentation (Wickler, 1967). This seems unlikely since genital presentation is generally a sign of submission, whereas a face-to-face position is likely to be confrontational/aggressive or neutral. Additionally, as Grubb (1973) pointed out, this auto-mimicry has not developed in drills, who seem to have a similar social system to mandrills. (d) Facial colours are important in sexual selection. Grubb *(op. cit.)* pointed out that colour probably evolved in conjunction with the elaborate behavioural displays and facial expressions of mandrills and may contribute to rank determination in males. However, since females also have coloured faces, albeit less bright than those of males, this explanation cannot wholly account for face colour. In the CIRMF mandrills, with the exception of the alpha male whose red nasal mid-rib was conspicuously brighter than those of other males, there was no clear relationship between dominance rank and facial colour. In females there was no correlation between rank and facial colour either. Although the two most subordinate females had faces that were largely black, individual differences in colouring were great and colouring seemed to have a heritable component since there were family resemblances between offspring and their mothers. It seems likely that facial colouring may be a result of both inherited, developmental, and social factors, the last probably being more important in males than in females. This could be tested by removing the alpha male of a group. I would predict that the male who replaced him would rapidly develop the brightest facial colouration. I would not expect to see changes in facial colour if a similar manipulation were done among females.

Turning to colouration of the rear, the blue rump of mandrills is certainly readily visible in the forest undergrowth (pers. obs. of wild and CIRMF mandrills) and it may be that the patches of white hair behind the ears (see Frontispiece), which are especially conspicuous in adult males, may also act as a visual signal (as they seem to in tigers, in whom they act as visual cues for cubs to follow). Colour may also function as a physiological marker of, for example, testosterone level in males and reproductive state in females, shown for example by the reddening of the perineum during pregnancy (see Chapter III). This suggestion is supported by work on an immature male drill (Zuckerman and Parkes, 1939, cited in Hill, 1970) which indicated that injections of testosterone evoked the full colour pattern typical of a mature adult male drill, particularly intensifying red. Cessation of the injections left secondary sexual characters unaffected except for a lessening of the reddening on face, trunk, and buttocks. The coincidence of the brightest colouring and highest blood testosterone levels in the alpha male of the CIRMF mandrill group may be related to this. This suggestion is discussed in a later section. The likely multiplicity of function of colour in the mandrill supports the idea that signal structure in mandrills 'suggests correlations between species-specific signals and ecologically determined behaviour that is equally specific' (Kingdon, 1988).

Olfaction

A most unusual feature of mandrills and drills is their possession of sternal glands. It is possible that this feature is related to the limited opportunities for effective visual communication for semi-terrestrial forest-dwelling primates.

The occurrence of sternal glands among primate species has been reviewed by Geissmann (1987). Briefly, cutaneous glands are relatively common among the prosimians and Platyrrhini but very few Old World monkeys possess them. Four species of *Cercopithecus* monkeys are reported to engage in olfactory marking; feral *C. aethiops pygerythrus* (Gartlan and Brain, 1968) and captive *C. hamlyni*, *C. neglectus*, and *Allenopithecus (C.) nigroviridis* (Gautier and Gautier, 1977; Loireau and Gautier-Hion, 1988). Of the Papioninae only the mandrill and drill possess a sternal gland. The sternal gland was first described in the drill (Hill, 1944); a similar structure was later reported in the mandrill (Hill, 1954). The gland is a triangular area in the middle of the chest and is covered with modified hairs, longer than the surrounding hairs, and whose follicles have wide crateriform openings. There are three types of gland: (1) specialized massive sebaceous glands associated with the follicles of the modified hairs; (2) a layer of enlarged apocrine sweat glands; and (3) a deep carpet of unusual coil glands (clumped into lobules and surrounded by a vascular network) deep in the dermis (Hill, 1954, 1970).

Neither species has been observed to scent-mark in the wild, but this behaviour has been seen in captive drills (Hill, 1944; Böer, 1987c; Cox, 1987; Hearn *et al.*, 1988), in captive mandrills (Hill, 1954; Jouventin, 1975a; Mellen *et al.*, 1981), and was observed in the semifree-ranging mandrills which were the subjects of the present study (Chapter IV).

The functional significance of scent-marking is difficult to assess. I think it likely that in mandrills, and probably also in drills, the behaviour may serve more than one function. The two types of gland, sebaceous and apocrine, may produce secretions with different characteristics and different functions. Glandular secretions were collected (under light anaesthesia) from two of the CIRMF male mandrills for chemical analysis to try and address this question but unfortunately chemical analysis was unsuccessful (M. Gorman, pers. comm.). Scent-marking may have both a territorial and social function, and Jouventin (1975a, p.517) suggested four possibilities: (1) it affirms the status of the dominant male and repels rivals; (2) it facilitates orientation within the home-range; (3) it allows encounters between individuals or groups; and (4) it facilitates regrouping of a troop.

Previous reports of scent-marking in captive mandrills (Mellen *et al.*, 1981) provided only brief qualitative description, however in the present study quantitative description of observations of 115 instances of scent-marking by the CIRMF mandrills were made and allow the assessment of the various functions of scent-marking, proposed by Jouventin.

There was some support for the first hypothesis. Older males were the most active markers; the alpha male accounted for 30% of the marking by sub-adult and adult males and he scent-marked significantly more than other males (Chapter IV). His gland appeared more active at certain times, for example, during the breeding season when it appeared very greasy and the long sternal hairs were stained yellow, contrasting with the surrounding white fur on his chest. It is also posssible that scent-marking facilitates orientation within the range (hypothesis 2). About half the scent-marks were deposited at less than two metres height, and thus were easily accessible to terrestrial individuals. As all rapid travel was done on the ground, and some low marks were on mandrill travel routes, scent-marks may indicate occupancy or recent traversing of the area by a group of mandrills. Observations of zoo animals indicated that scent-marking rates increased when males were introduced to new substrates such as branches (drills, Hill, 1944) or new enclosures (mandrills, Mellen *et al.*, 1981), which may indicate a territorial function. The same phenomena have also been observed in captive de Brazza monkeys (Gautier and Gautier, 1977; Loireau and Gautier-Hion, 1988). There were no data which either supported or refuted hypotheses (3) and (4). The enclosure was so small in relation to a natural range and the animals knew it so well that orientation and regrouping were never a problem. If groups of individuals did become separated they found each other using vocal communication.

Evolutionarily, it is interesting to note that scent-marking is considered a primitive character and that mandrills and drills may represent the ancestral condition for baboons (Szalay and Delson, 1979). Markable substrates in grassland savanna habitats are probably relatively rare. All the four cercopithecines reported to scent-mark are semi-terrestrial, and many lines of evidence (anatomical, karyological, and paleontological) suggest that the semi-terrestrial guenons belong to a more ancient radiation than the arboreal forms (Muleris *et al.*, 1986; Gautier-Hion *et al.*, 1988; Loireau and Gautier-Hion, 1988). The three guenon species in which scent-marking has been observed in captivity are forest-living species; the lack of observation of scent-marking in feral populations of these species and in feral mandrills is likely to be related to the small number of field studies done and the extreme difficulty in observing semi-terrestrial forest primates. There are insufficient data to say definitely whether or not the forest-dwelling, semi-terrestrial species of the *lhoesti* group also show scent-marking behaviour. Preliminary observations of captive individuals suggest that they do not (Loireau and Gautier-Hion, *op. cit.*; pers. obs. of *C. solatus*). Only further study of semi-terrestrial forest primates including intensive study of habituated wild mandrills and drills may give clues as to which aspects of the forest habitat when coupled with phylogenetic history are related to this unusual behaviour.

Vocalisations

Many authors have commented on the rich vocal repertoire of mandrills (e.g., Tate, 1955; Jouventin, 1975a). It may be that the frequent and varied vocalisations of mandrills are an adaptation to an environment in which visual signals are relatively ineffective over any distance except at very short range.

The properties of tropical forest, e.g., limited visibility, may not only require emphasis on sound in communication, but may also severely constrain the use of acoustic signals (Waser and Waser, 1977, p.239). Absorption, reflection, and refraction by factors such as foliage, air turbulence, temperature gradients, and ground effects, can rapidly degrade the structure of a transmitted signal. Degradation can be particularly severe in tropical forest, habitats which are also very noisy. Although a low frequency sound window exists in tropical forest (Waser and Waser, 1977; Waser and Brown, 1984) it is only available to the elevated signaller, since near the ground no clear sound window is present (Waser and Brown, 1986). None of the calls given by mandrills can be described as classic type 1 loud calls, characteristic of the arboreal forest guenons (Gautier and Gautier, 1977). There is also an absence of specialised long-distance calls in semi-terrestrial forest guenons, e.g., the *lhoesti* group also lacks type 1 calls (Waser and Brown, 1986; Gautier, 1988). However, the mangabey *Cercocebus galeritus*, which is also largely terrestrial, does have them, but calls from an elevated position (Homewood, 1976 cited in Waser and Brown, 1986). This behavioural adaptation was also observed in the CIRMF mandrills. Crow calls were frequently, but not always, given from elevated positions and the male roars were always from arboreal locations. Both these calls could be heard at distances of several hundred metres.

There has been only one study of mandrill vocalisations (Kudo, 1987) and the author asserted that the 'social structure of mandrills is considered to be multi-male troop type' (p.307) on the basis of analyses of vocalisations. Several calls reported by Kudo, as well as others not included in her study, were also heard in the mandrill group at CIRMF and were described in Chapter IV. Methodological problems in Kudo's study (see below) meant that individual identity and behaviour could rarely be matched to a vocalisation. Although sonographic analysis of vocalisations was not carried out in the CIRMF study, the ability to watch individually-recogniseable mandrills vocalising meant that a detailed description of the function and use of a particular call was obtained, and these data could be used to assess and interpret the vocalisations described in Kudo's study, recorded from wild mandrills in Cameroon.

The results of Kudo's study will be examined in some detail, because Kudo drew a number of conclusions about mandrill social organisation based on her study and also because the study highlights the confusion surrounding mandrill social groupings in terms of whether a one-male unit is the basic social grouping or whether it is a multi-male group.

Kudo's study of vocalisations has a number of drawbacks. The difficulty of studying mandrills resulted in only 30% of following time being within 20m of the mandrills; different groups could not reliably be distinguished so were dichotomously classified as small (about 20 individuals) or large (about 100 individuals); individuals could not be distinguished, so vocalisers also were divided into only two categories, adult males and others (p.290).

The two most frequently recorded mandrill vocalisations in Kudo's study were the two-phase grunt (2PG) and the crow call. Kudo classified these calls as long-distance calls on the basis of their acoustical features - low frequency (less than 4kHz) and a repeated part or harmonic structure - on the grounds that other studies have found that these features are effective in long-distance transmission (Waser and Waser, 1977). Kudo gave no indication of the distance over which these 'long-distance' calls were audible, but stated that that they were both 'frequently heard in situations of short distance vocal communication' (p.297). Thus 'it is characteristic ... in mandrills that long distance calls are used frequently regardless of actual distances from receiver' (p.297). Kudo reported that the functional significance of the 2PG, which was given exclusively by adult males, was for group integration and its continuous emission signalled a calm aggregation of members without subgrouping. Crow calls were reported to be emitted during formation and splitting of the subgroup and were given by others. A subgroup was said to contain 20 to 40 individuals. It is unclear from Kudo's study (and other studies at Campo) exactly what constituted a subgroup, since the small group seemed to be similar in size to a subgroup. For example, 'the one-male group is not a temporary subgroup of a multi-male group but a stable social unit ... on the other hand, multi-male groups seem to be composed of some one-male groups (or subgroups), because a small subgroup (one-male group) was occasionally formed from a multi-male group by subgrouping' (Hoshino *et al.*, 1984, p.305). An established terminology for mandrill groupings (such as seems to be in use for hamadryas multi-levelled societies) would clarify matters and it is one of the aims of this discussion to attempt to provide a solution, at least in terms of the basic social unit in mandrills.

The two-phase grunt was hardly ever heard at CIRMF although I heard it in the forest of central Gabon and it was audible over several hundred metres. The lack of 2PG in the CIRMF mandrills can be explained by the reduced 'need' for a rallying call in an enclosure which was small in relation to the natural range of a group of mandrills, and intimately known to them. The lack of other one-male groups may also have been important. In contrast crow calls were frequently heard, e.g., at the sleeping site, when animals were moving across the enclosure to the feeding site, etc., and were also audible over several hundred metres.

Short-distance vocalisations were reported by Kudo as being infrequent (<0.5 per 5 mins). Kudo stated that grunts 'do not function in group integration, ... are given only in an aggressive context' (p.301), that mandrills have a low rate of vocal exchange (since all calls except 2PGs were emitted more frequently alone, i.e., there was no response within 5 secs, than during exchange) and lack a short-distance contact call. As pointed out in Chapter IV, this was not the case in the CIRMF mandrills, who communicated with each other by contact grunts, particularly while foraging. The lack of this observation in Kudo's study was no doubt related to the fact that she was rarely close to the mandrills, and that when she was, they were probably aware of her presence and ceased emitting relaxed contact grunts.

Kudo based her interpretation of mandrill social structure largely on the occurrence of 2PG, crow-calls, and the (false) absence of short-distance contact vocalisations. Although Kudo had previously asserted that mandrills had a multi-levelled society resembling that of gelada or hamadryas baboons (Hoshino *et al.*, 1984), this was revised on the basis of a comparison of vocal patterns. In gelada and hamadryas baboons most vocal exchanges occurred between members of a one-male unit and analyses of spatial proximity suggested that the one-male units were closed (Kummer, 1968; Dunbar and Dunbar, 1975). As this was not found to be the case in mandrills, since Kudo asserted that frequent vocal exchange between females and juveniles in separate vocal clusters existed, an adult male responded to the vocalisations emanating from several different subgroups, and each subgroup did not always include an adult male emitting 2PG (p.304) she concluded that mandrill subgroups were not closed and were therefore not one-male units. An alternative explanation is that the mandrill social unit does indeed contain a single male emitting 2PG, and that small (sub)groups of females and juveniles (likely to be kin groups) disperse during foraging, maintaining contact amongst themselves by contact grunts, and with other subgroups by crow calls. In the CIRMF study, on the rare occasions that small (sub)groups of mandrills were widely separated in the enclosure (e.g., by about by 200 m) they communicated by frequent exchange of crow calls. However, the alpha male did not vocalise during these exchanges, which were dominated by the crows of adult females. It is likely that the identity of the caller as well as the location is communicated by these crow calls since I was able to distinguish individuals on the basis of their calls. Thus I assume that crowing mandrills can communicate not just where they are but who is where. This probably applies to many of their calls, since for example male roars were also individually recognizeable to me. Crowing also functioned as a lost call (see Chapter IV) when an individual lagged behind the group. These crow calls were distinguishable to me by their 'emotiveness'. Only a detailed observational field study of marked individuals will resolve this question.

The other evidence that Kudo presented to suggest that mandrills may not have a one-male unit can also be criticised. Kudo rejected one-male units for mandrills on the basis of work on captive mandrills showing that adult males rarely participated in social interaction, group cohesion, and visual attention (Emory, 1975; Mellen *et al.*, 1981) and that social orientation to the dominant male was weaker in mandrills than in baboons with one-male units (Emory 1975). However, although both hamadryas and gelada baboons have one-male units, these are maintained by completely different relationships, thus the argument that social relationships in mandrills differ from geladas is not evidence that mandrills do not form one-male units. My study also indicated that although the alpha male participated in social interaction with females more than other males, he was far from being the focus of affiliative attention for females, who did most of their grooming, when anoestrus, with their own offspring and other females (Chapter V). The 'separateness' of the alpha male may be a characteristic feature of mandrill social organisation. The results of the captive studies reported above may be an artefact of captivity *per se*. For example, small groups of mandrills housed in small cages are unlikely to have much scope for group cohesion. If little interaction between adult males and females is a characteristic of mandrills (outwith oestrus) then little visual attention to the alpha male is to be expected. Additionally, gelada and particularly hamadryas one-male units are much smaller than mandrill groups, they inhabit much more open areas where visual contact is probably easier, and since females may receive aggressive herding from males if they stray too far, they need constantly to be monitoring the male and hence are likely to show high levels of visual attention. This is not the case for mandrills who appear to live in bigger groups, in densely vegetated habitats, and in whom herding has not been reported.

It was also suggested by Kudo that 2PGs reflected 'a kind of inter-male conflict' (p.304). Vocal exchange between adult males was monopolised by a few males, although no data were provided quantifying the ratio of vocalising males to all males present; the vocally prominent male was observed at the back of the group; and duration of '2PG in bout 2PG-2PG exchanges tended to be longer than if 2PG was given by only one adult male'; 2PG-2PG exchange decreased when distance between callers exceeded 50 m. This presumably indicated separation of groups or subgroups, since at 50 m apart groups would probably be out of visual contact, particularly if travelling on the ground. A long-distance call reputed to function as a contact call might be expected to increase in emission with increasing distance if its purpose is to maintain contact between widely dispersed groups, rather than to decrease. The decreased frequency of 2PG in the small group, in comparison to emission in the large groups, was interpreted as indicating that the single fully adult male did not have to emit the 2PG to display to other males in the group, and that the 2PG was unnecessary for group integration in a small group since individuals were likely to be less widely dispersed.

In conclusion the exact nature of social groupings in wild mandrills is still unclear. The smallest stable group appears to contain a single mature adult male, several females, and a high proportion of juveniles (Jouventin, 1975a; Hoshino *et al.*, 1984). However, larger groups containing multiple males have also been reported. Many of these reports were based on the number of males heard vocalising, but a ratio of vocalising males to males present has not been reported (e.g., Kudo, 1987).

An examination of the sexual and reproductive behaviour of mandrills and the relationships between individuals may provide a means to test predictions related to the occurrence of single- or multi-male groupings in primates. In all discussion of social groupings in primates, the mating system should be clearly differentiated from the social organisation. Assertions about mating system should be based on observation of copulatory behaviour and not simply on relative numbers of males associated with groups of females. Thus observations of multiple males associated with groups of mandrills does not necessarily imply that mandrills have a multi-male (polygynandrous) mating system.

Single- vs. multi-male groups

The phenomena of seasonality and reproductive synchrony in the CIRMF mandrills are of interest in testing results from analyses by Dunbar (1988) from which it was concluded that seasonal breeders are unlikely to have single-male harem-type social systems. This confirmed an earlier review (Ridley, 1986) showing that multi-male groups occur significantly more often in species that have short breeding seasons, whereas in non-seasonal breeders one-male groups occur significantly more frequently. If mandrills are strongly seasonal breeders, which the data presented in this thesis indicate, then they would be expected to occur in multi-male groups. Bearing in mind that primates can be found in multi-male groups yet have a single-male breeding system, the mandrill data collected in this study were applied to the model presented by Dunbar (1988) to see whether the prediction that mandrills would live in multi-male groups would be upheld by an analysis using reproductive parameters from the CIRMF mandrill group.

It is suggested that the ability of a male to restrict access to sexually receptive females depends on the probability of multiple females being in oestrus on the same day. The greater the probability, the more difficult it would be for a single males to prevent access by other males to oestrous females. Before testing these predictions with the mandrill data from the present study, the nature of 'oestrus' in the CIRMF mandrills merits discussion.

Data presented in Chapters III and VI on the reproductive biology and behaviour of female mandrills, particularly in relation to the coincidence of copulation with maximum swelling, have not before been available, and are of interest in relation to Loy's (1987) paper on the question of oestrus in African monkeys. The data from the CIRMF study suggest that mandrills may be an exception to the reported cercopithecoid pattern proposed by Loy. Oestrus can be characterised by the following features (Loy, 1987): (1) copulation occurs only at this time - when a female is anoestrus she is sexually inactive; (2) during oestrus the female is willing to copulate, whereas she avoids copulation attempts at other times; (3) copulation at this time can result in conception; and (4) oestrus is generally restricted to a brief time period. Sexual behaviour fitting this description of oestrus is common among mammals such as Norway rats (*Rattus norvegicus*), guinea pigs (*Cavia parellus*), domestic cattle (*Bos taurus*), and dogs (*Canis familiaris*) (references in Loy, 1987). Among primates this type of oestrus is also characteristic of most prosimians (references in Loy), such as galagos (*Galago senegalensis*), ring-tail lemurs (*Lemur catta*), and mouse lemurs (*Microcebus murinus*). However, Loy argued that 'in the vast majority of African monkey species, females do not limit their sexual behavior to oestrus' (1987, p.184) and therefore that it is inaccurate and misleading to describe their behaviour in terms of an oestrous cycle. Despite some species having cyclical sexual swellings and seeming to show classic oestrous cycles mangabeys, talapoins, and baboons engage in sexual behaviour at times other than near ovulation (references in Loy, 1987). The only mention of *Mandrillus* in Loy's paper is of sexual activity in early pregnancy in both mandrills and drills in a captive colony (Hadidian and Bernstein, 1979) and Struhsaker's (1969) reported observation of ejaculate on a wild unswollen drill. In relation to Beach's (1976) model of Attractiveness, Proceptivity, and Receptivity (APR model) Loy argued that in most African monkeys, proceptivity and receptivity were strongly situation-dependent. Oestrus in the classic sense can be defined as the coincidence of APR at the same time in the female reproductive cycle - namely around ovulation (which is exactly what occurs in the prosimians and rodents mentioned above). The data presented in Chapter III indicated that mandrills also can be described as having 'true oestrus' in that virtually all intromitted mounts occurred during maximum tumescence; females accepted and even initiated copulations during this period; copulations resulted in conception (conceptions occurred in 61% of oestrous periods); and that oestrus was temporally restricted (an average of 14 days a year occurring in the months July to October). In this respect mandrills differ from baboons of the genera *Papio* and *Theropithecus*, as well as from other African cercopithecoids.

Given that females associate in groups, whether or not a single male can effectively monopolise access to oestrous females depends on the probability of multiple females being in oestrus on the same day. The more females who are synchronously in oestrus the less the male's chances of effectively defending them from competing males. The probability that two or more females will be in oestrus together can be calculated from Dunbar's formula (1988, p.140):

$$P(x \geq 2) = \sum_{x=2}^{n} \binom{n}{x} p^{x} (1-p)^{n-x}$$

where $P(x \geq 2)$ is the probability that two or more females will be in oestrus at the same time (on the same day), n is the number of females in the group, x is the number of females in oestrus at the same time, and p is the probability that any one female will be in oestrus on any given day. The probability p is calculated by the proportion of days that a female spends in oestrus during a full reproductive cycle. This can be calculated as the number of days of the menstrual cycle spent in the oestrous phase, multiplied by the number of cycles to conception. For example, in mandrills the modal duration of oestrus was 14 days, and on average females conceived in two cycles thus $p = 14 \times 2 = 28/365 = 0.077$ if mandrills bred throughout the year. However, since they are seasonal breeders, if the season lasts four months, $p = 28/123 = 0.228$. This is thus the probability of a female being in oestrus on any one day of a four month breeding season. Based on the transition in gelada baboons from one male to multi-male groups, which occurs at about eight reproductive females, Dunbar proposed that a P of approximately 0.2 represented the threshold for switching from single-male to multi-male groups. Data presented on capuchin monkeys, *Cebus apella,* supported this finding (Janson, 1984, cited in Dunbar, 1988). The probability of two or more females being in oestrus on the same day (the value P) was calculated for the CIRMF mandrills. The data were calculated separately for the years 1986 and 1987.

In 1986 there were eight reproductively active females in the group, conception occurred in 2 cycles, and females were in oestrus (modal duration 14 days) over five months. The probability of any one female being in oestrus was $p = 0.183$. From Dunbar's formula, P was 0.434. This was considerably higher than the proposed threshold of 0.2 and suggested that mandrills should be found in multi-male groups. The data for 1987, using slightly different parameters (nine females in the group, conception in one cycle, and oestrus during four months) gave $p = 0.114$ and a P value of 0.277. In practise, probabilities of greater than five mandrills being simultaneously in oestrus can be ignored since the contribution they make to P is almost negligible due to the very small value of p ($p < 0.000$). Interestingly, five was the maximum number of female mandrills ever observed in oestrus on the same day.

In both years the results of the calculation, although less conclusive for 1987, suggested that mandrills should occur in multi-male breeding groups. This finding supported the predictions of Ridley (1986) and Dunbar (1988) that seasonally breeding primates should occur in multi-male troops. However, since there is some evidence that mandrills occur in single-male groups other explanations should be sought. The above results could be explained by features of the model as well as by the possibility that characteristics of the CIRMF mandrills were not representative of wild mandrills.

Various parameters in the model were based on approximations, for example the duration of the breeding season and the length of oestrus. The calculations above indicated that the probability of more than two females being simultaneously in oestrus varied between the two years. This suggests that any characterisation of a species as being single- or multi-male is only accurate for one particular moment in time, and thus that classing a species as single- or multi-male on the basis of the model is a generalisation. Furthermore, the different results in the two years suggest that under some circumstances, depending on the value of P, primate groups would switch from single-male to multi-male groups in different years, or different breeding seasons (or possibly within them as the number of females simultaneously in oestrus varied). This has been observed in some species (*Cercopithecus:* Cords, 1987; Henzi and Lawes, 1987; *Erythrocebus:* Harding and Olson, 1986). If applied to mandrills this suggests the possibility of considerable flexibility in social organisation. The multiplicity of terms and grouping reported for mandrills, outlined above, lends some support to this idea, although the quantification of group composition in mandrills is still too vague to allow an accurate assessment. Since there are as yet no field reports of oestrous females or copulatory behaviour, the coincidence of change in group composition with the mating season in mandrills must remain purely speculative. However, although the relevant observations are lacking, some circumstantial evidence exists. Mandrills are reported to form very large congregations numbering several hundred individuals at times of relative fruit scarcity (reviewed in Chapter IV) or at least, these enormous groups were more frequently observed at these times than at times of fruit abundance. In Gabon, fruit is relatively scarce during the long dry season, June to September. This period coincided with the observed mating season in the CIRMF mandrills of July to October. The representativeness of these CIRMF data is supported by the limited field reports of seasonality in birth approximately six months later. Thus, accepting that the mating season observed at CIRMF occurs in feral populations in Gabon also, it appears that females come into oestrus at a time when more males are likely to be 'around', even if 'attached' to their own groups, and also when the alpha male of a one-male unit has most to lose by losing tenure of his group. Numerous solitary males have been

* Refining the parameters used in the calculation has the effect of decreasing the probability of two or more females being simultaneously fertilizeable (peri-ovulatory). This would be true for all species and the threshold for single vs. multi-male groups would therefore be lower. Data from a variety of species would be needed to fix the new threshhold with any certainty and thus allow the definite assessment of mandrills as being in either single or multi- male groups on the basis of this formula.

observed associated with and following these large aggregations of mandrills (A. Gautier-Hion, pers. comm.). This has implications for social strategies and male-male competition as well as for female choice. Additionally it would allow female transfer between groups.

Generalisations in the model could also limit its accuracy. The model used the duration of oestrus in the calculation of p. In geladas this was about 10 days, in mandrills about 14. However, conception is not equally likely on all oestrous days and fertilisation of a female is possible on only a small proportion of days during oestrus. In baboons conception is most likely on the days D-4 to D-2 (Hendrickx and Kraemer, 1969; Wildt *et al.*, 1977; Shaikh *et al.*, 1982) and assuming this also to be the case for mandrills, the calculation could be refined by considering only the days when copulation by a male would be likely to result in impregnation of the female. Thus the probability values for mandrills were recalculated using three as the number of days of possible conception and limiting the mating season in the manner defined in Chapter III, namely as comprising the period from the day a maximum sexual swelling was first seen to the last day such a swelling was observed. The probability of more than two females being synchronously peri-ovulatory given the restricted period during which females were in oestrus was calculated. The adjusted P value for 1986 was 0.046 and for 1987 was 0.029.* These figures suggested that mandrills may be found in single-male groups since one male should effectively be able to monopolise peri-ovulatory females, given the assumption that nearness to ovulation is not concealed from males. In fact, this is what was observed in the CIRMF mandrills. Although females sometimes copulated with more than one male in any one oestrous period, an average of 87% (range 71% to 100%) of ejaculated copulations (thus conception was possible from the male perspective) on days D-4 to D-2 (thus conception was possible from the female perspective) of four founder females (Nos. 2, 6, 10, and 12) in 1986 were by a single male, the only fully mature male in the group, No. 7, the alpha male. Additionally, the data presented in Chapter VI on mate-guarding showed that it occurred preferentially in the peri-ovulatory period and that the alpha male swopped females on consecutive days indicating that proximity to ovulation was not concealed.

Since the above discussion suggests that mandrills may form one-male units, their behaviour is compared below to that of other baboons whose basic unit of social organisation and whose mating system is the one-male unit, namely hamadryas baboons (*Papio hamadryas*) and gelada baboons (*Theropithecus gelada*). These comparisons are based mainly on the studies of Kummer (1968a) and Dunbar (Dunbar and Dunbar, 1975; Dunbar, 1984). These two baboons are found in multi-levelled societies (Stammbach, 1987). However, since field data on the larger groupings of mandrills are rudimentary, comparisons with mandrills will be limited to interactions within the one-male unit and will focus on interactions between adults, as relationships of immatures were not quantified in the mandrill study. First, relationships during anoestrus will be discussed, followed by an assessment of the effect of oestrus on these relationships.

Mandrills, geladas, and hamadryas baboons

Spatial relationships among the CIRMF mandrills indicated that, with the exception of the alpha male, on average males had no founder mandrills in 71% of point samples at 0-5 m, and none in 50% at 5-10 m (Chapter V). This may be an indication of general group dispersion, but that this may be a social effect is suggested by the finding that the percentage time spent with no neighbours correlated with dominance rank, with subordinate males spending less time alone than more dominant individuals. This corroborated the finding that among males dominance rank correlated negatively with sociability index with subordinate males being more sociable than more dominant individuals. Thus subordinate subadult males, far from being peripheral, were more 'involved' in the group than were the older more dominant males. This was supported by observations of subordinate males playing with juveniles, which more dominant males were never observed to do. The alpha male was significantly different from other males on both these measures, spending less time with no neighbours at both distance categories, and having a higher sociability index. Simply on these two measures he was immediately distinguishable from other males - which would tend to support predictions of a functionally one-male group structure in mandrills. Data reported in Chapter IV confirmed this, indicating that the alpha male was significantly different from other males, not just on various social behaviour but also in maintenance behaviour such as monitoring, foraging, and climbing.

Anoestrous female mandrills, both when pregnant and lactating, spent significantly less time without founder neighbours at both distance categories than males and were also significantly more sociable than males. Given that these analyses were based on quantified interactions between founders, i.e., offspring were excluded, they indicate that females associated more than males did. In contrast to the situation for males, the alpha female was not significantly different from other females and there were no clear relationships between dominance rank and measures of spatial relationships. During pregnancy and at some distance categories during lactation, females spent relatively little time in close proximity. It is possible that this was due to feeding competition.

Grooming relationships among members of hamadryas and gelada one-male units differ considerably. In the hamadryas unit, grooming by adult females is primarily concentrated on their own infants and on the unit leader and females compete with each other to groom him (Kummer, 1968a). By contrast, in gelada baboons females form grooming dyads composed of an adult female and her mature daughter (Dunbar, 1984). The adult male's main grooming partner is usually a female who has no female relative with whom to groom. An examination of the data presented in Chapter V on grooming relationships in the CIRMF mandrills indicated that they conformed to neither of these two patterns.

First, in general male mandrills were involved in very little grooming. For example, two of the six group males were never recorded grooming, and those that were (excluding the alpha male) spent on average only 1% of point samples grooming. The exception was the alpha male who groomed significantly more than other males. There was considerable individual variation in the pattern of grooming, although all grooming by males was with females, i.e., no male-male grooming was observed. Two of the males groomed only with adult females and received nealy all their grooming, whereas two other males groomed also with adolescent females and gave a proportion of their grooming. Groomer/groomee roles between males and females were very skewed, with in most cases the female grooming the male. However, generally speaking male mandrills were rarely observed grooming and the absence of this behaviour was quite striking.

This relative lack of male-female grooming in mandrills was very different from Kummer's observation of hamadryas baboons at the sleeping rock where 'adult males were grooming in 12% of the observation minutes and were being groomed in 19%' (1968a, p.44). Since focal data on mandrills were not collected after 1800 hours, when the mandrills were in their sleeping trees and thus likely to be relaxed and in a situation similar to the hamadryas at their sleeping cliff, it could be argued that grooming records collected during focal sampling were likely to under-estimate this behaviour. However, *ad lib.* observations after 1800 hours indicated that there was no increase in male-female grooming at this time. In fact, for many males social grooming was not possible since they often slept alone, apart from the group. Thus, although the alpha male mandrill participated in more grooming than other males he was not a focus of female grooming attention and there was no indication that females competed to groom him. The same was not true in relation to females, who did sometimes displace each other from female grooming partners (Chapter V).

Analyses of female grooming relationships indicated that most females groomed only with their own offspring and with other founders, but that these founders were mostly females. Of the three adult female founders who had adolescent daughters, two had strong grooming relationships with them, receiving much of their grooming from them. This was reminiscent of the situation in geladas. Only study of a more mature group containing older established matrilines would allow an assesment of whether female mandrills develop strong dyadic grooming relationships with their kin. In geladas, although relationships between females appear to maintain the unit, from the male's point of view he maintains his bond with the females by grooming with them. This was clearly not the case in the CIRMF mandrills since male-female grooming was rarely observed and the alpha male was seen grooming with only three of the seven adult females in the group.

Agonistic relationships in the CIRMF mandrills were characterised by stable, linear dominance hierarchies within each sex and considerable reversals in male-female dyadic interactions. In hamadryas baboons females also were arranged in a linear dominance hierarchy but aggression between females was always carried out in front of the unit leader (Kummer, 1968a). Dominance hierarchies among female geladas were also strictly linear, and as in mandrills, no cases of non-transitive dominance and few wins against the hierarchy were observed (Dunbar, 1984). Perhaps the major difference between the agonistic interactions observed in mandrills and those reported in gelada and hamadryas baboons concerns the use of herding, which is particularly salient in the latter species. 'Aggression by the male hamadryas is produced by anything that reduces the behavioural and spatial integrity of his unit' (Kummer, 1968a, p.46). A bite on the nape of the neck or on the back is the most severe reaction a female hamadryas baboon receives if she strays from the male, and it induces the following response. In geladas, 'males may herd females for straying too far from them, though there is much individual variation among the males' (Dunbar and Dunbar, 1975, p.38). In addition, herding may result in the female threatening back and chasing the male. Female chases of males were also observed in the CIRMF mandrills but were usually in response to a perceived threat against an offspring. Herding was not observed in any of the CIRMF male mandrills although it has been described in wild subadult male drills (Gartlan, 1970). Aggressive behaviour by males towards females was generally followed by an increase in distance between the two rather than the increased proximity which resulted from male aggression to females in hamadryas baboons. Thus a one-male unit of mandrills is unlikely to be maintained by coercion by the male as it is in hamadryas baboons. It seems possible that in mandrills, as in geladas, considerable female choice exists, which is not the case in hamadryas baboons in whom females are herded, secluded, and protected within a small part of the troop from the early juvenile stage onwards for the rest of their lives by adult males.

Relationships among founder mandrills were altered by the occurrence of oestrus. All founder mandrills spent less time with no neighbours during periods of oestrus than anoestrus. Among males, dominance rank correlated with percentage time without neighbours, with dominant individuals spending less time alone than subordinates - which was the opposite relationship to that found during anoestrus. As before, the alpha male was significantly different from other males, spending only about 5% of point samples alone. The same phenomenon, that of a reversed correlation with dominance during oestrus in relation to anoestrus was also seen in male sociability indices. Dominant males were more sociable than subordinates, and the increase in sociability from anoestrus to oestrus was greater for more dominant males. These two examples of a reversal in social tendency among males with occurrence of oestrus provide an immediate contrast to gelada baboons in whom 'sex is perfunctory and interferes rather little with the participants' established pattern of relationships' (Dunbar, 1984, p.52). In female mandrills, time with no neighbours decreased and sociability indices increased during oestrus in comparison to pregnancy. Generally, although fewer males were in close proximity to each other during oestrus, they spent more time at 2-5 m than they did during anoestrus. If males increase their proximity to oestrus females, a result of this is that they are also likely to be nearer other similarly-behaving males. Proximity to oestrus females was dominated by the alpha male, whether mate-guarding or not. He spent 12 to 15% of time very close to (< 1 m) females in oestrus in comparison to only 1% spent by other males and this pattern also occurred at other distance categories (Chapter VI).

In addition to spatial relationships, grooming relationships in mandrills were also altered by the occurrence of oestrus. Females spent more time grooming when in oestrus than they did when pregnant and groomed only with their offspring and with founders. When females were fully swollen nearly three-quarters of their grooming was with founders. During oestrus males received nearly all the grooming given to founders, whereas when pregnant, females gave three-quarters of their grooming to female founders. Oestrous females also received more grooming than pregnant females, they received more from founders, as opposed to offspring, and over 60% of it was from founder males. During pregnancy females received less grooming from others and nearly all of it was from adult females. Thus female grooming relationships changed dramatically with a change in their reproductive status from being sexually inactive to sexually receptive. Male behaviour was also altered; subadult and adult males groomed more, with the alpha male grooming twenty times more frequently than other males and grooming twice as much when females were in oestrus than when anoestrus. However, fewer males were recorded in grooming relationships with females during oestrus than were during anoestrus suggesting perhaps that some males were excluded or that they were not chosen as grooming partners by oestrous females. Males restricted their grooming partners to adult females during oestrus. Although male-female grooming was increased during oestrus it was unclear how much this grooming contributed to the mate-guarding relationship. The alpha male was not observed grooming with every female he mate-guarded and grooming did not follow copulation. In this respect the mandrills resembled geladas in whom grooming also is not asociated with copulation (Dunbar, 1984) and differed from hamadryas baboons in whom it is (Kummer, 1968a).

However, in other respects mandrills differed considerably from geladas. In the latter species mating is reported to occur throughout the female's cycle although its frequency increases in the peri-ovulatory period (Dunbar, 1984). This contrasts strongly with the CIRMF mandrills in whom virtually all mating was at periods of maximum swelling. In gelada baboons females initiated 75% of copulations, whereas in mandrills only 12% were initiated by females. Dunbar proposed that in a one-male group access to oestrous females is uncontested once a male has acquired a harem so that the male can 'allow females to notify him when they are receptive' (Dunbar *op. cit.*, p.52). In connection with this geladas were reported to mate at lower rates than multi-male *Papio* baboons and to have relatively small reproductive organs. The limited data available from the present study indicated that a pair of mandrills mated about once every 71 minutes. This was intermediate in relation to rates of once every 50 minutes in yellow baboons (Hausfater, 1975) and once every 110 minutes in geladas (Dunbar, 1984). Predictions about testis size in mandrills are considered later.

In summary, substantial differences exist between the inter-adult relationships of mandrills, hamadryas, and gelada baboons, though none of these differences in themselves provide conclusive evidemce against the existence of one-male groups in mandrills. Given that mandrills do not much resemble these two species, perhaps aspects of their social interactions can better be understood in the light of a continuum of variation in behaviour among baboons. Popp (1983) suggested such a continuum and in the following section the data presented in this thesis are examined in relation to Popp's predictions of the position of mandrills on the continuum.

Popp's baboon continuum

Popp (1983) argued strongly for the ecological determination of baboon life history strategies (and hence social organisation) through environmental variables, such as food resources, which affect reproductive success, in terms of reproductive effort and its distribution over the life history of the individual. These variables constitute a strong selective force leading to divergent evolution in behaviour and morphology and operate via increased energy intake through feeding, as this 'extra' energy may be used to increase reproductive output.

In baboons, parental investment by males is relatively low in comparison to female parental investment, so that a male can maximize his reproductive success by maximising the number of females he impregnates and the number of times he impregnates each. Popp suggested that a one-male unit would be the preferred male reproductive strategy as all other males are excluded from the breeding group and a single male can thus maximize the number of females that he impregnates. If exclusion of other males was not possible, the 'next-best' strategy might be to diminish or subordinate the role of other males in breeding by competition at critical points, e.g., over peri-ovulatory females, for example by forming dominance hierarchies. If neither of the above strategies were feasible then a third alternative would be to avoid other males and to try to enhance contact with females through techniques other than male aggression, for example by establishing affiliative bonds by grooming them. These strategies can be summarised as (1) male-male exclusion, (2) male-male competition, and (3) male-male avoidance (Popp, 1983, p.199).

The most energetically costly is the first strategy as it involves high rates of male-male aggressive competition. Reproductive payoffs are likely to vary considerably depending on outcome - a dominant male may have sole access to reproductive females, whereas an excluded male may have almost no reproductive opportunities. Intense competition from other males pursuing this exclusion strategy suggests that duration of male tenure and male reproductive life-span may be correspondingly short. Popp predicted that this type of social organisation (effectively a one-male unit) would be most prevalent in relatively energy-rich habitats. The second strategy should operate in moderate-energy habitats and requires moderately high amounts of aggressive competition and sexual dimorphism. These moderate habitats may be highly variable and Popp predicted a degree of plasticity in male strategy and in social organisation at both ends of the moderate energy continuum. In energy-poor habitats the third strategy, that of male-male avoidance, should predominate. Behavioural consequences of an energy-poor environment should include low rates of intra-sexual aggression, low rates of reproductive effort per unit time, but long reproductive lifespans. Morphological consequences might be reduced body mass and dimorphism in relation to individuals in higher-energy habitats.

The ecological variable Popp proposed to determine life history strategy was mean annual rainfall. This was because primary production and plant species diversity are positively correlated with mean annual rainfall (where there are controls for altitude, evaporation rate, periodicity etc.). Since baboons can be described as generalised herbivores, their food supply and hence energy available through foraging, is correlated with rainfall.

Popp predicted that energy-rich habitats would contain large, highly sexually dimorphic males with high rates of intra-sexual aggression. At the other end of the spectrum, energy-poor habitats should contain relatively smaller, less sexually dimorphic males with lower rates of male-male conflict. Inbetween are intermediate baboons. These predictions, that particular sets of features relating to male reproductive strategies are associated with habitats of particular energy level as measured by precipitation, can be tested by examining baboon populations from areas of differing mean annual rainfall. This is exactly what Popp did, using 13 sets of data from behavioural studies of gelada, hamadryas, savanna baboons, and mandrills.

Three principles coordinate his theory:

(1) *that body mass of adult males and females is positively correlated with mean annual rainfall*;

(2) *that the degree of sexual dimorphism in body mass increases with increasing rainfall and that male body mass increases geometrically as a function of adult female body mass*; and

(3) *that as habitat quality improves, male-male competition increases for access to mates. Rates of escalated male-male conflict are positively correlated with annual rainfall.*

The data on mandrills presented in this thesis are of relevance to all three principles and can be used to substantiate or refute Popp's ideas, since he had only limited biological data on mandrills and no data on social behaviour.

The data on body weight of the CIRMF mandrills (Chapter III) support the first principle and confirm that male mandrills are not only the largest of the baboons, but also of any of the monkeys. The second principle was also supported, mandrills were shown to be extremely sexually dimorphic in weight (Chapter III). The second principle has recently been criticised by Vitzthum (1988) on the grounds that the mean weight Popp reported for mandrills was 'likely to be a substantial overestimate of the average body weight of wild mandrill males' (p.135). Vitzthum argued that if the mandrill example was excluded a linear regression of mean body weight data produced a line statistically indistinguishable from that of constant body dimorphism of 200%. Popp's mandrill data were from two captive males (49 kg, 52 kg) and two captive females (14 kg, 18 kg) giving a sexual dimorphism ratio of 216% (where male weight was given as female weight plus % female weight). A similar degree of dimorphism was obtained (207%) from the CIRMF mandrills, using the weights of the two fully adult males (53 kg, 27 kg) and seven adult females (mean = 13 kg) to calculate the measure of dimorphism. If all males were used (giving an underestimate as five had not yet reached full growth) the ratio was 166%. This underestimate is counterbalanced by bias in the opposite direction in that the criticism applied to Popp's data, that data from captive individuals represent an overestimate of body weight in feral animals, could apply here also since the CIRMF mandrills were provisioned. However, even using data from wild-shot mandrills (Malbrant and Maclatchy, 1949) a ratio of 145% is produced, which is still higher than that of any other baboon population examined by Popp. Thus it seems reasonable to conclude that mandrills are at the extreme end of the array of increasing sexual dimorphism among baboons.

Thus, data from the CIRMF mandrills on body weight and sexual dimorphism corroborate principles 1 and 2. High body mass and extreme sexual dimorphism are predicted to be associated with both the male-male exclusion and male-male dominance strategies, but particularly the former.

The analyses of social behaviour in mandrills presented in this thesis allow an assessment of Popp's third principle. Which of the strategies proposed by Popp - exclusion, dominance, or avoidance - do male mandrills most resemble? Do the data from the CIRMF mandrills support Popp's predictions of high rates of male-male competition in wet habitats?

The third principle is more problematic in that although Popp referred to rates of 'escalated male-male conflict' (p.207) and cited data from focal samples of aggressive behaviour of *Papio* baboons, he did not define escalated conflict. The mandrill data from this study and any other relevant information supporting or refuting each strategy will be considered in turn.

(1) Male-male exclusion

I witnessed only one fight among the male mandrills at CIRMF (described in Chapter VI), which was between the two fully mature males present in the enclosure, and occurred in the presence of an oestrous female. However, the appearance of wounds indicated that other unobserved conflicts had occurred. Whether or not these unobserved fights were over possession of the group and alpha status is unknown, although the observation that the alpha male was never seen with a wound suggests that they were not. It seems more likely that that they were contests among the other males over relative dominance rank. Given the alpha male's predominant role in breeding (Chapter VI and above), it seems possible that a male-male exclusion strategy could have been in operation in the CIRMF mandrills.

The process by which maturing males become peripheral and solitary was not observed and is unknown. The alpha male did not act aggressively towards the subadult males in a manner that appeared to be 'forcing' them from the group and, with the exception of the witnessed fight, no clear dyadic winner-loser interactions between the two fully adult males were observed (Chapter V). The male-male exclusion hypothesis, which should result in a single-male group, at least functionally at a breeding level, would suggest that the alpha male should be readily distinguishable from other males. This was shown repeatedly to be the case for the alpha male mandrill at CIRMF. His behaviour was significantly different from other males, not only in terms of his social interactions, but as mentioned earlier also in terms of foraging, monitoring, and movement pattern (Chapters IV, V, and VI). His 'special' position was also demonstrated by the following experiment. When a (slightly larger than life-size) model of a male mandrill was presented to the CIRMF mandrills, the alpha male was the only male whose initial reaction to the model was to threaten it. Other males showed submissive and appeasement gestures, displacement behaviour, and were ambivalent in their reaction (unpublished observations). One interpretation is that the alpha male treated the model as he would an unfamiliar conspecific, i.e., by threatening a potential competitor. (It should be remembered in this context that the solitary male in the enclosure was well-known to the members of the group, having been released with them in 1982). Further evidence in support of the male-male exclusion hypothesis is provided by the relatively frequent field observations of solitary subadult and adult males (mean 15% of sightings, Chapter IV) indicating that many males spend some time excluded from social groups. Jouventin (1975a) reported that numerous hunters in Gabon described fights during which supernumerary males or an old leader male were expelled from the group (p.522).

Evidence against the operation of this strategy is furnished by observations of multiple males associated with mandrill groups (Jouventin, 1975a; Hoshino *et al.*, 1984). For example, I observed a group of about 40 mandrills in the forest in the Lopé Reserve, Gabon in which two large adult males were present. However, the males could easily be distinguished. One was somewhat larger and much more brightly coloured than the other. Additionally, observations of multiple males were usually concomitant with those of large groups (Jouventin, 1975a; Hoshino *et al.*, 1984), which does not exclude the possibility that the large groups were aggregations of several one-male groups. In the CIRMF group of mandrills although two fully mature males were present in the enclosure, only one was associated with the group, and in terms of producing infants the group was effectively a one-male unit. The exact composition of mandrill groups is difficult to judge in the forest, but additionally, as emphasised above, the presence of more than one male in a group does not mean that the additional male has a role in breeding, and in terms of mating strategy, even a group with more than one male could operate on a male-male exclusion strategy if the second male was excluded from access to peri-ovulatory females, as was the situation between the two fully mature males at CIRMF. An example of this is provided by the gelada baboon. One-male units sometimes contain a second follower male, but he does not have sexual access to oestrous females (Dunbar, 1984).

(2) Male-male dominance

Agonism between males in the group of mandrills at CIRMF seemed generally to be 'low key' and rates of aggression were low (Chapter V). The males were ranked in a stable linear dominance hierarchy and several subadult males were consistently associated with the group. This suggests that Popp's male-male dominance strategy might have been in operation. Competition at critical points, i.e., over peri-ovulatory females occurred and the most dominant male was able to monopolise access to these females by mate-guarding them and warning off other males. This male was very likely the father of many of the youngsters in the group, as was shown in Table VI.8.

(3) Male-male avoidance

There was little evidence in favour of this strategy from observations of the CIRMF mandrills. Outwith oestrus, male mandrills interacted very little with females and showed very little of the affiliative behaviour such as grooming which is predicted by the male-male avoidance strategy.

In summary, the data from the present study at CIRMF allow the rejection of the male-male avoidance strategy for mandrills. It is difficult to be so definite about the other two strategies given that numerous males were associated with the group (although all these males were subadult in that they had not reached full growth) and could be ranked in terms of a linear dominance hierarchy, supporting the male-male dominance strategy, yet although more than one male was observed to copulate, the alpha male was clearly predominate in breeding and the group could be classed as a functionally one-male unit supporting the male-male exclusion strategy. Further detailed data from wild mandrills are needed before a conclusion could definitely be reached.

In fact, Popp's hypotheses about male-male strategies may be over-simplified and only allow very broad classification. In practice, male baboons may use different tactics. For example, in a multi-male savanna baboon troop (suggested by Popp to represent the intermediate male-male dominance strategy) males may compete aggressively for access to oestrous females as consort partners (Hausfater, 1975) and also develop strong affiliative bonds involving frequent grooming with anoestrous females (Smuts, 1985). Thus the same individuals may show behaviour characteristic of both the exclusion and avoidance strategies. This point was also discussed by Dunbar (1984) in relation to the different tactics available to male gelada baboons.

Mandrills do not appear to resemble savanna, hamadryas, or gelada baboons (Feistner, unpubl. manus.). Since all these baboons live in very different habitats from mandrills there seems no clear reason why mandrill social structure should fall neatly into any category. Recent work indicates that baboons (*P. ursinus*) typically considered as living in multi-male troops live in one-male groups under some circumstances (Whiten *et al.*, 1987; Byrne *et al.*, 1987; Anderson, 1989). Given the considerable flexibility of these primates it may be more 'helpful' to concentrate on a thorough description of environmental variables, particularly in relation to distribution and availability of food resources, and to attempt to refine methods of data collection, for example by the use of radio-telemetry, than to try to fit the relatively limited and inconclusive field data currently available on group structure in mandrills into patterns manifested by other baboons in very different habitats.

Since mandrills closely resemble none of the other baboons in either ecological conditions or in social structure, it may be of interest to look further afield and examine a species which does seem to show many similarities with mandrills and which appears to represent the analogue in Asia of the African mandrill. An Asian monkey which is relatively large-bodied, mainly frugivorous, semi-terrestrial, and inhabits primary rain forest is the pig-tailed macaque, *Macaca nemestrina nemstrina.* An examination of the ecology and behaviour of this species based on a long-term (29-month) field study (Caldecott, 1986a) provides the information for the comparison of pig-tailed macaques and mandrills described below.

The pig-tailed macaque as an ecological analogue of mandrills

The pig-tailed macaque's diet, as assessed by percentage of feeding observations, consisted of 74% fruit, nearly all of which was ripe, 12% invertebrates, and 14% other plant parts and vertebrates. In this respect its diet resembles that of mandrills who eat about 87% fruit, 5-8% invertebrates, and 6% other plant material, as assessed by analysis of dry weight of faecal samples (Hoshino, 1985; Lahm, 1986). Such an analysis may underestimate the importance of invertebrates which, although forming only a relatively small percentage weight of dried faecal and stomach contents, may take considerable time to acquire. Norris (1988) found that 11% of food-items taken from terrestrial sources by mandrills were animal matter, although none was reported as being acquired arboreally. However, on several occasions I observed the CIRMF mandrills obtaining invertebrates from above-ground sources. Both species can feed both on the ground and at all levels in the canopy. Contrary to mandrills who live sympatrically with a number of semi-terrestrial primates (as discussed earlier), the pig-tailed macaque's competitors are exclusively arboreal. However, in both species there may be intra-specific differences based on size-class, with large males excluded from foraging on some of the smaller arboreal sources where thin twigs may not be able to support their weight (Caldecott, 1986a; pers. obs.). Adult male pig-tailed macaques used the ground and large supports more than expected and females and juveniles used branches and foliage more than expected, and this was similar to observations of mandrills reporting that adult males were mainly seen on the ground and that females and juveniles used the higher strata of the forest (Jouventin, 1975a). Both Hoshino (1985) and Norris (1988) proposed that terrestrial food sources were the mainstay of the mandrill's diet. In fact, Hoshino (*op. cit.*) even suggested that 'food availability may be greater for the arboreal monkeys than for the terrestrial monkeys, *since the terrestrial monkeys have access to fruit only after it falls to the ground*' (p. 267, my italics). This seems completely to ignore the fact that mandrills are capable climbers and can quite readily gain access to arboreal fruit sources. As an example, Harrison (1988, p.223) reported an observation of 52 mandrills emerging from a single fruiting tree.

Both species are found in groups of similar sizes; pig-tailed macaques lived in groups of about 30 individuals (range 15 to 40). From observations of 28 social groups of mandrills, 13 contained 20 to 50 individuals, and the median size of these groups was 29 (Jouventin, 1975a).

The ratio of adult males to adult females was also similar in both species, with each having the most skewed ratio relative to other members of their taxonomic groups. In pig-tailed macaques, of 1715 spot observations 19% were of fully adult males and 36% of adult females, giving a ratio of 1:1.9. However, most males were either peripheral or solitary and only a few were consistently associated with groups. When solitary and peripheral males were excluded, only 5.3% of observations were of fully adult group males, giving an intra-group male to female ratio of 1:7.9 (Caldecott, 1986a). This was the highest of any wild macaque group yet studied (see Caldecott, *op. cit.* Table XXXIX, p.171) and resembled the pattern for mandrills. From three detailed group counts by Jouventin (1975a) a ratio of adult males to adult females of 1:9 (1:10, 1:10, 1:8-9) can be calculated. This is the highest of any papionine with the possible exception of the drill in which group composition appears similar to that of the mandrill (Gartlan, 1970). No estimate of male:female ratio was available from the studies of mandrills at Campo, in Cameroon, because observed individuals were classified only as adult male or other (with one exception, but the number of females was not reported) and in calculation of group composition based on distribution of weight of fresh faeces the faeces of adult females were not distinguishable from those of subadult males (Hoshino *et al.*, 1984). The proportion of the group which was immature was about 32% in pig-tailed macaques and about 50% in mandrills (Jouventin, 1975a; Hoshino *et al., op. cit.*).

Both pig-tailed macaques and mandrills appear to divide into several different social units. Various authors have defined these groupings differently for mandrills and given them different names, as mentioned earlier. As pointed out by Caldecott (1986a, p.173) 'temporary fissioning and fusing of groups makes it particularly difficult to establish group size in wild, forest-dwelling macaque populations' and the same can be said of mandrills. Both species appear to exhibit considerable social and spatial variability (Caldecott, *op. cit.*; Jouventin, 1975a; Hoshino *et al.,* 1984; Kudo, 1987). Subgroups in both species are thought to have both a social and ecological role, and it was suggested that the grouping patterns of pig-tailed macaques may be explicable in terms of the aggregation and separation of one-male harem units with permanent female membership (Caldecott, 1986a, p.149). The size of such units, their density, and their tendency to aggregate would presumably be controlled by food supply. In this respect there appears to be considerable convergence between pig-tailed macaques and mandrills, although nothing is yet known of the temporal stability of membership of mandrill subgroups. However, data presented in Chapters V and VI indicated that females may form the stable core of mandrill groups; females spent more time in proximity to each other than they did to males, most grooming during anoestrus was with other females and offspring, and adult females generally had close relationships with their adolescent daughters, suggesting the development of cohesive matrilines. That aggregation of groups is influenced by food supply is supported by the indication that the very large congregations of mandrills, numbering 100 to 300 individuals, presumably formed by the fusion of several one-male units, groups, or subgroups, were more frequently observed during periods of relatively low availability of fruit (Jouventin, 1975a; Hoshino *et al.*, 1984; C.E.G. Tutin, pers. comm.; A. Gautier-Hion, pers. comm.).

Solitary individuals were observed in both species and were always subadult or adult males, but no all-male bands have been reported in either species. Adult male pig-tailed macaques neither travelled not fed in parties, except when paired with consorts, and thus represented independent foraging units, whether group-living, peripheral, or solitary. Jouventin (1975a, p.528) suggested that male mandrills fed largely terrestrialy and that only a single dominant male mandrill was found in a group of mandrills because of feeding competition between adult males foraging on the forest floor. If this were the case, a male mandrill might also be considered to represent an independent foraging unit. Small groupings of two to six monkeys have not been reported in mandrills but were the smallest unit, termed a party, in pig-tailed macaques and appeared to be a foraging unit. As was pointed out earlier for both mandrills and white-collared mangabeys, subgroups have been reported as being similar in size to groups, and the same was reported for pig-tailed macaques - subgroups were composed of several parties and contained 'perhaps 15 to 30 individuals' (Caldecott, 1986a, p.89). These macaque subgroups were comparable in size to the subgroups reported in mandrills - about 20 individuals (Hoshino *et al.*, 1984). Feeding traces from mandrills indicated that they travelled and foraged in a dispersed manner across a broad front (pers. obs.) and parties of macaques were reported to forage in a similar way.

Very large aggregations, containing several hundred mandrills have been reported and pig-tailed macaques were observed in 'super-groups', numbering 60 to 100 individuals.

Thus in several aspects related to group size and general ecology pig-tailed macaques show considerable similarities to mandrills. The various similarities and diferences in social behaviour are examined below.

An analysis of nearest-neighbour proximity in pig-tailed macaques revealed that juveniles (small and medium-sized monkeys excluding infants and adolescent males) associated together, adolescent males (large juvenile and adolescent males) associated together, and adult males and adult females (those with and without swollen perineal skin) associated together. When this analysis was refined by inclusion of social interaction data, females could be classed by sexual swelling state, and the association between swollen females and adult males increased in significance. Thus juveniles tended to travel, forage and sit near one another, and avoided adolescent and adult males. This was similar to my observations of the CIRMF mandrills, although juvenile relationships were not quantified. Youngsters frequently played together and travelled together. Older juvenile males did associate with subadult males and sometimes played with them, in contrast to the relationships described for pig-tailed macaques, but female juvenile mandrills did not. Juveniles of both sexes avoided the alpha male although agonistic interactions were relatively rare.

A 'policing' role by the alpha male mandrill was observed at CIRMF. He interfered in disputes with the result that aggression diminished. Adult male pig-tailed macaques associated with groups appeared to play a similar role. They were seen to approach sources of disturbance, and inferred to quell them (Caldecott, 1986a, p.155). Additionally, in pig-tailed macaques the group male's displays and antagonism were thought to be responsible for his avoidance by juveniles and for the peripheral status of sub-adult and other adult males. Data relating to male-male agonism in mandrills were reviewed above. The mechanism by which males become increasingly peripheral and solitary is unknown. Daya from CIRMF did not suggest that they were aggressively driven out by the alpha male. The data seem to suggest that pig-tailed macaques may form one-male harem units (Caldecott, *op. cit.*, p.149). However, this has yet to be confirmed by a study of long-term membership of groups and a detailed analysis of social interactions in wild pig-tailed macaques. If the basic reproductive grouping of pig-tailed macaques is indeed a one-male harem unit, this enhances the analogy with mandrills (see below).

Adult male pig-tailed macaques formed consortships with adult females with swollen perineal skin. These were identified by observations of a known male having a sustained liason with a particular female. Consort behaviour in pig-tailed macaques was described as follows (Caldecott, 1986a, p.159) 'the male often followed the female around and mounted her, sometimes in response to her presentations, sometimes spontaneously; the female meanwhile remained close to the male, groomed him, and seemed to keep her sexual skin oriented to him for much of the time'. Consort pairs were often peripheral to the group. Some aspects of consort behaviour in pig-tailed macaques are reminiscent of the mate-guarding behaviour of the alpha male mandrill described in Chapter VI, although the peripheralisation of the consort pair more closely resembles that reported for *Papio* savanna baboons (A. Collins, pers. comm.). The male mandrill maintained close proximity to the female he was guarding, following her movements. He mounted her, occasionally in response to her presentations, but most copulations were male-initiated. Grooming increased during oestrus over anoestrus and this was also reported in the pig-tailed macaques, in whom grooming between adult males and unswollen females was never observed. This resembled the pattern described for mandrills in Chapter V; grooming between adult male and adult female mandrills was rare. Furthermore, the relationship between adult males and non-swollen females was similar in both species, and was characterised by an absence of grooming, mounting, or sustained proximity.

The data presented in Chapters III and VI showing sexual behaviour in mandrills to be almost entirely confined to periods of maximal swelling are similar to the data on pig-tailed macaque consort behaviour. These data support information, reviewed in Caldecott (1986b), suggesting that in wild macaques sexual behaviour does not occur continuously throughout the cycle and that in macaque species in which imminence of ovulation is revealed by a large perineal swelling (as it also is in mandrills) female sexual behaviour is strongly associated with the late follicular phase of the cycle, as shown for mandrills earlier in this thesis. Thus sexual behaviour of wild *Macaca nemestrina* was concluded to be 'oestrus-like in its sudden onset, intensity and rapid cessation' (Caldecott, 1986b, p.211) and in this respect resembles that for mandrills who were also shown to exhibit 'true oestrus' (see above).

Popp's analyses, examined above, predicted the effect of ecological conditions, specifically food resources broadly measured by mean annual rainfall, on male behaviour in baboons. A similar analysis, predicting the effect of ecological conditions, specifically food resources, broadly assessed by dipterocarp abundance, on female behaviour in macaques and on males adapting their strategy to 'fit in' with female strategy was proposed by Caldecott (1986a).

A comparison of the sexual behaviour of *Macaca nemestrina* and *Mandrillus sphinx* is of particular interest since Caldecott (1986a, 1986b) attempted to connect sexual behaviour with male grouping tendency and ecological conditions in macaques. Given the broad similarities between pig-tailed macaques and mandrills, this perspective may provide insight into the socio-ecology of mandrills. Additionally, this comparison has not been attempted before because the relevant data on mandrills were lacking. The results of the present study of the CIRMF mandrills thus enable new interspecies comparisons of sexual interaction to be made.

In free-ranging conditions, in contrast to the confinement of captivity, female macaques are able to avoid males. Avoidance of males by female mandrills was also observed in the naturalistic semi-free ranging conditions of the present study. This phenomenon - ease of avoidance by females - should be particularly salient in habitats with complex three-dimensional structure, such as lowland tropical forest, where a variety of supports of differing sturdiness exists. As a result of considerable sexual dimorphism in size and weight, females should be able to climb to places where adult males are unable to follow them. This was observed in the CIRMF mandrills and was inferred in pig-tailed macaques from an analysis of support use which indicated differential access to the environment (ranging from the ground to foliage) (Caldecott, 1986a). All but 8 of 123 observed copulations in the CIRMF mandrills took place terrestrially and all observed copulations in pig-tailed macaques were on the ground or on boughs (Caldecott, *op. cit.*). Thus females of both species can be considered as having the ability to avoid copulations should they wish.

The data on pig-tailed macaques indicated that unswollen adult females were significantly less often in proximity to adult males than would be expected and it was suggested that adult females avoided adult males due to feeding competition, since food sources, particularly fruit, were sparse in Dipterocarp-rich forest (Davies *et al.*, 1983). This was presumed partly to account for the considerable dispersion observed among foraging pig-tailed macaques (Caldecott, 1986a). This explanation may apply also to mandrills since males and females spent little time in proximity. However, it is unclear to what extent male and female mandrills are in competition for food. In the CIRMF mandrills, males displaced adult females from foraging sites, but this was relatively rare in comparison to displacements between females. [Frequent displacement of females by males has been reported for savanna baboons however (Smuts, 1985)]. The importance of terrestrial foraging in mandrills, much of which is for ubiquitous herbaceous plants or items in the leaf litter would tend to reduce feeding competition. Competition might be expected to be greater for arboreal resources such as fruit, although differential access due to sexual dimorphism would reduce the competition, depending on the nature of the fruit and its position in the tree. Caldecott reported an impression that close male-female proximity interfered with food acquisition by adult female pig-tailed macaques and changes in activity in both sexes during consortships has been reported in savanna baboons (*Papio ursinus*, Bercovitch, 1983; *P. cynocephalus*, Rasmussen, 1985). In pig-tailed macaques females appeared to avoid males, unless their sexual motivation was high. Since a male could not 'sequester the female against her will'

(Caldecott, 1986b, p.212) a male macaque would need to adjust his behaviour to 'fit in' with female sexual strategy. Mate-guarding behaviour seen in mandrills, in which the male seemed primarily responsible for maintaining proximity by following the female, and in which no herding behaviour was seen - i.e., the male did not appear to constrain the female's movement or behaviour - might indicate adjustment of male to female behaviour in this species also.

Consortships in wild pig-tailed macaques lasted up to three days (Caldecott, 1986a) although this may represent an underestimate, since observation conditions were less than ideal. In mandrills, females were mate-guarded on two to ten consecutive days and the duration of mate-guarding depended on the temporal distribution of oestrous females as shown above.

Caldecott divided macaques into species in which females participated in consortships lasting hours or days (including pig-tailed macaques) and those lasting only a matter of minutes. Females of the first group typically copulate with only a few, generally high-ranking males and were termed selective copulators; the latter group copulate with a large number of males and were termed promiscuous copulators (references in Caldecott, 1986a, 1986b). Under this scheme, the CIRMF mandrills would be classed as selective copulators since females copulated to ejaculation with on average two males per period of oestrus (data from 1986, n = 6 females, n = 12 cycles).

Female pig-tailed macaques with swollen sexual skin were mounted only by group adult males, which were few in number. Repeated mountings and evidence from captive studies (cited in Caldecott, 1986a) indicated that pig-tailed macaques are multiple-mount ejaculators

Six species of macaque can be divided on the basis of whether males are single- or multiple-mount ejaculators, and whether females are selective or promiscuous copulators. The divisions yield the same groups of species and Caldecott concluded that species such as the pig-tailed macaque have multiple-mount ejaculating males and selectively copulating females, indicating that in macaques 'single-mount ejaculation appears to be appropriate to brief consortships, and multiple-mount ejaculation to prolonged ones' (1986b, p.213). However, mandrills are clearly single-mount ejaculators (this study; Feistner and Dixson, in prep.) and they differ from pig-tailed macaques in this respect.

A comparison of mandrills with macaques is summarised in Table VII.2. Caldecott suggested that, given female selectivity, a male macaque should attempt to sustain the female's interest as long as possible, both to deny other males access to her and to reward her selection and solicitation of him. It was suggested that sustained male potency would be important and is achieved by deferring ejaculation and ejaculatory fatigue by multiple mounting. Additionally intra-vaginal ejaculation, if coordinated with female orgasm, could assist sperm transport (Allen and Lemmon, cited in Caldecott, 1986b). Since mandrills appear to resemble pig-tailed macaques in many respects except the mounting pattern why might it be advantageous to male mandrills to ejaculate in a single mount and not after a series of mounts as many macaques do?

The reason may be influenced by seasonality of reproduction in mandrills, which has previously only been refered to anecdotally (see Chapter IV). The present study is the first to present several lines of evidence (see Chapter III) pointing to clear seasonality in reproduction in mandrills and thus confirming these earlier anecdotal reports. The reproductive seasonality in the CIRMF mandrills is also found in all sympatric monkeys for which the data are available, with the exception of the black colobus *Colobus satanas*. A pattern of reproduction with mating in July, August, and September and births in December, January, and February is found in 85% of guenon populations (Butynski, 1988). The timing of guenon reproductive events, and by analogy those of mandrills, is affected by rainfall through its influence on food supply, which is mainly fruit and arthropods for both guenons and mandrills. There are correlates between the distribution and amount of annual rainfall, the period over which nutrients are most available, and the timing of gestation, birth, lactation and the

Table VII.2. Attributes related to mating system in macaques and mandrills

Attribute	Group 1 macaques	Mandrills	Group 2 macaques
Female mate choice	Selectivity	Selectivity	Promiscuity
Consortship duration	Hours to days	Days	Minutes
Copulation pattern	Multiple-mount	Single-mount	Single-mount
Inter-male relations	Anatagonistic	Antagonistic?	Relaxed
Mean adult sex ratio	1 male:1.7 to 8.0	I male:8	1 male:0.9 to1.2
Paternalism	Generally weak	Generally weak	Generally strong
Male emigration	Common	Common	Rare
Inbreeding	Relatively low	Relatively low?	Relatively high
Species example	*M. nemestrina*	*M. sphinx*	*M. sylvanus*

Data for macaques from Caldecott (1986, p. 215, Table IV)

Mandrill data from this study and review of field studies (Chapter IV) transition from a milk to plant-arthropod diet in guenons (Butynski, *op. cit.*). Reproductive seasonality, probably based on food supply in relation to the energetic demands of the female in terms of the energetic costs of pregnancy and lactation, has implications for male behaviour and mating strategy as was discussed earlier.

If female mandrills are only reproductively available to males for a limited period each year, male reproductive effort may be concentrated into a relatively short period and a male might experience a 'boom or bust'. The possible need to inseminate a number of females over a relatively short time period, even in the context of multiple consecutive consorts with selective females, may have implications for testicular function in mandrills in terms of sperm production and mounting pattern. Relatively large volumes of semen and sperm, delivered in single-mount ejaculations, may be required. This argument could be applied to seasonally breeding macaques such as rhesus monkeys, *Macaca mulatta,* but they are also, like pig-tailed macaques, multiple-mount ejaculators. However, female mandrills at CIRMF appeared to exhibit not only a marked degree of oestrous synchrony, but also considerable temporal proximity in ovulation, as estimated by the period D-4 to D-2 (as described in Chapter VI). Thus a male mandrill may need to 'swop' females in order to 'track' the likely periods of conception. He may thus need to maximise his production of sperm to increase the chance of fertilising each female. The pattern of mate-guarding by the male would be predicted to vary according to the number of females simultaneously in oestrus and peri-ovulatory. In the CIRMF mandrills, at the height of the breeding season, when up to five females were in oestrus on the same day, periods of consecutive days of mate-guarding of any one female were relatively short, of two to three days duration, (cf. pig-tailed macaques, above) and the alpha male mandrill at CIRMF was observed swopping between females and mate-guarding different females on consecutive days (Chapter VI). In contrast, when Female 6 came into oestrus in December and January, after an abortion, outwith the mating season, and was thus the only female with a tumescent sexual swelling, the alpha male was observed mate-guarding her for ten consecutive days.

As suggested above, the temporally concentrated availability of female mandrills in oestrus may have implications for testicular function in terms of sperm production. It was indicated earlier that male mandrills copulated to ejaculation about once every 71 minutes. If a male needs to sustain this output over several consecutive days in order to inseminate a number of females this may select for increased testicular function and testis size. Thus mandrills might be predicted to have relatively large testes. However, Dunbar (1984) predicted that males of one-male units would have relatively small testes. Harcourt *et al.* (1981) reported that gelada male reproductive organs were small in relation to those of an average savanna baboon and that they had a small testis-to-body-weight ratio. I was unable to test the prediction for mandrills since comparative studies use testis weight rather than testis volume and the relevant data for mandrills are unavailable. I was not able to take measurements of the male mandrills sufficiently regularly to assess seasonal changes in testicular volume or testosterone level, but it seems plausible that such changes may occur. In two consecutive years the alpha male in the CIRMF group had the highest blood testosterone concentration among males (Chapter III), as measured in October, the last month of the mating season. He was also by far the most brightly coloured male in the group and he became more brightly coloured during the mating season than he was at other times of the year. The increase in the red components of the CIRMF alpha male mandrill's colouring, which intensified during the mating season, may thus have been due to an increase in the production of testosterone, as was suggested by work on a drill, described earlier. The regular monitoring of hormone levels in mandrills living in naturalistic social groupings under natural climatic regimes (as were the mandrills at CIRMF) would allow this idea to be tested. However, this was not done in this study due to the disruptive effect of regularly capturing the group.

It was concluded by Caldecott (1986a) that forests high in dipterocarps support low macaque biomass and dipterocarp-poor forests support a greater macaque biomass. Since in relatively food-poor zones male-female feeding competition is predicted to be higher than in food-rich habitats social organisation in the former habitat should be governed by avoidance of males by females except during oestrus. This conflicts somewhat with Popp's assertions of tropical forest as the highest energy habitat, yet supports Jouventin's (1975a) suggestion that the forest floor is a food-poor zone. Mandrills appear to fit into the schemata proposed by both authors, which could be linked as follows.

Caldecott (1986a, p.121) suggested that a terrestrial, large-bodied macaque colonising Asia and adapting to more or less productive forests may have parallels among the African Papionini and suggested that a baboon-like ancestor could have differentiated into forest-dwelling mangabeys and mandrills and open-country baboons. However, he suggested that the *Mandrillus* lineage is strongly adapted to terrestrial foraging, rather than the arboreal foraging and terrestrial travel of *Macaca nemestrina.* There is some support (not referred to by Caldecott) for this view, since Hill (1970) and Jolly (1970) both suggested that the hands and feet of *Mandrillus* were adapted for branch walking. This weakens the analogy between pig-tailed macaques and mandrills. Instead, Caldecott suggested that *Mandrillus* may be similar to *Macaca arctoides*, the stump-tailed macaque. However, the lack of field study of this macaque precludes a comparison of the two species. Mangabeys of the genus *Lophocebus* are exclusively arboreal yet also have relatively large home ranges. However, although the semi-terrestrial *Cercocebus* mangabeys were reported by Caldecott as having small ranges (less than 40 ha), explicable by the relatively high productivity of riverine forest, the recent study of *C. torquatus* by Mitani (1989, reviewed above) cited relatively large home ranges of 250 ha. Although this is small compared to those of pig-tailed macaques (800 ha) and especially of mandrills (up to 40 km^2) this comparison merits further study.

Caldecott asserted that there is no *M. nemestrina*-like forest-dwelling African cercopithecine, and suggested that the radiation of the arboreal Cercopithecini 'discourages the evolution of an arboreally-foraging but terrestrially-travelling African rain-forest papionin' (1986a, p.122). If this is the case, and this niche is not occupied by the mandrill, then I suggest that the terrestrial traveller and arboreal forager in a large home range in African forest may be represented by the chimpanzee. The data on *P. t. troglodytes* to test this hypothesis are currently lacking.

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APPENDIX II.   CHECKSHEETS

	INFANTS									JUVENILES		
Date:	Skin colour					Coat colour				Skin colour		
	Palms	Soles	Body	Muzzle	Ears	Back	Limbs	Head	Chin	Rump	Genitals	Muzzle
2A												
2B												
2C												
5A												
5B												
6A												
10A												
10B												
12A												
12B												
12C												
17A												

Comments:

Date: ID: Time start: p:

Forage																		
Travel																		
Climb																		
Still																		
Rest																		
SolicitG																		
Self-G																		
Allo-G																		
Self-Play																		
Allo-Play																		
Head bob																		
HB+call																		
T. Rush																		
Inspect																		
Smile																		
S+Shake																		
Present																		
Scream																		
Display																		
Mount																		
Mastub																		
Yawn																		
Mark																		
T. out																		
Misc																		

Time	Act.	<5m	5-10m	I.D.	Date	Time	State
0				Focal: A T			
1							
2							
3							
4							
5							
6							
7							
8							
9							
10							
11							
12							
13							
14							
15							

Comments

Appendix III.1. The decline in health of juvenile male 12B, April 1986

1 April 1986
12B is sitting quietly on the ground. Earlier he was hiding near the stream. He seems depressed.

2 April 1986
12B is by himself sitting on the ground.

9 April 1986
12B is still depressed. He is at the back of the group sitting on the ground doing nothing.
1548: He ignores 5A and 2A playing less than 6 m from him. He sits with his eyes shut and shows no reaction to an infant's screech or to the dominant male rushing off.

12 April 1986
0930: 12B is at the periphery of the group sitting on the ground. <u>All</u> other juveniles are playing or foraging.
1041: 12B forages at the periphery of the group.
1130: He is wobbly and the third last in a progression along one of the transects.
1210: 12B is wobbly and looks thin. He is the last mandrill and sits on the ground with his eyes closed.
1804: He is groomed by his older sister 12A.

13 April 1986
1651: 12B is by himself. His stomach looks bloated.
1801: He is obviously in pain. His abdomen is very bloated and he sits as if pregnant, leaning back with his legs apart. He climbs/part falls out of vines to wobble after his mother Female 12, as she makes her way to the sleeping site. He stops for a rest by a log on the transect. Male 18 nuzzles him in passing. He moves and defaecates. I collect the faecal sample. He continues slowly but I lose him in the undergrowth.

14 April 1986
0657: I cannot locate 12B, and presume he is dead.

In the late afternoon of the 13th April I carried anaesthetic and syringes with me in the hope of sedating him and removing him for treatment, but I was unable to do this. The following morning I did the same, but could not find him. Analysis of the faecal sample collected on the 13th revealed the presence of cysts of *Endolimax nana*, *Entamoeba coli*, and *Ancylostoma*-type ova. (Further details on parasitic infestations are presented in Chapter III.)

Appendix III.2. The decline of Female No. 1's infant, January 1986

26 January 1986
1115: Female 1 is first seen with a newborn infant. Its head and fur are still damp. She appears attentive to it. She has dried blood on her vulva.

27 January 1986
The baby is seen rooting and on the nipple. She is attentive to it but when she sits down she often positions the baby too high, near her shoulder instead of on her ventrum. Her nipples are small and barely visible in her fur.

28 January 1986
She is seen grooming the baby and attending to it early in the morning. However it seems to spend very little time on the nipple despite rooting a great deal. She often places it on the ground to groom it. During the morning it weakens visibly.
1130 to 1200: The infant ceases to cling properly, but is still making rooting movements. She supports it with one hand during travel, walking tripedally.
1300: The baby's head is lolling and it is obviously very weak.
1530: She is no longer supporting the baby against her ventrum but carrying it in her hand, supporting it under the belly like one would a kitten. It is either dead or unconscious. She continues to groom it.

29 January 1986
She still has the infant who is now definitely dead. She carries it carelessly, walking quadrupedally and thus sometimes stepping on it. She holds it by a limb rather than clasping its body. It has cuts on its chin, presumably from abrasion. Flies are attracted to the corpse.

30 January 1986
No observation made.

31 January 1986
She is no longer carrying the corpse.

Appendix III.3. Comparison of female infants 5A1 and 5D at 48 days of age.

	5A1	5D
Date of Birth	5 Mar 1988	6 Mar 1988
Gestation (days)	175	172
Weight (kg)	0.64	1.23
Weight (kg) of mother	12.95	14.92
Teeth	$i_1 \quad i_1$	$c\ i_2\ i_1 \quad i_1\ i_2\ c$
	$i_1 \quad i_1$	$c\ i_2\ i_1 \quad i_1\ i_2\ c$
	n = 4	n = 12
Face	ears pink tinged with red	ears pink
	muzzle pale pink	muzzle just light grey
Pelage	of newborn	
	black natal cap	black natal cap
	sparse white fluffy fur	fur agouti on limbs
	(especially on arms)	
	fur pale round face	agouti fur round face
Skeleton		
L. hand:	digits 3 + 4 completely fused	normal
	digits 4 + 5 fused to 3rd phalanx	
R. hand:	digits 3 + 4 + 5 completely fused	normal
	pads and nails of all fingers	
	bend medially.	
Feet:	phalanges short and stubby	normal
Face:	"rat-like", nose ridge straight	normal
	and prominent	
Condition	thin and weak	vigorous
Temperature (°C)	low (34.7 - 35.6)	normal (37.1 - 38)

Appendix III.4.. Canine tooth length (in cm) in male and female mandrills at CIRMF

	Identity	Upper Right Lower Right	Upper Left Lower Left
Males	7	UR 4.2	UL 4.0
		LR 2.7	LL 2.7
	3	UR 4.7	UL 4.5
		LR 2.4	LL 2.5
	14*	UR 4.8	UL 3.9
		LR 3.1	LL 3.2
	9*	UR 4.5	UL 4.7
		LR 2.5	LL 2.5
	13*	UR 4.2	UL 3.9
		LR 2.5	LL 2.5
	15*	UR 3.3	UL 3.3
		LR 2.2	LL 2.2
	18*	UR 1.6	UL 1.7
		LR 2.5	LL 2.9
Females	2	UR 1.0	UL 1.0
		LR 1.0	LL 1.0
	5	UR 0.8	UL 0.8
		LR 0.7	LL 0.7
	6	UR 1.0	UL 1.0
		LR 0.8	LL 0.9
	10	UR 1.0	UL 1.0
		LR 0.9	LL 0.9
	12	UR 0.9	UL 0.9
		LR 0.9	LL 0.9
	17	UR 1.3	UL 1.3
		LR 1.1	LL 1.1
	16	UR 1.0	UL 1.1
		LR 0.9	LL 1.0

Mandrills shown in order of decreasing dominance rank within sex
Mean lengths except * which are latest (April 1988) measurements

Appendix V.1. Focal samples for part 2 proximity study

Identity	State	No. focal samples	No. point samples	
			<5 m	5-10 m
Females				
No. 2	Pregnant	48	699	165
	Lactating	9	132	32
	Oestrus	18	288	72
No. 5	Pregnant	28	447	109
	Lactating	32	487	105
No. 6	Pregnant	60	960	221
	Oestrus	13	208	49
No. 10	Pregnant	53	816	189
	Oestrus	31	487	118
No. 12	Pregnant	29	464	111
	Lactating	32	485	115
No. 17	Pregnant	41	642	149
	Lactating	24	367	85
No. 16	Lactating	62	970	220
Males				
No. 7	Non-oestrus	49	763	169
	Oestrus	11	171	43
No. 3	Non-oestrus	51	793	190
	Oestrus	9	143	35
No. 14	Non-oestrus	50	799	187
	Oestrus	9	144	36
No. 9	Non-oestrus	49	775	186
	Oestrus	15	229	55
No. 13	Non-oestrus	49	764	182
	Oestrus	11	175	42
No. 15	Non-oestrus	51	800	189
	Oestrus	11	176	43
No. 18	Non-oestrus	49	779	188
	Oestrus	12	192	48

Within sex mandrills are presented in order of decreasing dominance rank

Male 3's data were excluded from analysis of proximity

Appendix V.2. Male hierarchy at feeding site

Loser

Winner

	7	3	14	9	13	15	18	
7			2	3	1	3	5	14
3				2		2	1	5
14				3	2			5
9					8		2	10
13						2	2	4
15							2	2
18								n = 40

Appendix V.3.Female Hierarchy at Feeding Site

Loser

Winner

	2	5A	5	6	10	10A	12	12A	17	16	
2		3	15	4	1		2	2	2	1	30
5A			7		3			1			11
5				6	6	1	8		3	4	28
6					2				2	1	5
10							3		2	1	6
10A											
12									3	5	8
12A										1	1
17										10	10
16											

n = 99