SOCIAL BEHAVIOUR AND PATTERNS OF MATING AMONG ADULT YELLOW BABOONS

(PAPIO C. CYNOCEPHALUS. L. 1766)

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Declaration

I declare that this thesis has been composed by myself, and that the data-collection, analysis, and writing were carried out by myself except where explicitly acknowledged in the text.

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Abstract

Results are presented from three months' observation of 30 adults in a troop of 70 yellow baboons in Tanzania. Data were collected by sampling subjects' location and association, and by *ad libitum* observation of social interaction. An attempt was made to correct for observability bias in the latter.

The troop showed a tendency to spatial patterning of individuals, both stationary and during progression; while some of its features may have provided predator-protection, it appeared that its proximal causes were largely social factors described below.

Mothers with young infants tended to associate together, and attracted much grooming from other females; they contrasted strongly with pregnant females, who associated and interacted much less. Affiliation between the sexes involved cycling females with higher ranking adult males and mothers with prime adult males. Males' differences reflected age; subadults interacted merely with cycling females; young newcomer adults interacted often with cycling females and peripheral pregnant females; the prime adults had also established relations with the mothers; while older adults either were no longer favoured by females or were excluded from them by prime males. These contrasts were reflected in that males who associated with mothers were spatially central in the troop (i.e. 'focal' males).

Presenting and mounting were also frequent between cycling females and high-ranked adult males, but mothers were little involved. Mounting with*in* each sex tended to be from dominant to subordinate, and females mounted each other more often than elsewhere.

Agonistic interactions revealed a linear hierarchy in both sexes, which predicted individuals' rates of several behaviours. However agonism between males was more frequent and more often uprank than that between females. Between the sexes, males supplanted cycling females often, reflecting their mating associations. The males who spent most time with mothers also interacted frequently with their infants, including in protectiveness and buffering against one another as well as against newcomers. These focal males also allied together often, while the newcomers rarely allied but were often the victims of alliances.

Among females, interaction (but not association) tended to be more frequent between closer-rankers. In affiliation, this may reflect kinship: in antagonism, it may reflect the maintenance of dominance relations between close-ranked matrilines; but other explanations are discussed.

Features of mating were a tendency for series-mount copulations, and for the copulation-call to be more frequent near midcycle and when the male ejaculated. Mating caused appreciable male-male competition, and male-male aggression was more frequent when more females were in oestrus. In this, high-rankers were at an advantage, and mated more. However, middle-rankers increased their relative mating success by alliance, by possessiveness to particular females, and by capitalising on lapses in the high-rankers' consortships. Females appeared to prefer high ranking males, but such preferences could be over-ridden by male-male interactions.

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CHAPTER 1

INTRODUCTION

1.1 Previous studies

The earliest field studies of baboons were conducted in S. Africa by Marais (1939) and Zuckerman (1932), and later Bolwig (1959): but quantitative studies were not initiated until more recently both there (Hall, 1962; Stoltz & Saayman, 1970) and in E. Africa (DeVore & Hall, 1965; Rowell, 1969a; Altmann & Altmann, 1970). These agree that savanna baboons, the olive, yellow, and chacma, form multi-male troops numbering usually between 10 and 100. These troops use large overlapping home ranges, with core areas, and their distribution is limited by permanent water and safe sleeping sites.

Some of the early studies focussed on the adaptive aspects of group-life, such as progression order and predator-defence, as a possible model for hominid behaviour (e.g. Washburn & DeVore, 1961). They also described many details of social behaviour, but their description included two misconceptions which have since been widely quoted. The first was that baboon society, which comprised closed groups, was organised around the dominance hierarchy of adult males (Hall & DeVore, 1965). However, subsequent studies showed that troops are not closed (Rowell, 1969a; Altmann and Altmann, 1970; Ransom, 1971): males generally leave their natal troop by adulthood, to breed elsewhere, and may transfer again subsequently (Packer, 1975, 1979a). Furthermore, male dominance relations are not very stable, although usually hierarchical (Hausfater, 1975; Packer, 1979b). In contrast, females very rarely change troops (Ransom ibid.; Rasmussen, K. pers. comm.), so that the troop comprises matrilines of females and their offspring, and the adult males are not permanent members (Rowell ibid.). Also, dominance relations between females are more stable than those between males (Hausfater, 1975), and daughters take dominance ranks close to their mothers' (Moore, 1978). Kinship therefore determines much interaction (Nash, 1978b). Thus the male dominance hierarchy is not the main element of social structure: in the long-term, bonds between females are probably more important (also Hausfater ibid. p.68).

The second misconception, related to the first, was that male dominance was connected with particular behaviours or roles, such as mating, aggressiveness, group defence, and protection of infants (Hall & DeVore, 1965). However this pattern probably only applies in troops with one conspicuously dominant adult male, because in troops with more males these behaviours vary independently (compare Rowell, 1967a; Saayman, 1971b; Hausfater, 1975; Seyfarth, 1978a & b). There are also no a priori reasons why dominance ranks should determine roles (Hinde, 1978).

Current field studies have moved from general descriptions to include fine analyses of relationships (Seyfarth, 1976; Altmann, 1980), or examination of specific questions (Packer, 1979a,b). The original purpose of this study was to test hypotheses about male dominance, mating success, and mate selection in a well documented baboon troop. However, for reasons financial and political, the fieldwork had instead to be completed in a shorter time and at a new study site, so the scope of the study was widened to include a description of social structure. This description is presented in detail, in the belief that our understanding of baboon social behaviour can be increased in two ways. The first is to monitor long-term changes in particular troops, as is being done at Amboseli, Gilgil, Gombe, Mikumi and Moremi. The second is to compare a larger sample of troops, covering all kinds of baboon in a variety of habitats and over a range of troop-compositions. This study is a contribution to the second of these, and describes social behaviour of one troop at a new study site. The majority is therefore descriptive and uses specific hypotheses mainly as a key to that description: the original hypotheses about mating are tested in the final chapters.

1.2 Social structure

Social behaviour is affected by environment largely through the pattern of availability of foods (Clutton-Brock & Harvey, 1978), which determines whether females feed separately or in groups: this in turn dictates the mating strategy of the males, and thus the social organisation (i.e. whether one-male or multi-male troops etc.) (Wrangham, 1980). As permitted by these factors, male and female must establish relationships which allow them to reproduce, and it is the pattern of these relationships among adults and immatures which comprise the social structure of the group (Hinde, 1976).

The data for this study are the social interactions recorded between its subjects. Any description of social structure based simply on interactions has one important caveat: to consider simply 'who does what to whom' may not recognise all the affinities between animals, since the same affinity may be expressed in a variety of ways (Mason, 1978) and some affinities may not be expressed at all, through inhibition or competition (Vaitl, 1978). In treating of interactions, Hinde (1976) proposes that by analysing their content, quality, and patterning we may resolve them into relationships, and these relationships in turn into social structure. Furthermore, comparisons of social structure across groups may reveal universal processes, which he terms deep structure (e.g. Seyfarth _et al_., 1978). The data in this study do _not_ lend themselves to an accurate description of relationships: this is first because the study was so short that scant data are available for some pairs: secondly it is because the data were collected by _ad libitum_ sampling, which meant that the proportion of different kinds of interaction in any pair reflect in part the diffential _observability_ of each kind of interaction. Also the study design was biassed to selective recording of certain behaviours. Therefore the interaction _content_ in any relationship may be misrepresented. The approach in analysis has instead been to examine the patterning of each kind of behaviour separately, and then to compare these patterns to detect the underlying relationships.

Descriptions of interactions themselves may become complicated, because they often involve more than two animals. It is well-established that interactions and relationships are both greatly affected by the presence of other group-members (e.g. Kummer, Gotz & Angst, 1974; Vaitl, 1978), and the possible combinations of participants, interactions, and outcomes increase as group-size increases. This problem is further discussed in terms of agonistic behaviour (6.2.2b; 6 part 7).

An important feature of social structure is that it is not static. Relationships continually change as animals mature, change groups, and die, while groups themselves may grow and divide (Rowell, 1967c; Nash, 1976) or even change with season (Hladick, 1975). This study was particularly short in relation to the lifetime of its subjects, and data were usually insufficient to monitor changes in pairs' interactions over time. However some behavioural changes coincident with birth of infants, resumption of cycling, and menstrual cycle stages have been assessed (esp. Chapters 7 & 8).

Another feature of social behaviour is that individuals may vary greatly: they may take different behavioural routes to the same goal, possibly within a range in which natural selection is of little effect (Hinde, 1975). Although there are models of mixed heritable strategies of behaviour which provide a promising approach to this variability (Maynard Smith & Price, 1973), it is not clear that they can account for the great range of variations observed. Particular attention has been paid here to individual differences, because they may suggest social factors other than gender, dominance rank, reproductive state etc. that may affect behaviour: the males have been compared especially, in part because more data on them were available.

There is increasing evidence that social interaction is affected by kinship (e.g. Nash, 1978b; Sade, 1968; Walters, 1981) although it is hard to separate the effect of kinship from that of familiarity alone. There was no information on kinship among the adults in this study: it was merely assumed that adult females and natal males shared a similar range of relatedness, but that immigrant (i.e. adult) males were not closely related to them nor to each other (2.IIIb; Packer, 1977a, Appendix A).

Chapters 3 to 6 of this thesis present data on social structure in terms of spatial factors, and different categories of interaction, in turn. The third chapter describes the spatial distribution of troop-members: thereafter are described affiliation, in terms of association and grooming (Ch. 4), and agonistic behaviour including aggression (Ch. 6). Sociosexual behaviours (presenting, mounting etc.) are treated separately since they combine elements of affiliation, agonism, and sexual behaviour (Ch. 5). The distribution of each behaviour between subjects is analysed according to the same general hypotheses and as far as possible by the same methods. Initially the sexes are compared, on the basis that they differ in size, kinship, and reproductive constraints (4.1.1, 6.4.1, 6.4.6). Then classes are compared within each sex: adult and subadult males differ *a priori* (2.IIIb): and reproductive state affects females through nutritional needs, affiliation with males, and the attractiveness of infants.

Secondly, the effects of dominance rank (estimated as in 6, part 3) are examined: this is expected to affect affiliative behaviour, since high rankers may be more attractive (Seyfarth, 1976) or more successful in access to favoured partners (4.3.9a): and to affect agonistic behaviour because position in the hierarchy reflects the number of others to whom a subject may give, or from whom receive, agonistic interaction (6.5.1).

Thirdly, interactions between partners close in rank are compared with those more distant: affiliative behaviours may be more frequent between close rankers (as explained in 4.3.1). Conversely, agonistic interaction and competition may be more intense between opponents of similar competitive ability (6.6.1).

Finally, comment is made on the context and quality of interaction. This is in the firm belief that it is impossible to interpret quantitative data without knowing the kinds of situation in which each behaviour occurs, and that particular interactions may reveal affiliations or inhibitions which are not apparent during the normal course of events.

1.3 Mating and sexual selection

Chapters 7 and 8 of this thesis are concerned with mating. The first of these portrays behavioural changes occurring over the menstrual cycle, notably in interaction between male and female including consortship. These data are presented for comparison with those of Rowell (1967a), Saayman (1970), Hausfater (1975) and Seyfarth (1978a), and details of mating behaviour are discussed. Essentially however this provides a background to Chapter 8, which investigates what factors caused the large differences in male mating success. This question originally arose because DeVore's (1965) study concluded that baboons lived in closed groups in which one or a few males fathered most offspring, ideal conditions for rapid evolutionary change (Wright, 1940). Later research suggests that the opposite is true: migration is frequent (above) and evolutionary rates have been low (Bush *et al*., 1977). The phenotypic differences seen between troops (Byles & Sanders, 1980) are more likely to reflect female kinship lineages, or habitat quality. However the intensity of mating competition reported by DeVore suggested also that there might be strong sexual selection for the attributes of mating success (e.g.

male dominance), and a number of studies have examined this in baboons and macaques (8.3.1).

Sexual selection occurs because one sex (usually the female) invests more than the other in the production and nutrition of gametes (Darwin, 1871; Bateman, 1948), and in parental care (Trivers, 1972). The reproductive success of the female is therefore limited by the number of offspring she can rear in her lifetime, and the main way in which she can increase this during mating is by ensuring the <u>quality</u> of her mates. In contrast, the male invests so much less in each offspring that, unless paternal care is essential, he is free to mate elsewhere: his reproductive success is limited only by the number and fecundity of his mates. A male's priority is therefore to increase the number of his matings, and this leads to competition so that males vary much more in reproductive success than do females. The <u>intensity</u> of sexual selection is measured by this variance in reproductive success in the competing sex. Although in some species the relative investment of each sex may be equalised or reversed, leading to monogamy (Kleiman, 1977) or polyandry (Jenni, 1974), yet baboons conform to the typical case outlined above which tends to produce polygyny.

The female's priority to choose good mates may provide a powerful selective force. Fisher (1930) emphasised that if males showed any external sign of heritable quality, females who could recognise it would leave more offspring: this would initiate runaway selection both for the sign and the ability to recognise it (Maynard Smith, 1958; O'Donald, 1962). Favoured traits might be those with high survival value (e.g. in predator defence), or of advantage in mating competition (McLaren, 1967), or in attracting mates (Weatherhead & Robertson, 1979). A female so choosing would confer these benefits on her sons. Alternatively, females might favour those males most likely to enhance immediate survival of their offspring, e.g. protective males (Trivers, 1972; Williams, G.C. 1975). Female choice is evidently effective in insects (e.g. Crankshaw, 1979), fish (Farr, 1980), amphibians (Ryan, 1980), many birds (e.g. Searcy, 1979) and some mammals (Beach, 1970) including primates (8.4.1).

Conversely, any genetic traits enhancing competitive ability will be favoured in the competing sex. Many species show competition in which the large males (Davies & Halliday, 1979) or the high-rankers (Geist, 1971; Grubb, 1974; LeBoeuf, 1974; Lott, 1979) are more successful, and losers may even be killed (Wilkinson & Shank, 1976). Few studies have yet indicated that male competition leads to lifetime differences in reproductive success (e.g. Gibson & Guinness, 1980). Male competition is related to female choice in that even if females do not choose, intense competition will still ensure that their mates are of high quality; females may therefore accept the outcome of such competition, and may even incite it for this purpose (Cox & LeBoeuf, 1977, also 7.11.1b & d).

Evidence for the importance of competition comes from two other sources. First, many species have a breeding sex-ratio which is female biassed. This may result from increased mortality during male competition (McLaren, 1967; Trivers, 1972). But it also arises when there is delayed maturation in the males, by which they defer their reproductive effort to the age at which they are most likely to succeed (Selander, 1972; Wiley, 1974; Clutton-Brock & Harvey, 1977). The skewed sex-ratio in savanna baboons is at least in part because males take longer to reach adulthood (Altmann et al., 1977).

Secondly, the sexual dimorphism is often interpreted as the result of competition in one sex: the theory of sexual selection was in part proposed to explain dimorphism (Darwin, 1871). This is most convincing for dimorphic features which are definitely used in competition, such as antlers (Clutton-Brock et al., 1980). However, dimorphism can seldom be attributed to intrasexual competition alone: it may also have been favoured by female choice, or by selective factors independent of mating, such as predator-defence. This is almost to be expected, since females may benefit from choosing features which enhance competition and defence, as explained above: the large size and canine teeth of male baboons provide a good example. Dimorphism merely implies that the selective forces acting upon males and females are different (Fisher, 1930; Ralls, 1976). The nutritional load of reproduction may favour small size in females (Roberto Frisancho et al., 1973; Downhower, 1976), and this may apply to baboons, where competition with males has increased female canine size but not body size (Harvey et al., 1978). Conversely, largeness in males may represent the energetic optimum without these demands of motherhood: or be to counter predation-risk when transferring troops. Despite these caveats there is considerable agreement that much primate dimorphism has been selected sexually (Clutton-Brock & Harvey, 1977). This applies particularly to sexual swellings (7.11.1b) and to the independent variation of body size and genital size in different mating systems (Short, 1979; Harcourt *et al.*, in press).

The importance of male-male competition, and the effectiveness of female choice in primates, are discussed by Crook (1972), Goss-Custard *et al.* (1972), Rowell (1974), Bernstein (1976), Hanby (1976), Kolata (1976) and others (refs. also in 8.3.1, 8.4.1). The crucial deficits in our knowledge are that no study has been long enough to show that primate males differ in *lifetime* reproductive success, let alone relate success to any male characteristics: and that we lack quantitative data on female choice and its effects. The present study was too short to remedy either, but Chapter 8 demonstrates several mechanisms affecting competition and choice. Comparison with other studies may allow us to assess the importance of these mechanisms.

CHAPTER 2

Location, Animals and Methods

A. Location and Animals

2. I. Preliminaries

The field study was made during five months beginning in mid-August 1975. A preliminary period of general observation and study-design was followed by 84 days of data collection, between Oct. 10th 1975 and Jan. 15th 1976. The troop had been observed and habituated over the previous year by Peter Ngatwika and Leonidas Mathias of Tanzania National Parks. These two, with Juliet Oliver and Phyllis Lee of Cambridge University, provided valuable background data which are credited to them when cited below.

2.II a) Habitat

The study was conducted in Ruaha National Park, Tanzania ($7^{\circ}40'$S. $34^{\circ}55'$E: altitude 3000-5000 ft). The vegetation has been described by Bjornstadt (1976, 1977). The troop ranged over 60 square kilometres (Oliver pers. comm.), comprising upland savanna of which three zones were distinct. The first was the channel of the Great Ruaha River. The river bed provided broad swards of *Cyperus*, and the banks supported belts of *Tamarindus-Newtonia* riparian forest with the stands of *Acacia albida* in which the troop usually slept. The second zone was the floodplain of the river, with grassland of *Chloris* and *Sporobolus*, and open woodland of *Acacia tanganyikensis*. The third and largest zone comprised gentle slopes bordering the floodplain, covered by bushland of *Combretum* and *Turraea* and crossed by seasonal streams lined by *Anisotes* and *Feretia*. The river was the only permanent water-source, but these streams, and inland pools, were plentiful in the wet season.

2.II b) Fauna

The troop's range overlapped with those of at least eight other baboon troops (Oliver, pers. comm.), and there were numerous vervet monkeys (*Cercopithecus aethiops pygerythrus*) and bushbabies (*Galago* spp.). Ungulates were common, especially impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), buffalo (Syncerus caffer), waterbuck (Kobus defassa) and elephant (Loxodonta africana). Predators included lions (Panthera leo), leopard (Panthera pardus), hyaena (Crocuta crocuta), wild dog (Lycaon pictus), jackals (Canis adjustus), crocodile (Crocodylus niloticus), and raptorial birds.

III. The baboons

2.III a) Taxonomy

The baboons at Ruaha are yellow baboons similar to those studied at Amboseli (Altmann & Altmann, 1970) and Mikumi (Rhine et al., 1979). The five kinds of open-country baboon, hamadryas, guinea, olive, chacma and yellow, have been considered separate species (Jolly,C.1966; Napier & Napier, 1967; Hill, 1970). More recent evidence of gene flow between them suggests that some or all are conspecific (Thorington & Groves, 1970; Jolly & Brett, 1973; Szalay & Delson, 1979), unless evidence of reduced hybrid fertility can be obtained. The study troop are therefore assigned to Papio cynocephalus cynocephalus (Linnaeus, 1766), and they and other subspecies are referred to here by their common names.

2.III b) The study troop

(i) Age-sex classification

The troop chosen, Msembe troop, comprised between 70 and 72 baboons classified as follows:

Adult males: Males of full body size, canine eruption, and mane.

Subadult males: Males larger than adult females, but without full development of canines or mane (discussed below).

Adult females: Full-sized females, showing normal sexual cycles if not pregnant or lactating.

Immatures: All other animals, subdivided irrespective of sex as:

- Juveniles: All immatures older than one year
- Brown infants: Of known age between six months and one year. Predominant coat colour brown.
- Black infants: Of known age up to six months. Predominant coat colour black in most cases.

The troop's composition is summarised in Table 2.I. All the adult females were known to have had at least one offspring by the end of the

Table 2.I Troop composition

	Females	Males
Adults	19	8 - (7)
Subadults	-	4 - (3)
Juveniles	11	16
Brown infants	5	3
Black infants	3 - (1)	5

Table 2.II Absences of males, and reproductive changes of females

Subject	Event	Date/Duration	Time observed (hrs)
A1	absence	26 Oct (part)	435.4
	"	27 Oct & 28 Oct (part)	
	"	3 Jan (part)	
	"	4 Jan (part) 5 & 6	
A2	"	4 Jan (part)	440.7
S1	"	10-21 Oct	248.3
	"	14 Dec onwards	
S3	"	10 Dec	444.6
A6	death	7 Jan	399.5
F1	onset of cycling	9 Dec	264.0 + 181.6
F6	" "	14 Nov	150.4 + 295.2
F7	" "	9 Dec	264.0 + 181.6
F11	" "	9 Dec	264.0 + 181.6
F13	" "	13 Dec	283.0 + 162.5
F17	" "	8 Dec	261.0 + 184.6
F12	birth of infant	14 Dec	336.9 + 108.7
F18	" "	23 Dec	288.7 + 156.9

study. Two juvenile females showed adolescent sexual cycles but did not conceive. It is unlikely that more than three of the male juveniles were fertile (from Altmann _et al._, 1977; Packer, 1979a).

The rationale for distinguishing adult from subadult males was that in all long-term field studies it is clear that males approaching adulthood leave the troop in which they were born, and reside in other troops to breed (Packer, 1975, 1979a and refs. therein). The evidence at Ruaha agrees with this: between May 1975 and December 1978, six males, who were either large juveniles or subadults at the time of this study, left the troop: and nine adult males joined the troop to reside (Ngatwika, pers. comm.). Therefore the distinction between subadult and adult males coincides with Packer's separation of natal and transferred males, and it is almost certain that the subadults were offspring of females in Msembe troop while the adults were not.

2.III b.(ii) Female reproductive classes

Adult females were distinguished according to reproductive condition as:

Pregnant: Females between the cessation of full perineal cycles and the birth of an infant. Recognisable latterly by the deep red colour of the paracallosal skin.

Mothers: Females with a dependent black infant, below six months old.

Lactating: Females with a dependent brown infant, or who had not resumed cycling.

Cycling: Females showing menstrual cycles with perineal swelling.

The females' classification as pregnant, mothers, lactating or cycling will be referred to as their _reproductive state_. This is to be distinguished from the stages of the menstrual cycle, referred to as _cycle state_, and classified as follows:

Inflating: the sex skin increasing in size, usually bright red and shiny.

Full: the final week of inflation, thus the seven days before the onset of deflation. The sex skin attains maximum size (discussed further below).

Deflation: the sex skin decreases in size, becoming limp and wrinkled.

Flat: the sex-skin quiescent, not swollen.

The period of full-swelling is so defined because conception may occur during the seven days before deflation (Hendrickx and Kraemer, 1969): in some cycles the swelling did not reach full size until four days before deflation, but all seven days were considered as "full". Notation of the days within the cycle is described in Chapter 7. Inflation and full swelling together are referred to as turgescence, deflation and flat as detergescence.

2.III c) The subjects of the study

All adult males and females, and the four subadult males, were selected as the subjects of this study, total 31 animals. They were individually named, and are here referred to in the text by using the prefixes A for adult male, S for subadult male, and F for adult female, and the suffix in each case of their dominance rank within their class. Thus adult males number A1 to A8, subadults S1 to S4, and females F1 to F19. (The assignment of dominance ranks is described in Chapter 6). All were present for the 445.6 hours of data collection, except for the absences listed in Table 2.II, which also shows the duration of observations before and after each of eight females changed reproductive state.

2. III c.(i) Age

The age of non-adults was estimated from their size. Age of adults was estimated from condition of body and coat, tooth-wear, and skin-texture of face and ears. These criteria permit only crude estimates.

The adult males were classified as young (A1 and A2), prime (A3, A4, A5), ageing (A6 and A7) and aged (A8). The subadults ranged from just above female size (S4) to adult male size (S1), with S2 and S3 similar and intermediate.

2. III c.(ii) Seniority

Seniority refers to the relative length of time transferred males have been resident in a troop (Packer, 1979a). The eight adult males could be divided on this basis into two newcomers, A1 and A2, who joined the troop five months before the start of data collection, and the remaining six residents who had all been present at least twelve months (Ngatwika & Mathias, pers. comm.).

2.III c.(iii) Subjects excluded from analysis

Two subjects became ill. A6 died during the final week of the study, after nine days of a respiratory ailment. Because his symptoms were slight, and his normally low interaction rate little altered, all of his data have been retained in analysis. F11 suffered hairloss and weakness in the hindlimbs and lumbar region for most of the study, and her behaviour was unusual. She moved slowly, usually peripherally, interacted little, and during her menstrual cycle she was not attractive to males although she appeared hypersensitive to tactile stimuli. Her data have therefore been omitted from analyses of rates of female-female and male-female interaction, and of reproductive and cycle state changes. However, because she interacted no less frequently than other peripheral animals, and presumably had kin in the troop, she has not been excluded from portrayal of the network of relationships in the troop.

Because F1 resumed cycling while still classified as a mother, her interactions after December 8th have not been included as representative of either mothers or cycling females.

Interactions between adults and immatures have been retained for analysis, on the grounds that they contribute to the social relations of each adult. However, because they were not all reliably identified or even sexed in the field, their interactions have not been analysed in detail. The juveniles were the focus of separate studies by Oliver & Lee (1978) and Lee and Oliver (1979).

B. Methods

2.IV. Data collection

The baboons were habituated to the presence of humans within 5-15 metres, and observations were made while moving on foot among them. Data were recorded on check sheets, and binoculars were used to aid identification of distant subjects.

It was intended to study the behaviour of all 31 subjects. Although focal animal sampling would have yielded high quality data, there was not enough time available to obtain enough data on all subjects by this method. Instead, ad libitum sampling was chosen (Altmann, J. 1974), in which data are recorded from all subjects in view at once. Although the data are of lower quality, this method permits the recording of far more interactions, and was suitable in the good visibility conditions found at Ruaha. Another reason for this decision was the risk of coming upon buffalo and elephant at dangerously close range: ad libitum sampling involves constant scanning over a wide area, therefore reducing this risk, and also allows unscheduled breaks in observation, to avoid confrontation.

The major disadvantage of ad libitum sampling is that not all subjects are in view for an equal amount of time, and observations may also be biassed by the observer's interests (Altmann J. 1974). Accordingly a schedule of instantaneous samples on each subject in turn was introduced, to force the observer to search continually through the troop and to increase the chances that each subject would be seen equally in any behaviour. This sampling schedule will now be described (Sections V to VIII below).

2. V. Instantaneous samples of spatial data

This procedure was devised to record association between subjects, and to record their location in the troop. Both association and location are states that vary continually, so that instantaneous (point) sampling is an appropriate method to record them (Altmann J. 1974).

2.VI. Choice of subject

The ideal method for ensuring that subjects are chosen for sampling without respect to their association or location at the time is to sample in sequence from a predetermined randomly ordered list. However, subjects took too long to find and it was not possible to sample all 31 within one day's observation period by this means. Therefore, to speed up sampling, some choice was introduced: the random-ordered list was divided into triplets, and the subject chosen for each sample was the first member of the next triplet seen who satisfied the following criteria. To be eligible, the subject had to be at least 25 metres from the site of the previous sample, could not have featured in it as an associate, and must not have been sampled in the previous hour nor more than once that day. In some cases, members of triplets were given priority if their sample total to date had lagged behind, or if they had changed reproductive state, but such priorities were assigned before the start of the day's sampling.

2.VII. Sample interval

Each sample was taken on the first minute after the subject was chosen. It was important to ensure that consecutive samples of association were independent, even though they had different subjects. Thus if B was A's associate in one sample, the likelihood that B would be C's associate in the next would be affected by C's tendency to associate with A, unless sufficient time had elapsed to allow mixing. Pilot-data was collected to estimate the rate of mixing. All subjects then known (27 of the 31) were followed for an average of 51 minutes each, and the identity of the nearest male and female neighbour within 15 metres were recorded on every minute. The 1381 records so obtained included 378 associations between pairs: of these, 40% persisted over two consecutive minutes, 24.7% for three, 13.9% for four, and only 7.8% for five. Therefore, over the whole study, samples were taken on every 5th minute or as soon as possible thereafter. The mean sample interval was 6.6 minutes, with 5 minutes the mode, and 90 the maximum.

2.VIII. Data recorded

An average of 130.8 samples was taken on each subject (range between 81 and 142), and at each sample the following procedure was carried out:

a) Association. An instantaneous sample was made on the minute recording the identity of the nearest male and female subjects within 15m of the focal subject. Immediately a focal animal sample was made on the same subject through the ensuing minute, recording the identity of all other subjects passing within 15m of the focal subject. The focal subject's grooming partners were excluded from the on-minute records, but included in the through-minute ones.

The distance of 15m was chosen as a reasonable distance uniting animals which appeared to travel together within the wider limits of the troop. Records did not distinguish whether subject or associate was responsible for their proximity.

The on-minute data are the basis for the analyses in Chapter 4. The more plentiful through-the-minute records were used for more detailed analyses of male-male agonism (Chapter 6) and cycle-state changes (Chapters 7 and 8).

b) Location. On the minute was recorded the focal subject's location in the troop. If there were five or more baboons (of any age, but excluding the subject's dependent infant) within 25m radius, the subject was in a cluster. If there were fewer than five, but there were no more than two baboons beyond the subject in a general direction away from the troop's centre of mass, subjectively judged, the subject was at the edge. But if there were more than two, it was in the middle. If the troop was travelling, the edge was divided in relation to the line of travel of the troop's centre of mass as front or rear (if in line) or the sides.

c) Troop state. At the time of the sample, the activity of the majority of the the troop was classified as static - the majority not travelling, most resting or feeding - or in slow progression - the majority travelling and feeding, often widely dispersed - or in fast progression - all baboons travelling in the same direction, within a relatively small area for the troop.

Spatial data of these three kinds were recorded even when the troop was moving rapidly, in contrast to the procedure of Kummer (1968) and Deag (1974).

2.IX. One-zero sampling of consortship

Sexual consortship between male and female (Chapters 7 and 8) is another state, but one which cannot usually be recognised instantaneously. It was therefore recorded by one-zero sampling: observation-time was divided into 15-minute time-blocs, and in each of these each cycling female was designated in or out of consort with an adult or subadult male, on the basis of ad libitum observation through that time. Of those consortships judged to be continuous, the mean length was 99.3 minutes (range one to 420), an estimate limited by the duration of observation on those days which averaged 313 minutes. However, 30% of these consortships were less than 15 minutes long, so that one-zero sampling may have inaccurately estimated the consort-time of any pairs who typically had short consortships (Dunbar, 1976; Tyler, 1979). Therefore little weight is given to findings on this measure. The 15 minute sample was also used to record the presence of any male subject within 25m of the consort pair (excluding any male who was at the time in consort with another female). These data are used in Chapters 7 and 8.

2.X. Ad libitum recording of social behaviour

Ad libitum observations were made in the intervals between instantaneous samples, often while searching for focal subjects. All social interactions involving at least one of the 31 subjects were recorded, noting the type of interaction (described below), the identity of the participants, and the time. If either participant could not be identified, the interaction was retained for analysis of the behaviour of the other.

The social behaviours recorded were chosen to reveal patterns of affiliation (grooming and some socio-sexual behaviours), agonism (approach-retreat interactions, aggression, and some socio-sexual behaviours), sexual behaviour (intromitted mounts), and possessive behaviours (triadic interactions in which one animal is denied access to a second by the behaviour of a third). The definitions of these behaviours are given in Appendix I.

The categories of interaction were only grossly defined, because in ad libitum observation, often at a distance, it is not possible to reliably record fine details, nor always to determine which partner approached or left the other. Although most behaviours were events of short duration two were not: grooming was of relatively longer duration, but was recorded as an event since bout-length could not be measured *ad libitum* (Chapter 4). Secondly, aggression often involved prolonged exchanges of gestures, the recording of which is described in Chapter 6.

2.XI. Sources of bias in the data

2.XI a) Bias in instantaneous sampling

The likelihood that any subject had at least one male or female within 15m was much affected by whether the troop was static, or in slow or fast progression, at the time of sampling (Table 2.III). Unfortunately subjects were not sampled equally in the three troop states, and so their records of association with each sex might not have been comparable. For each subject was calculated the expected number of its samples for which male and female neighbours would have been present; first on the nul hypothesis that individuals would not differ; and secondly on the nul hypothesis that individuals would have neighbours present entirely in proportion to the number of their samples taken in each troop state, in relation to the neighbour probabilities found in those states (from Table 2.III). Data in Table 2.IV show that the two sets of expected scores were almost identical, but that observed scores differed markedly: since the individual differences could not be the product of sampling bias, it has been discounted in analysis.

2.XI b) Bias caused by unequal sampling of subjects

Instantaneous samples were not taken equally on all subjects: so that more interactions might have been recorded for those who were sampled more. Most females were sampled for an average of 129.5 times (± s.d. 1.6), but the high priority females, those who resumed cycling or gave birth, were sampled on average 140.6 times (± s.d. 1.4). As a result the low priority females might have been seen in only 92.1% as many interactions as the high priority ones. But data in Table 2.V show that they were only seen in 65.5% of the number of the high priority females' interactions. This is a significant difference (Mann-Whitney $U = 15$, $N_{8,10}$, $p < .05$), and it is not explained by

Table 2.III

The percentage of association samples in which subjects had at least one male or female neighbour within 15m, subdivided according to Troop State at the time of the samples

Troop State	% with female	% with male	Total samples
Static	64.3	50.8	2628
Slow progression	51.7	34.0	1337
Fast progression	65.3	38.7	75
Overall	60.2	45.0	4040
χ^2	59.79	102.35	
probability (df 2)	$p < .001$	$p < .001$	

χ^2 values are derived from comparing the proportion of all samples with or without neighbours across the three troop-states.

Table 2.IV

Chi squared values derived from four 2 x 31 comparisons between the number of association samples in which each subject had male or female neighbours, and the numbers expected from two nul hypotheses described in the text

	Female neighbours	Male neighbours
Expected compared with troop-state expected	0.141 p 0.99	0.359 p 0.99
Troop-state expected compared with observed	56.937 $p < .01$	95.085 $p < .001$
	N=2448 samples between 31 subjects	N=1824 samples between 31 subjects

Table 2.V

Differences between the interaction scores of females given high- and low-priority in instantaneous sampling

Mean number of interactions with all partners by females in high- and low-priority groups

	Low priority (N=10)	High priority (N=8)
$\bar{x}$	197.5	301.5
sd.	22.6	90.8

sampling bias because even when the high-priority females' scores are reduced to 92.1% of their original value, they remain significantly above those of the low priority females ($U = 17$, $N_{8.10}$, $p = 0.05$). The effect of sampling bias is therefore trivial in relation to other differences between the sets of females, and has been discounted in analysis.

2.XI c.(i) Bias in ad libitum recording

Biases may arise in *ad libitum* sampling in at least three ways (Altmann J. 1974).

First, an observer who is more interested in particular animals or behaviours may tend to miss those in which he is less interested. The prime interests in this study were the relations between the sexes, especially involving cycling females, and the agonistic relationships within each sex. It is undeniable that less interesting interactions may have been overlooked when the interaction rates were high, yet rates were usually low enough to scan equally all subjects in view. It is also undeniable that the interactions of the more conspicuous animals, such as adult males, may have been noticed more.

The second possible bias is that animals may behave differently under cover than when in view: low-ranking males may be inhibited from mating in the sight of high-rankers. However, at Ruaha baboons spent little time in thick vegetation, and it is by no means inevitable that when out of the observer's sight they were out of sight of other baboons. But for those who *were* out of sight more than others, the usual reason was not that they were under cover, but rather on the periphery, where there was probably less opportunity to interact.

This point introduces the third bias, which is that if animals are not in view for equal amounts of time they will not be seen interacting equally often. During sampling it was difficult to tell how much time each subject *was* in view, and this is important because most observation time was inevitably spent in the more crowded parts of the troop. Therefore an attempt was made to measure differences in observability between animals, to see whether they alone could account for the observed differences in behaviour.

2.XI c.(ii) Observability ratings

The observability of each animal was assessed by making 360° visual scans, dictating the names of all subjects seen into a tape recorder. In order that visibility at such times differed as little as possible from conditions during routine data collection, the scans were interposed between the instantaneous samples of daily observations, on ten days between November 23rd and January 10th. The scans were made immediately after each focal sample, from the same location, and took between 20 seconds and two minutes each. On average 55.4% of the subjects could be seen in each scan. Scans were apportioned equally after the focal samples of every subject, as far as possible, to ensure that they were made equally from all parts of the troop.

The observability rating of each subject was the number of scans in which it was seen as a percentage of the number of scans in which it might have been seen. That is, from the 391 scans taken were excluded all those made when the subject was absent from the troop. Also excluded were all scans taken immediately after the subject's <u>own</u> instantaneous samples: this is because subjects were certain to be seen in the scan after their own focal sample, but they differed individually in the proportion of scans for which this was the case. This exclusion reduced mean observability ratings by 2%, but allowed accurate comparison of subjects. The subjects' observability differences were consistent between the first and second halves of the scanning programme (comparing ratings before and after December 31st, Spearman rank correlation, r_s 0.590, $n = 29$, $p < .02$) so that all data were used in compiling the overall ratings which appear in Fig. 2.1. Subjects' observability ranged from 38.1 to 65.3% ($\bar{x}$ 53.9, s.d. 6.5).

2.XI c.(iii) The effect of observability

To assess the extent to which individuals' variance in interaction rate could be attributed to observability differences, subjects' rates of behaviour exchanged with all partners were compared with their observability ratings by Spearman rank correlation coefficient (Table 2.VI). Comparisons in each behaviour were made separately for males and females. Only two behaviours were significantly related to observability, and 25% of comparisons suggested a negative relationship. The proportion of the variance due to observability was nowhere very high: most strongly for male copulation, male-male

FIG 2.1 OBSERVABILITY

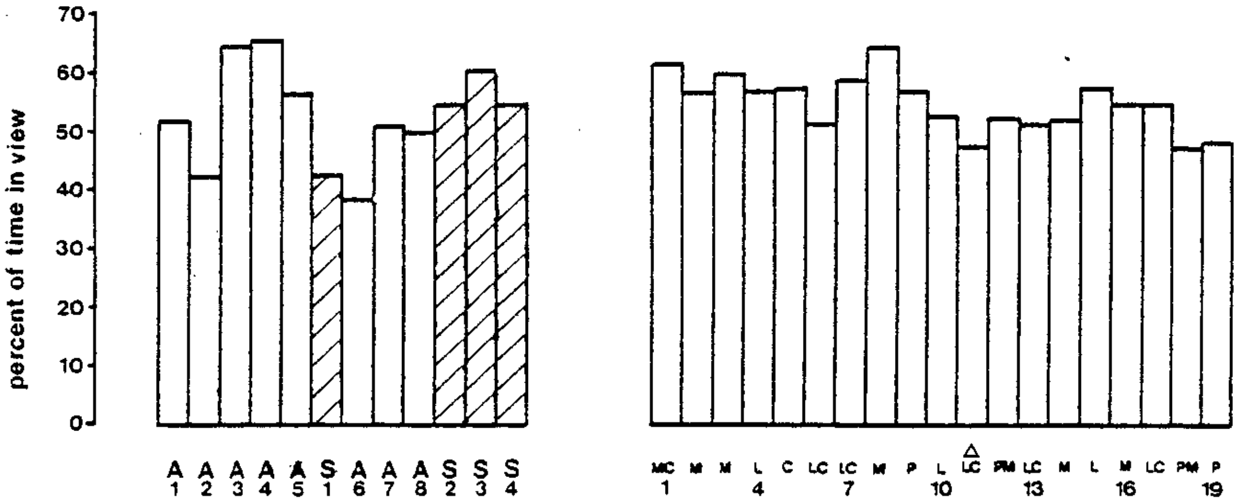

Fig. 2.1. Observability differences between subjects. The percent of time for which each subject was in view, estimated from 391 scans over 360°. Males and females in descending order of dominance rank from the left, subadult males cross-hatched, females' reproductive states shown as C - cycling, P - pregnant, M - mothers, L - lactating, and the sick female F11 indicated by △ .

Table 2.VI

The relationship between subjects' ranks for rates of behaviour given and received with all partners, and their ranks for observability. In each column is shown the Spearman rank correlation coefficient (r_s) and the square of that, as percent (which is the percent of variance in behaviour attributable to observability differences).

Behaviour		**Females:** (n=19)		**Males:** (n=12)	
		r_s	$(r_s)^2$x100	r_s	$(r_s)^2$x100
Grooming	-given	.020	0.0	.459	21.1
	-rec	-.037	0.1	-.004	0.0
Presents	-given	-.068	0.5		
	-rec			.144	2.1
Mounts	-given	.406	16.5	.466	21.7
	-rec	.011	0.0	-.063	0.4
Avoidance	-rec	.215	4.6	.070	0.5
	-given	-.341	11.7	.032	0.1
Supplant	-given	.393	15.4	.343	11.7
	-rec	.264	7.0	.106	1.1
Aggression	-given	.320	10.2	.322	10.4
	-rec	-.163	2.7	.378	14.3
Copulations	-given			.790**	62.4
Passes	-given			.049	0.2
	-rec			.176	3.1
Male contact	-given			.699*	48.9
	-rec			-.161	2.6
Male interacts with infant				.574	33.0

$^{*}p < .05$ $^{**}p < .01$

contact, male-infant interaction, male grooming, and male mounting. It was concluded that very little behavioural variance was caused by observability alone, but enough that it should be corrected for in analysis.

2.XI c.(iv) Correcting for observability differences

Although observability differences explained only a small proportion of individual variability, yet they may still have exaggerated or masked real individual differences. Therefore all analyses of individuals' behaviour were repeated using the observability correction of Drickamer (1974a). Each subject's observed rate was corrected to a rate expected had it been in view all the time. This was done by dividing the observed rate by the proportion of time for which the subject had been in view (i.e. the subject's observability rating expressed as a proportion). This has the effect of relatively increasing the rates of the less observable subjects. The results of the analyses of observed scores which follow are only accepted if they are also confirmed by the analysis of corrected scores, which is probably a conservative procedure, for the following reason.

J. Altmann (1974) and Symons (1978, p.165) describe objections to the use of such correction factors. A real objection in this study was that the less observable subjects spent less time near other baboons. The amount of time that subjects spent in clusters (Section VIII b) above) was correlated with their observability ratings (Spearman rank correlations: over all subjects, r_s 0.723, n31: males only, r_s 0.797, n12: females only r_s 0.691, n19: all probabilities $<.01$). This implies that the less observable animals may have had less opportunity to interact, so that to relatively increase their rates with the observability correction may produce even less accurate estimates of individual variability.

Despite this, the observability correction is retained here as a check on the analyses of raw scores. It usually produced only slight changes in the rank-orders of class members, or in the relative distributions of class scores.

2.XI d) Biases caused by the time of day of observations and seasonal changes

(i) Time of day

The number of focal samples and observation hours in each period of the day are shown in Table 2.VII. Most data were recorded before 3.00 p.m., which may have biased against certain types of interaction. The troop's activity pattern was usually predictable:

i) Early morning: a period of rest at the base of the sleeping trees, with grooming frequent. Seldom more than half an hour except in rain.

ii) The troop moves onto the river flats to feed on *Cyperus*. Supplanting frequent.

iii) The troop travels inland, foraging, starting 9.30-10.30: interactions less frequent, except sometimes for a period of rest and grooming at the far point of travel.

iv) Return to the river, to drink, at noon or shortly after. Usually a rest period, with grooming frequent.

v) Afternoon: slow foraging near the river.

The observation period sometimes included the early social period, always included the morning's feeding and supplanting, and usually also the mid-day rest and grooming. Instantaneous samples on each subject showed the same distribution over five two-hour time-blocks starting at 6.30 a.m. (x^2 99.5, d.f. 120, n.s.). However, time of day affected the distribution of adult social behaviour within and between the sexes (Tab 2.VIIIa); and also the types of interaction seen (Tab.2.VIIIb). Therefore the number of interactions of each type within and between each sex are compared as pooled mean rates per dyad-hour (Section XII c.(iv)) in Fig. 2.2. Most behaviours were most frequent before 9.00 a.m., decreasing steadily thereafter. However the routine of ending observation around 2.00 p.m. may have discriminated against recording grooming (especially between females), and supplants and aggression (especially between males).

2.XI d.(ii) Seasonal changes

Figs. 2.3 and 2.4 show time changes over the study in association and interaction among subjects. There were no clear changes in relations between males. Female-female association increased,

Table 2.VII Time of day of observations

The number of instantaneous samples, observation hours, and the number of days contributing, at each time of day

Time:	7	8	9	10	11	12	1	2	3	4		
Samples:	6	224	596	646	643	681	616	387	188	46	50	4083
Hours:	.6	25.2	62.8	73.6	73.3	72.8	63.6	41.9	20.9	5.4	5.6	445.6
Days:	2	49	74	77	75	74	73	56	33	9	4	max.84

Table 2.VIII Time of day of behaviours

a) The numbers of interactions between adults at different times of day

Time:	earlier	8	9	10	11	12	1	2	later	
Grooming:	98	59	73	87	101	139	71	66		
Presents:	28	45	37	24	23	22	11	17		
Mounts:	83	94	52	41	35	25	11	10		χ^2 258.01
Intromitted mounts:	43	85	81	56	37	56	37	18		df 42. $p < .001$
Avoids:	46	110	78	72	70	41	22	21		
Supplant	177	334	257	209	142	173	103	96		
Aggression:	90	223	164	135	126	118	97	61		

b) The distribution of interactions within and between sexes at different times of day

Male to male:	177	434	306	236	152	196	147	106	
Male to female:	228	378	333	254	234	214	113	108	χ^2 89.37
Female to male:	59	73	63	59	70	67	35	39	df 21. $p < .001$
Female to female:	128	186	139	133	136	148	102	81	

FIG 2.2

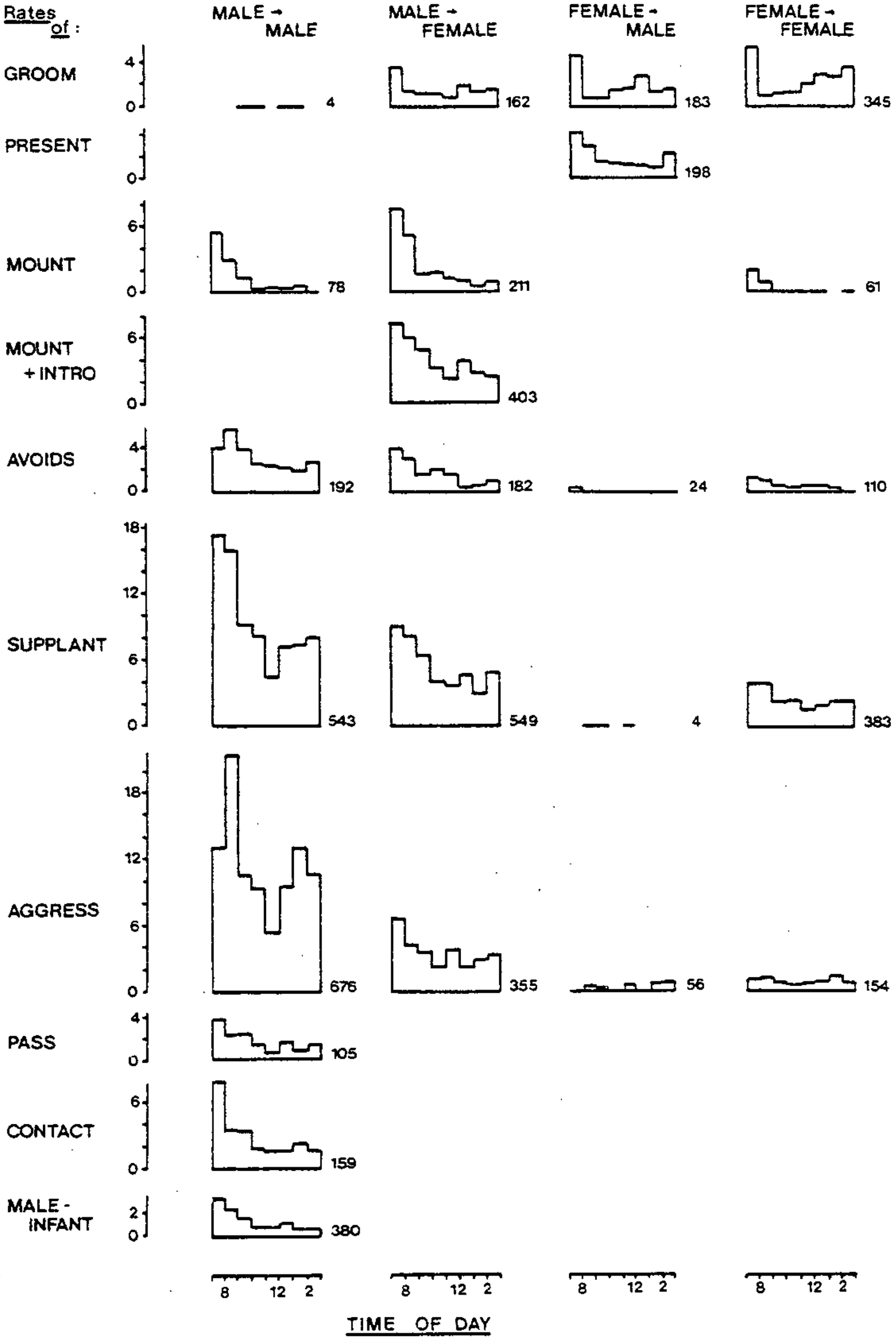

Fig. 2.2. Time of day of social behaviours. For each behaviour is shown the pooled mean rate per thousand dyad-hours in eight time-blocks through the day, from before 8.00 a.m. till after 2.00 p.m. Rates are presented separately according to sex of donor and recipient, with the number of interactions to right of each histogram. The rate of male-infant interaction is calculated per fifty male-hours, to save space.

FIG 2.3

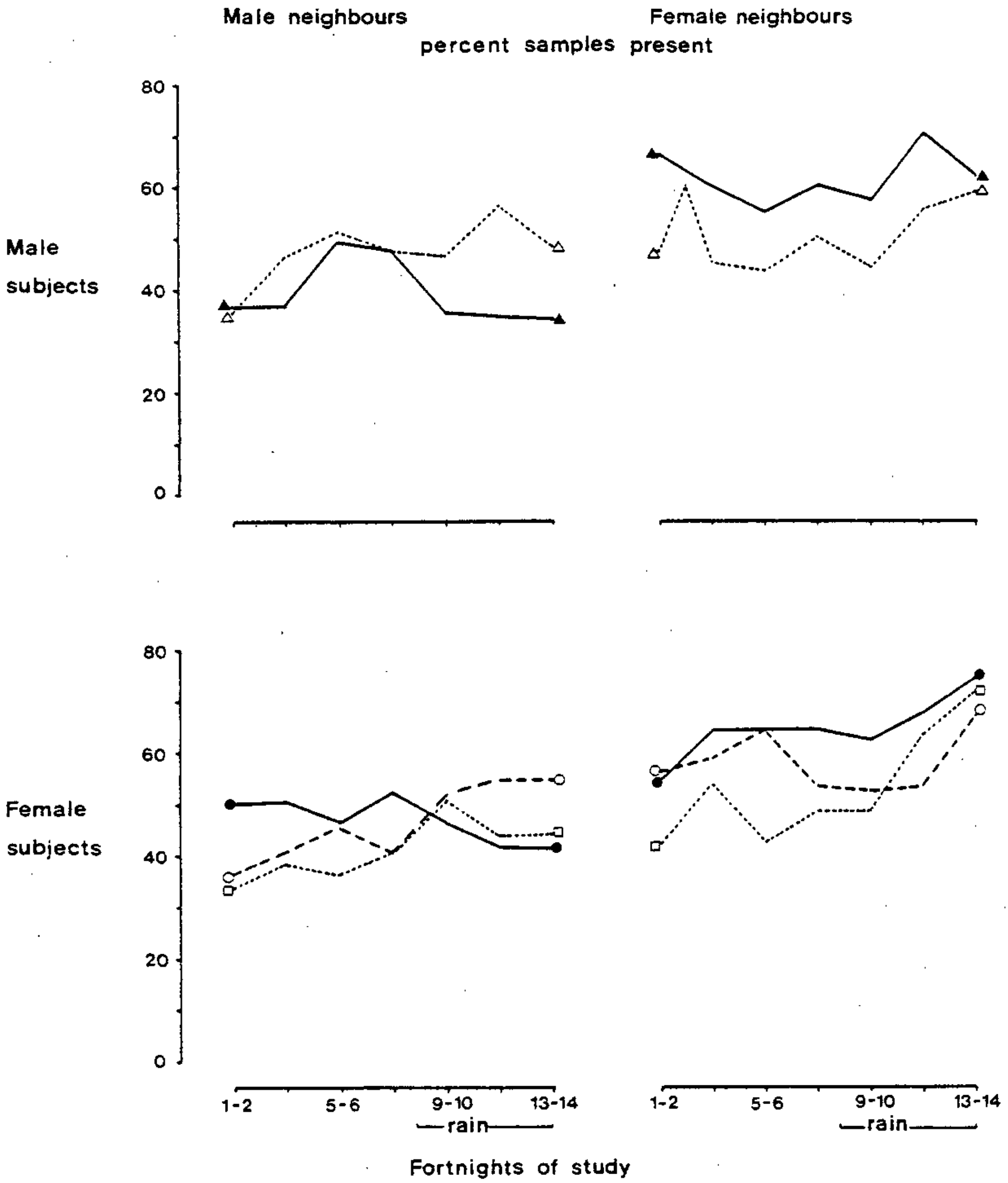

Fig. 2.3. Variation in the presence of male and female neighbours in each fortnight. For each subject was calculated the percent of its association samples in which male or female neighbours were present during each two-week period. The figure shows the means of these scores for: 8 adult males (▲—▲), 4 subadult males (△---△), 6 females who resumed cycling (○--○), 2 who gave birth (□····□), and 9 females who did neither (●—●).

FIG 2.4

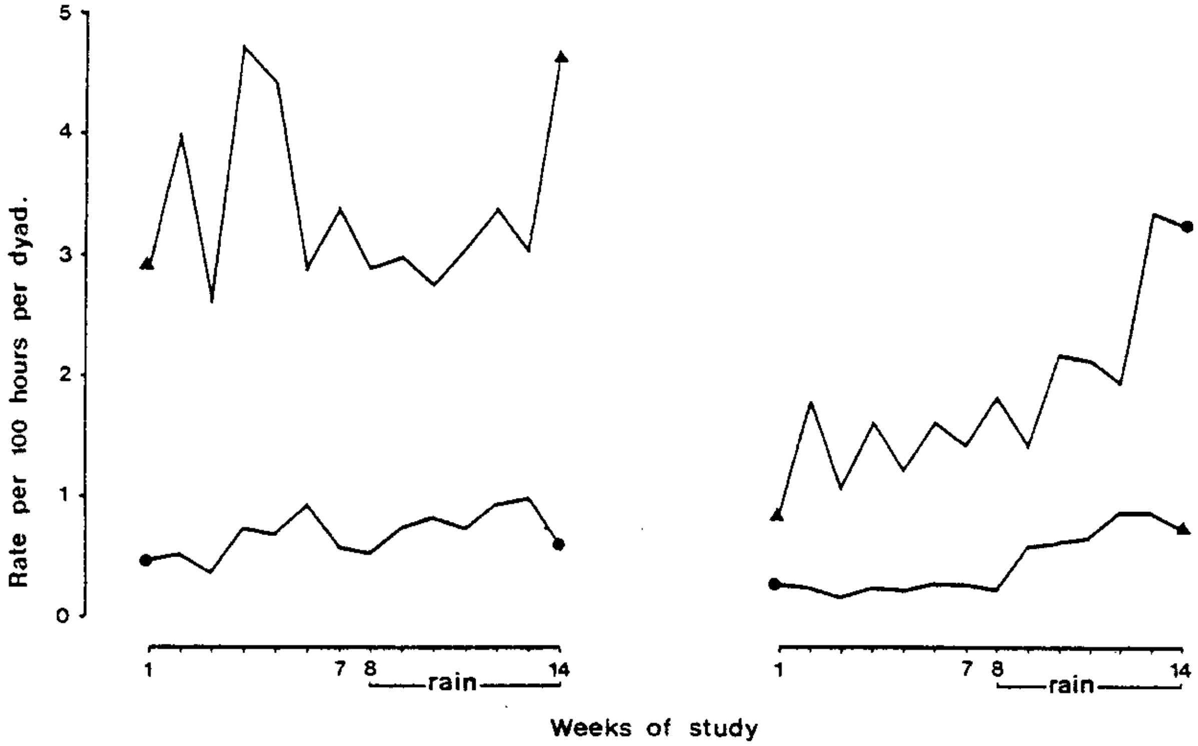

Fig. 2.4. Variation in interaction rates in each week of the study. The graph shows pooled mean rates of all interactions per hundred dyad-hours. Rates are presented separately of interactions between males (▲—▲), between females (●—●), from male to female (▲—●), and from female to male (●—▲). The rainy season began in week 8.

especially for females who gave birth and those who did not change reproductive state, but there was only slight increase in interaction. Associations between the sexes changed in that the females who resumed cycling, or gave birth, had male neighbours more often later in the study: this parallels an increase in interaction between the sexes, especially after week 8.

These changes might be attributed to the onset of the rains in week 8, which brought a flush of new vegetation, and the baboons fed and rested more, and travelled less (Oliver & Lee, 1978). Such changes may have permitted the increases in association and interaction. However this cause cannot be distinguished from the female reproductive changes: after the first rain, five females resumed cycling within two weeks, and two gave birth within the month. The data on association and interaction suggest that the behavioural changes were not general to all subjects, which implies that the reproductive changes were probably more important. In the ensuing analyses, comparisons of behaviour before and after the resumption of cycling, and the birth of infants, cannot therefore be attributed entirely to the reproductive changes, since ecological factors may have influenced rates of behaviour directly.

2.XII. Measures of behaviour

Because females changed reproductive state, and males were sometimes absent, behavioural measures have often been calculated over short periods within the study as well as over the entire study (Sections XII a) to c) below).

2.XII a) Whole and part sample data

Association frequencies, and interaction rates calculated over the whole duration of the study are referred to as whole-sample data. But measures calculated for a female before and after her change in reproductive state, or shorter permutations between females who changed state at different times, are referred to as part-sample data.

2.XII b) Neighbour frequency

Subjects' instantaneous samples of association records were used to calculate dyadic neighbour frequencies between subject and neighbour. The dyadic neighbour frequency was the number of times the partner was nearest neighbour to the subject, expressed as percent of the number of samples taken on the subject while the neighbour was in the troop. The same method was used to calculate part-sample neighbour frequencies, but using only the data from the relevant part of the study. These frequencies were used to calculate each subject's dyadic mean neighbour frequency with all members of particular classes. Part-sample frequencies based on less than 30 samples were excluded from analyses.

2. XII c) Interaction rates

Interaction rates were calculated for each subject both with and without accounting for the number of partners available, as follows:

2. XII c.(i) Subject rate

The number of times the subject gave or received a behaviour was divided by the number of observation hours for which it had been in the troop. This measure reflects the rate at which the subject performed or received the behaviour irrespective of partner availability.

2. XII c.(ii) Dyadic rate

The number of times the subject gave or received a behaviour with a particular partner was divided by the number of observation-hours for which they had both been in the troop. For part-sample rates, both interactions and time-base were limited to those during the period of the part-sample.

2. XII c.(iii) Dyadic mean rate

For each subject, this was the mean of its dyadic rates to each partner in the class under consideration. For behaviours which were not given randomly to dominants and subordinates, dyadic mean rates within sex were calculated separately uprank (to dominants) and downrank (to subordinates). Dyadic part-sample rates based on less than 1000 minutes of observation were excluded from analysis.

2. XII c.(iv) Pooled mean rate

For each subject, the number of interactions with all partners in a given class were divided by the sum of observation hours with all members of that class. If all partners were available for an equal amount of time this rate is the same as the dyadic mean rate. Pooled mean rate was used for rate calculations in each stage of the menstrual cycle, since dyadic mean rates based on such short periods were more susceptible to random fluctuation.

All interaction rates were expressed per 100 hours, because of the generally low rates per partner-hour. All are underestimates of real interaction rates, due to *ad libitum* sampling. During analyses, the observability correction (Section XI c.(iv)) was applied to all these rates except dyadic rates ((b) above).

2. XII d) Subject rate compared with mean dyadic rate

To answer questions such as "how often does each animal receive aggression?" subject rates are the appropriate measure. But for questions such as "do females interact with their own sex more than with males?" the number of partners becomes important, and mean dyadic rates are used. However there is an upper limit of the extent to which an increase in the availability of partners is expected to increase an animal's interaction rate. It is not clear where this limit lies, and no attempt is made to allow for it in most of the analyses here. However, because grooming is a more time-consuming behaviour, the maximum number of partners in a given time is presumably much lower, so that subject rates and mean dyadic rates are presented in parallel.

Subject rates are also used in analyses of interaction with immatures, because partners were not all recognised. Subject rates with immatures may be approximated to dyadic mean rates by dividing by 40, or for behaviours confined to male immatures by 24.

2. XIII. Analysis

The same procedures of analysis were used in Chapters 4 to 6, and will be described here. The analyses were devised to test nul hypotheses that interactions would be distributed randomly with respect to sex, class, and dominance rank of participants. The aim was to avoid using pooled scores, and to assess the effects of observability: thus all analyses were repeated using the observability correction. Whole or part-sample data were used as appropriate, and data from F11 and the second part of F1's data were omitted.

2. XIII a) Comparisons of sex and class

Subjects' mean dyadic neighbour frequencies, or mean dyadic interaction rates, were compared between successively smaller subdivisions of the data. The procedure is exemplified by the scheme for analysing differences between subjects in their rates of behaviour given to male partners. First, male and female subjects were compared: then the two male classes were compared with each other, and so were the four female classes: then, for each of these six classes in turn, was compared their rates given to each of the two recipient classes, namely adult and subadult males. Analysis of rates of behaviour to females followed exactly the same sequence, except that the final six tests compared each subject class's rates to recipients in the <u>four</u> different female classes. This routine therefore made full use of the data but maintained strict independence between successive tests.

The only exceptions to this sequence were that

1) for some behaviours, different permutations were compared in the <u>initial</u> tests between and within the sexes, but care was taken to ensure independence.

2) for some behaviours, data were too scanty for the final six tests: instead the <u>recipient</u> classes were compared for rates of receipt of interaction from all members of the donor sex.

Another variation in procedure was necessary when analysing behaviours with high direction constancy either uprank or downrank. Class-comparisons were not valid without accounting for rank-differences between classes, so that similar analyses were conducted only on dyadic mean rates downrank, (or, in a few cases, uprank). This procedure also reduces variance between subjects at opposite ends of the hierarchy: thus male subjects were avoided by other males four times as often as female subjects were avoided by other females, but the males' rate was not significantly higher because the low rankers in each sex had similarly low rates. However, comparison of mean rates to subordinates only revealed a significant difference between males and females (Chapter 6).

2.XIII b) Rank-correlations

The procedure for testing whether rates of behaviour varied with dominance rank was in all cases to rank subjects in order of their rate of interaction, assigning rank 1 to the highest score, and comparing the resultant ranks with dominance ranks by Spearman rank correlation.

2.XIII c) Dominance rank-difference

Rank-difference refers to the number of ranks separating two individuals in a dominance hierarchy. A number of hypotheses were tested that interactions would be more frequent between partners close in dominance rank, within sex. Two methods were employed.

2.XIII c.(i) The first tested the hypothesis that there would be an approximately linear relation between rank difference and interaction rate. Mean dyadic interaction rates were calculated over all pairs at each rank difference, pooling ranks at the greatest rank differences because of diminishing sample size. Mean rate and rank difference were then compared by Spearman rank correlation.

2.XIII c.(ii) The second hypothesis tested was that each subject's most frequent partner would tend to be within two places of dominance rank. For each subject who showed the behaviour, the most frequent recipient was designated first partner. The number of such first partners at each rank difference was counted (assigning equal fractions of one to tied first partners). The expected distribution of such first partners was calculated from the availability of partners at each rank difference (to those subjects who showed the behaviour). The numbers of first partners within and beyond two rank-places were compared with the numbers expected from partner availability, by chi square or binomial test as appropriate. This method was derived from an analysis of rank difference of first partners devised by B.B. Smuts (Harvard University).

2. XIII d) Statistical tests

Interaction rates, being derived from *ad libitum* sampling, were only approximate: further, their distribution very often departed from the normal distribution, so that non-parametric tests were used throughout. All probabilities were two-tailed, α 0.05. This was because in no case were directional predictions sufficiently strong as to reject entirely the converse. The tests, and the ways they are quoted in the text, are described below:

1) In comparison of two or more different classes Mann-Whitney U test (quoted as U) and Kruskal-Wallis one-way analysis of variance (quoted as H) were used respectively.

2) In comparing differences in the rate at which one class interacted with two or more other classes, the Wilcoxon matched-pairs signed ranks test (quoted as T) and the Friedman two-way analysis of variance (quoted as χ_r^2) were used.

3) Rank-orders of subjects were compared by Spearman rank correlation coefficient (quoted as r_s) throughout.

4) The other commonly used test, chi-square, is quoted as χ^2. Other tests used are indicated more fully in the text. All those above are described in Siegel (1956).

When tests have been repeated on scores corrected for observability the result is prefixed by "corr. obs.": if the result was exactly the same as the uncorrected test, it is written "± obs. corr.".

2.XIII e) Sociograms

Details of dyadic relationships have been represented by sociograms (Hanby, 1974a). The methods used have not been consistent throughout, because:

1) in different sociograms, different critical values have been used because rates of different behaviours differed so markedly.

2) the subjects have not been positioned in the same way in each. In some, subjects have been placed to minimise line-crossing (association); in others they have been placed to emphasise the focal position of a particular class (male-female grooming); but in most the subjects of each sex are arrayed in a circle, the order of dominance rank reading anticlockwise from the top.

CHAPTER 3

The Spatial Pattern of the Troop

3.I. Introduction

As a preliminary to describing social behaviour, data are here presented on how individuals were distributed spatially within the troop. A number of authors have distinguished 'central' and 'peripheral' group-members (e.g. Imanishi, 1963): but in so doing so they have sometimes confused spatial criteria with criteria based on social interactions (e.g. Hall and DeVore, 1965). It is important, however, to consider these types of criterion independently until they are shown to coincide (Deag, 1974).

Most authors agree that when baboon troops are stationary, animals are placed with respect to physical features, food sources, or their companions (Rowell, 1969a). Social subgroups may form, which include juvenile playgroups, and aggregations around mothers with newborn infants, or around adult males: while consort pairs are sometimes seen apart from the rest (Saayman, 1970).

There is much less agreement as to the pattern when the troop is moving. DeVore and his colleagues reported an order of progression which they held to be "invariable" in all troops, and to be adaptive against predators (Washburn and DeVore, 1961; DeVore and Washburn, 1963; Hall and DeVore, 1965). They described how the lower-ranking adult and subadult males travelled at the front and rear, forming a protective ring around the vulnerable females and young, with the dominant males in the centre.

With the exception of Maxim and Beuttner-Janusch (1963), however, other workers have failed to confirm this pattern. Qualitative reports do not mention it (Bolwig, 1959) or deny its existence (Rowell, 1966a; Bert et al., 1967; Altmann and Altmann, 1970; Stoltz and Saayman, 1970; Crook and Aldrich-Blake, 1968). Quantitative studies also refute such an invariable pattern, but they do provide evidence of non-random ordering which, as Rhine has emphasised, are consistent from different study-sites (Rowell, 1969a; Rhine, 1975; Harding, 1977; Rhine et al., 1979). However Altmann's (1979) detailed analysis suggests that with a few exceptions the order is essentially random.

The findings of these studies may be briefly summarised. Most authors agree that adult males tend to the edge of the troop, either the front (Harding, 1977), or the rear (Bolwig, 1959) or both (Rowell, 1969a; Tayler and Saayman, 1972; Rhine, 1975). S. Altmann (1979) found adult males sometimes under-represented in the centre, but only Bert and DeVore and their respective colleagues stress their presence there. Rowell contradicted DeVore's statement that particular males travelled in the centre, but Rhine noted high-rankers at the front, low-rankers at the rear, and both Harding and Altmann saw particular examples of this. Recently Rhine and colleagues' (1979) comparison of data from all quantitative studies concluded that subadult males tend also to the front.

There is little concensus about the placement of adult females. They may tend to the front (Harding, 1977), the front and rear (Rowell, 1969a), or the middle (Hall and DeVore, 1965; Altmann S. 1979). Those with young infants are said to avoid front and rear (Rhine and Owens, 1972) or to move at the rear (Bert et al., 1967), and they are often associated with adult males (DeVore, 1963). Females may tend to be outliers during pregnancy (Rowell, 1966a; Saayman, 1972) or during oestrus when consorting with a male (DeVore and Washburn, 1963).

Many of these studies have focussed on whether the pattern is adaptive against predation. Predators vary in abundance at different sites, but the most important are probably leopards and humans. Baboons' responses to them vary from indifference through mild avoidance (in which the adult males may be the last to avoid and so appear to form a rearguard (Rowell, 1969a)) to precipitate flight (Stotz and Saayman, 1970). But baboons of all ages sometimes combine to threaten or chase away predators (Altmann and Altmann, 1970; Baenninger et al., 1977). However it is very difficult to establish whether the progression pattern actually reduces predation.

All quantitative studies have focussed on the linear order of individuals in progression from front to rear, ignoring how they are dispersed laterally; and all except Rhine's (1975) have concentrated only on compact 'file' progressions. The data presented here are not a study of the linear order of different progressions, but of the proportion of time subjects spent in different zones of the troop, both stationary and moving. The results suggest that there is a spatial pattern in both conditions, but that the patterning comprises subtle tendencies and is not as clear-cut as implied by DeVore. The pattern is described in terms of individual and class differences, and examined to see if it might provide individual advantage in terms of safety from predators, feeding efficiency, or social benefits.

3.II. Measures of location within the troop

The measures of location were devised to differentiate between subjects firstly in terms of gregariousness, and secondly in terms of exposure to predators on the assumption that there is safety in numbers (Hamilton, 1971) and that risk is highest at the edge (Vine, 1971). Thus at each sample was recorded whether the subject was in a cluster, the middle or at the edge; and if the troop was moving, whether those at the edge were at front, side, or rear (the zones defined as in Chapter 2, VIII b)). The troop was seldom arrayed as in the idealised Fig. 3.1, which is to illustrate the model used during observations: a more realistic pattern is shown in Tayler and Saayman (1972, Fig. I). The schedule of instantaneous samples forced the observer to move continually through the troop, and allowed as accurate a judgement as is possible of the whereabouts of the troop's "centre of mass" (as in Rhine, 1975 and Altmann S. 1979). The location of the clusters was recorded for the first two weeks of the study: in the stationary troop, clusters were at the edge for 14.7% of the time, but this increased during travel to 31.3%, distributed equally at front, side, and rear.

Data on Troop State at the time of each sample (Chapter 2, VIII c)) show that subjects were sampled on average 83.3 times (s.d. 9.4) when the troop was static and 44.7 times (s.d. 5.8) during movement. Samples taken when stationary and when moving are analysed separately for each subject. The samples of location provide an estimate of how much time each subject spent in each zone calculated as the percent of its total samples which were in each. Data for females who changed reproductive state were calculated for whole- and part-samples (Chapter 2, XII a)). No attempt was made to describe or contrast particular progressions (cf. Altmann S. 1979).

FIG 3·1 Zones of the moving troop.

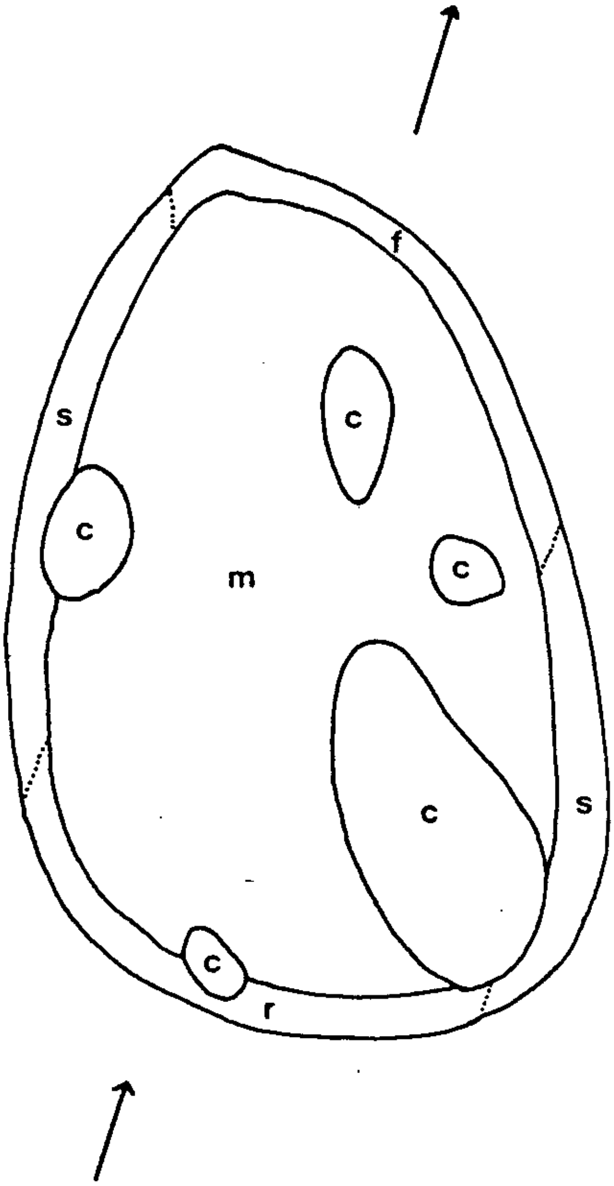

Fig. 3.1. Idealised plan view of the zones of the troop during progression. Arrows show direction of movement. The zones are: f - front, s - side, r - rear, m - middle, c - cluster.

3. III. Analysis: The comparison of adult-classes

Adult-classes were compared for the amount of time they spent in each zone, using part-sample and whole-sample data, and excluding samples on F11 and the second reproductive state of F1 (Ch.2: III c.(iii)). It was not possible to pool the samples of all class-members and then compare classes directly, for two reasons. First, there was considerable variation within each class: the total chi square for within-class heterogeneity during movement was 224.9, (d.f. 120, $p < .001$). Secondly, class-members did not contribute equal numbers of samples to their class(es), particularly in female classes containing part-sample data.

The aim in analysis was to assess the probability of finding a member of a given class in any zone, and then to compare the classes for their zone probabilities by chi square. A method of analysis which accounted both for heterogeneity and unequal sampling of individuals was designed and carried out by D.A. Williams*. The first step was to calculate a within-class variance parameter based on a Dirichlet multinomial distribution (an extension of the Beta-binomial model of Williams (1975) and Crowder (1978)). The contribution from each class-member to the class zone probability was weighted with a weight which depended on the estimated variance parameter and the sample size. The weight increased with the sample size, but the relationship was not exactly proportional as it would have been if there were no within-class heterogeneity. The class zone probability estimates were then compared between classes using chi squared statistics calculated by again weighting the contribution from each class-member. This method was used in all comparisons of classes in Sections IV b) and IV c) below.

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*Department of Statistics, University of Edinburgh.

3.IV. Results A: The overall pattern

3.IV a) Troop State and dispersion

The troop was seldom obviously demarcated into 'centre' and 'periphery' (cf. Hall and DeVore, 1965). Its members were often dispersed over 200-300m, sometimes to 500m (Oliver, pers. comm.). But only in 0.15% of samples were subjects recorded as 'out of the troop'; far from the rest and with no baboons audible or visible to the observer, although this probably occurred more than it was seen: these were all males.

The troop was stationary for more than half the time (Table 3.I). Fast progressions, most comparable to those sampled by other authors, were very rare. Data from fast and slow progressions are here pooled, because there are scant data from fast ones, and Rhine (1975) found no difference in progression order between the two types.

3.IV b) Spatial pattern in the stationary troop

Individuals differed in the proportion of their samples in each zone (χ^2 274.1, d.f. 58, $p < 0.001$). Subjects spent between 7.0 and 76.3% of time at the edge, and from 22.3 to 87.2% in the clusters. The zone probabilities of each class are shown in Table 3.II.

Classes differed markedly in the probability they would be seen in each zone (χ^2 30.2, d.f. 10, $p < 0.001$). Ranked in order of decreasing time spent in clusters (which corresponds to increasing time at the edge) the sequence runs mothers > lactating females > subadult males > cycling females $\geq$ adult males > pregnant females. This sequence is not a continuous one, however, since some classes can be pooled without causing significant increase in within-group heterogeneity. These are:

a) adult males, cycling and pregnant females
b) subadult males and lactating females
c) mothers

Pooling of groups (a) and (b) increases chi-square by 9.1 (at 2 d.f. $p < 0.02$), while pooling (b) and (c) produces an increase of 5.2 (at d.f. 2, $p \simeq 0.07$), so these groups remain distinct. Individual and class differences, illustrated in Fig. 3.3, are further discussed below.

Table 3.I

The proportion of time in each troop-state each month. Tabulated as the percent of all instantaneous samples for which each state was recorded.

Month:	Oct.	Nov.	Dec.	Jan.	Overall
Sample total:	861	1162	1294	723	4040
Stationary:	62.4	64.7	59.8	78.3	65.0%
Slow progression:	32.2	34.1	39.4	21.2	33.1%
Fast progression:	5.5	1.2	0.8	0.5	1.9%

Table 3.II The stationary troop

The mean probability of occurrence of each class in each zone, calculated by the method described in Section III.

Zones:	Edge	Middle	Clusters
Adult males:	.37	.06	.57
Subadult males:	.29	.10	.61
Cycling females:	.34	.09	.57
Pregnant females:	.43	.10	.47
Mothers:	.18	.09	.73
Lactating females:	.26	.10	.64
Mean:	.312	.090	.598

Table 3.III The troop during movement

The mean probability of occurrence of each class in each zone, calculated by the method described in Section III.

Zones:	Front	Side	Rear	Middle	Clusters
Adult males:	.18	.16	.10	.11	.44
Subadult males:	.19	.09	.03	.17	.52
Cycling females:	.12	.11	.07	.23	.47
Pregnant females:	.07	.31	.12	.17	.33
Mothers:	.03	.05	.12	.14	.67
Lactating females:	.07	.13	.06	.17	.57
Mean:	.110	.142	.083	.165	.500

3. IV c) Spatial pattern in the moving troop

Individuals differed also in the proportions of their samples in each zone during movement (χ^2, pooling the edge zones, 191.5, d.f. 58, $p < 0.001$). Subjects spent between 0.0 and 39.0% of time at the front, and between 25.0 and 85.0% in the clusters.

Classes differed in the probability they would be seen in each zone (χ^2 91.6, d.f. 20, $p < 0.01$): Table 3.III. Again, those classes which spent more time in the clusters spent less at the edge, and the same rank-order of classes was obtained. However, classes did not differ simply in terms of time spent in the clusters, since they also differed in their distribution about the other four zones (χ^2 69.4, d.f. 15, $p < 0.001$). Differences between classes were more apparent than when the troop was static, since attempts to pool even classes with the most similar patterns produced levels of heterogeneity that approached significance. Chi-square values obtained by pooling adult and subadult males were 9.7 (at d.f. 4, p 0.10-0.05), these and cycling females 14.6 (at d.f. 8, $p < 0.10$), and mothers with lactating females 17.3 (at d.f. 4, $p < 0.01$). Individual and class differences, illustrated in Fig. 3.4, are further discussed below.

3.IV d) The transition from stationary to moving

During movement, subjects were more often recorded at the edges and in the middle, and less often in the clusters, than when stationary (Table 3.IV: ^{2} 60.6, d.f. 2, $p < 0.001$). These tendencies were shown by respectively 20, 28 and 28 of the 31 subjects. Pregnant females showed the strongest tendency to move out of clusters, and mothers the least (Table 3.V).

3.IV e) The spatial pattern of oestrus females

Oestrus females and their consorts were often seen far from the rest, but the sample data give no indication that they spent more time away than usual. Not all of them increased the proportion of time at the edge on days they were consorted - only four of six when stationary, three of five when moving, - and pooling samples from both troop states, 29.4% of their samples were at the edge on non-consort days compared with 32.0% on consort days (n = 470 samples, χ^2 0.15, d.f. 1, $p < 0.70$).

Table 3.IV Comparison of stationary and moving troop, I: Samples from the stationary and moving troop compared for (above) the percent which fell within each zone, and (below) the mean difference over all subjects for the percent of their samples in each zone.

Zone:	Out	Edge	Middle	Clusters	Total Samples
Stationary:	-	30.2	8.5	61.3	2588
Moving:	0.4	33.9	15.2	50.5	1404
Mean difference:		+3.7	+6.8	-10.5	
s.d.		(10.8)	(5.2)	(8.5)	

Table 3.V Comparison of stationary and moving troop, II: Classes compared for the difference in their mean zone probabilities between stationary and moving troop. (Data from Tables 3.II & 3.III).

Class:	Pregnant	Ad.male	Cycling	Sub.male	Lactat.	Mother
Decrease in clusters :	-.14	-.13	-.10	-.09	-.07	-.06
Increase at edge :	+.07	+.07	+.03	+.02	=	+.02

3.V. Results B: Individual differences

Although much individual variation coincided with class-differences, there remained individual variability within classes, apparent in Figs. 3.3 and 3.4. These are now described in relation to agonistic rank and other factors.

3.V a) The effect of leadership

When the troop began to move, some animals would move conspicuously ahead, as though initiating or steering the progression. Individual scores for this behaviour, recorded ad libitum, are listed in Fig. 3.2. The subjects' ranks for this behaviour were positively related to their ranks for amount of time spent at the front (r_s across 8 adult males 0.619, across 19 adult females 0.649): since data for the two measures were not collected independently, the only conclusion is that those animals that appeared to lead at the start of progression also spent more time at the front.

3.V b) The effect of agonistic rank

Theories of social competition, and observations of primate groups, suggest that individual location in the troop may be influenced by agonistic rank. Dominance was assigned in each pair of subjects according to the prevailing direction of avoidances and supplants, and a linear hierarchy was found in each sex (Chapter 6). Accordingly the hypothesis was tested that the time subjects spent in each zone would be linearly related to their agonistic rank. Whole- or part-sample spatial data were used as appropriate within each female class, but whole-sample data were used for the females overall. The results of comparisons are listed in Tables 3.VI & 3.VII. In assessing the probability of each correlation, the middle zone has been ignored because there was not independence between zones (d.f. N-1), and the edge zone in the stationary troop has been ignored because subjects' time there was the inverse of their time in the clusters (for 12 males, r_s - 0.923, $p < .01$: for 19 females, r_s - 0.983, $p < 0.01$).

When the troop was stationary, higher ranking females were more often seen in the clusters, but this was not true of either male class. During movement, this pattern persisted, but the lower-ranking females tended more to the sides and the rear. Again, spatial pattern among males was unrelated to rank.

FIG. 3·2

LEADING - OFF

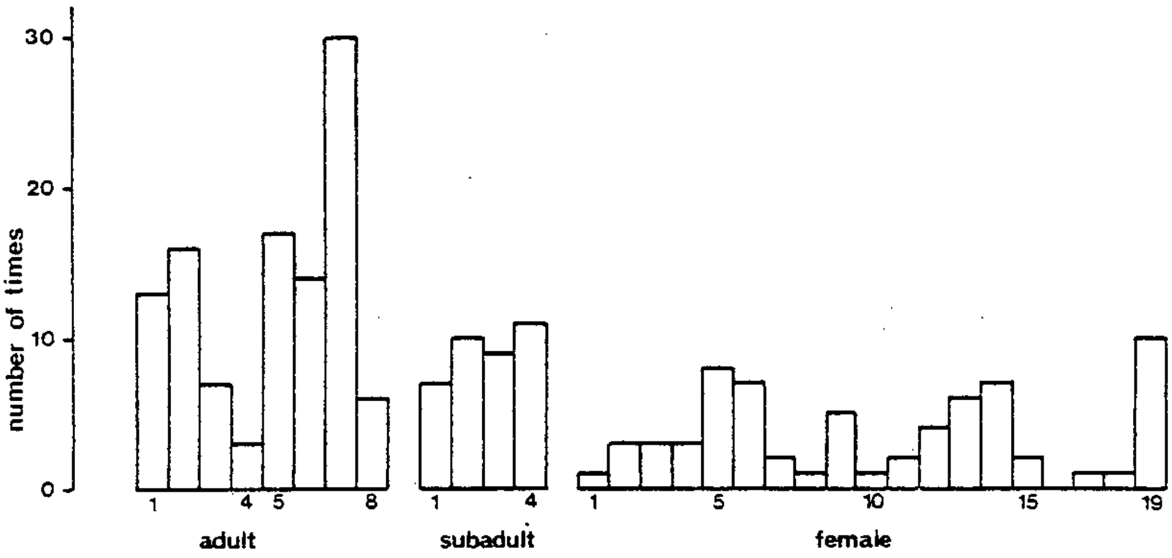


Fig. 3.2. The number of times each subject was seen "leading-off" at the start of progression. Individuals arranged in descending order of dominance rank within class, from left to right.

Table 3.VI

Agonistic rank compared with tendency to spend more time in each zone of the stationary troop. Spearman rank correlation coefficients. Probability estimated only for Clusters, $^{*}p < .05$

Class	n	Edge	Middle	Clusters
Adult males:	8	-.048	.048	-.214
Subadult males:	4	.400	-1.000	-.200
Cycling females:	5	.500	.000	-.700
Pregnant females:	4	-.800	.800	.800
Mothers:	8	-.833	-.071	.810*
Lactating females:	7	.250	-.821	.429
All females	18	-.467	-.183	.534*

Table 3.VII

Class	n	Front	Side	Rear	Middle	Clusters
Adult males:	8	.286	.119	-.690	.214	.190
Subadult males:	4	.200	.800	1.000	-.400	-.200
Cycling females:	5	.200	.100	-.154	.100	.400
Pregnant females:	4	.400	-1.000	-.800	.800	.800
Mothers:	8	.216	-.205	-.886**	.405	.934**
Lactating females:	7	.786*	.857*	-.571	-.714	.214
All females	18	.210	-.499*	-.768**	.020	.594**

Agonistic rank compared with tendency to spend more time in each zone of the moving troop. Spearman rank correlation coefficients. Probability not estimated for Middle, otherwise $^{*}p < 0.05$, $^{**}p < 0.01$.

Further spatial variation with rank will be discussed, separately for each class, below.

3.V c) Variation among females

(i) Cycling females

The mean zone probability of cycling females differed little from the overall average, apparently because they varied about equally above and below the mean (Figs. 3.3 & 3.4). Their variation was not related to their rank (Tables 3.VI & 3.VII). Resumption of cycling coincided with a decrease in time spent in clusters, more obvious during movement (all five females decreased) than when static (only three of five decreased). F5 was one of the few animals who spent more time in clusters when moving: F6 spent very little time there, and tended to travel at the side, while F17 often travelled at the rear.

3.V c.(ii) Pregnant females

Overall, pregnant females were the most peripheral female class (Tab 3.II & 3.III), and the two lower rankers were the most extreme: the tendency to travel at the side was in linear order of rank (Table 3.VII). F19 was unusual in that during movement her time at the edge increased by 20%.

3.V c.(iii) Mothers

Mothers spent more time in the clusters than any other class (Tabs 3.II & 3.III), but this was more pronounced for higher-ranking mothers (Tabs 3.VI & 3.VII). From Figs. 3.3 and 3.4 this is mainly because the four above median rank spent most time in clusters, and F2, F3 and F8 actually increased their time there during progression.

The two females who gave birth, F12 and F18, increased their overall time in the clusters thereafter by 8.0 and 22.2% respectively, but still did not spend as much time there as the mothers of older infants. Both tended to travel at the rear, along with F16 who was undersized and seemed encumbered by her infant. The tendency for lower-ranking mothers to travel more at the rear was a compound of the fact that these slower females were below median rank, and because the lower rankers among the other five also tended to the rear.

Figs 3.3 & 3.4 (next two pages). The spatial pattern of troop-members when stationary (Fig. 3.3) and during troop progression (Fig. 3.4). The layout of these figures is the same, except that the former has three zones, the latter five. The top row in both shows the mean probability of all classes in each zone. The body of the table shows the percent of time every class-member spent in each zone, expressed as the deviation above or below the overall mean (which therefore forms the x-axis of each diagram: thus the baseline for all Edge diagrams is 31.2%). This allows comparison of the classes for their tendency to be seen in each zone, while still representing the amount of variation within each class.

Class-members are arranged in descending dominance rank order from left to right. The number of samples from which each subject's score was calculated is indicated on the far right below the name of the class, in the same order as that of the individuals on the diagram: however some sample-numbers are offset vertically to save space, so that the order for mothers which corresponds to their order on Fig. 3.3 is 37, 85, 77, 87 etc.. The width of the vertical bars is related to these individual sample-size differences, in three categories from thinnest (< 20 samples) through medium (21 to 40) to thickest (41 or more); this is most apparent on Fig. 3.4.

Class-members within male classes may be identified by their rank position: thus for adult males, A1 is on the left, A8 on the right. Female subjects are dispersed about the classes as follows, listed in the order they appear on the tables. Whole-sample contributions are underlined.

Cycling;	F5	F6	F7	F13	F17			
Pregnant:	F9	F12	F18	F19				
Mothers:	F1	F2	F3	F8	F12	F14	F16	F18
Lactating:	F4	F6	F7	F10	F13	F15	F17	

FIG 3·3

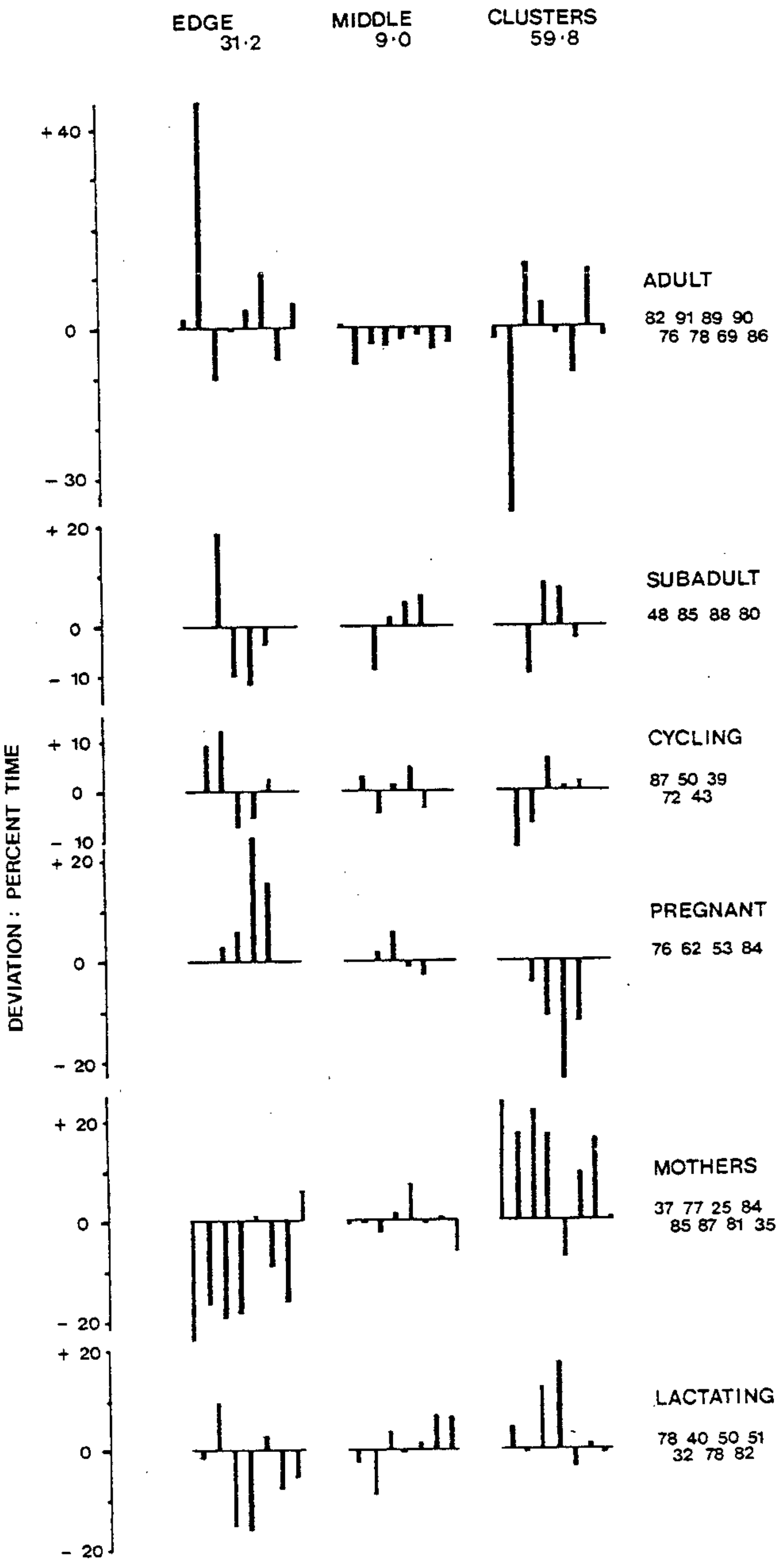
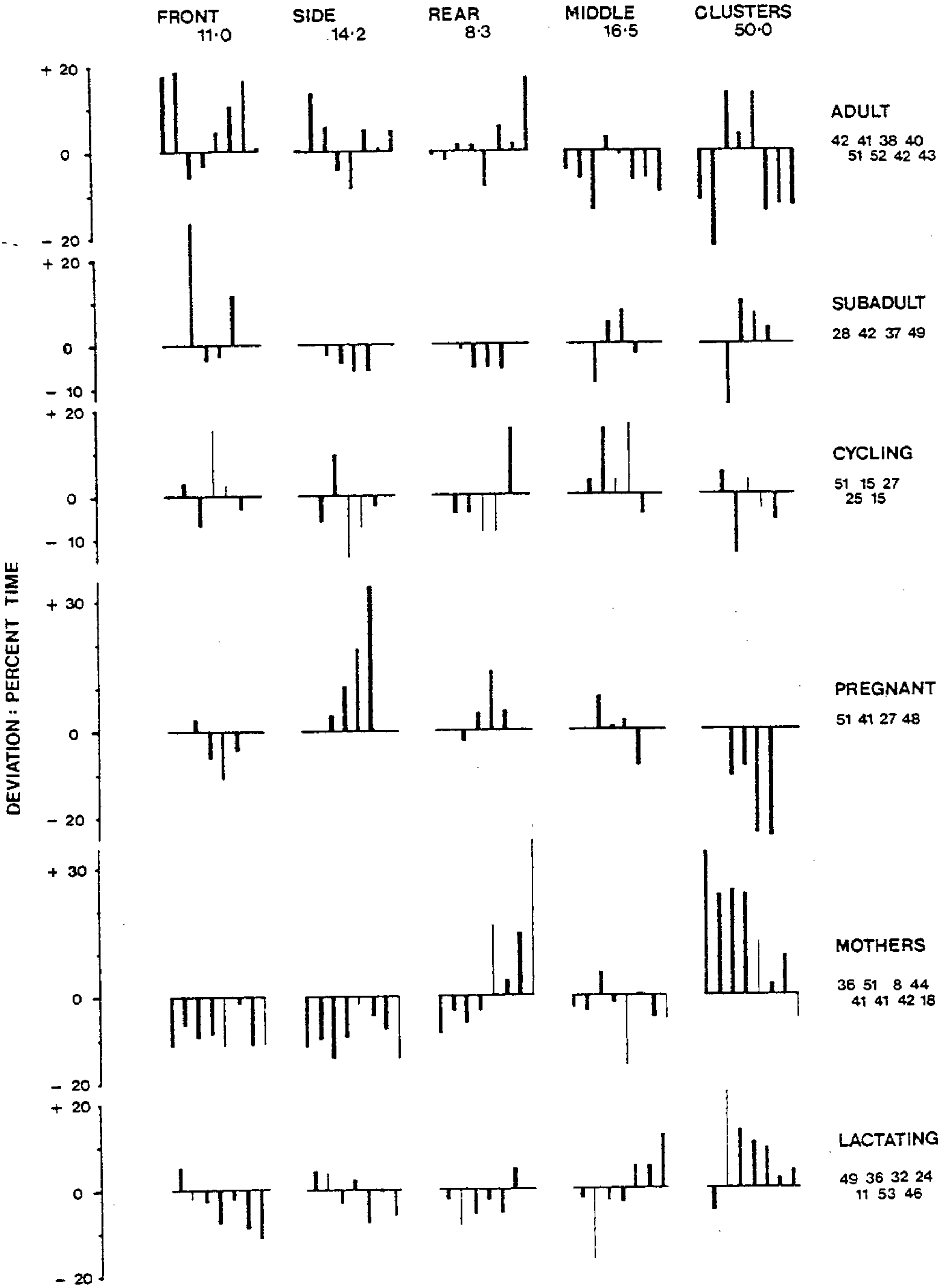

EDGE
31·2
MIDDLE
9·0
CLUSTERS
59·8
DEVIATION : PERCENT TIME
+ 40
0
− 30
ADULT
82 91 89 90
76 78 69 86
+ 20
0
− 10
SUBADULT
48 85 88 80
+ 10
0
− 10
CYCLING
87 50 39
72 43
+ 20
0
− 20
PREGNANT
76 62 53 84
+ 20
0
− 20
MOTHERS
37 77 25 84
85 87 81 35
+ 20
0
− 20
LACTATING
78 40 50 51
32 78 82

FIG 3·4


FRONT 11·0
SIDE 14·2
REAR 8·3
MIDDLE 16·5
CLUSTERS 50·0
DEVIATION : PERCENT TIME
+ 20
0
− 20
+ 20
0
− 10
+ 20
0
− 10
+ 30
0
− 20
+ 30
0
− 20
+ 20
0
− 20
ADULT
42 41 38 40
51 52 42 43
SUBADULT
28 42 37 49
CYCLING
51 15 27
25 15
PREGNANT
51 41 27 48
MOTHERS
36 51 8 44
41 41 42 18
LACTATING
49 36 32 24
11 53 46

3.V c.(iv) Lactating females

The lactating females' spatial pattern was similar to that of mothers, but less extreme. The high cluster score of F7 and F10 reflected frequent association with mothers (Chapter 4), but during movement F10 decreased her time in clusters by as much as 16.0%. The higher rankers tended more to the front and the sides (Table 3.VII), and this pattern was shown by F4 despite her being apparently the oldest female in the troop.

3.V c.(v) Atypical females (Chapter 2 III c.(iii))

The amounts of time that F1 and F11 spent in each zone are listed in Table 3.VIII. Comparison with the class zone probabilities in Tables 3.II & 3.III show that F1's pattern remained that of a mother despite her resumption of cycling, amounting to 86.6% of time in the clusters overall. The sick F11 also maintained her very peripheral position little affected by resumption of cycling. Her spatial pattern, with its tendency to the rear and sides, resembles most that of pregnant females.

3.V d) Variation among males

(i) Subadults

There were marked individual differences between subadults that bore little relation to dominance rank (Figs. 3.2 & 3.3). S1 was extremely peripheral and often travelled at the front. S2 and S3 resembled lactating females in their tendency to the clusters, while S4 was intermediate in that he showed some tendency to the clusters but also travelled at the front.

3.V d.(ii) Adults

Adult males differed markedly in their spatial pattern, but not in direct relation to their rank. In the stationary troop, A2 was exceptionally peripheral (being approached in this only by S4 and F11), A6 rather less so, while the others varied evenly with only A3, A4 and A7 very often in clusters (Fig. 3.3). During progression, however, two subsets emerged (Fig. 3.4); three adults remained in the clusters, A3, A4 and A5 (whose clustering score actually increased): whereas A1, A2, A6, A7 and A8 travelled at the edge. A7 was unusual in that he was prominent in the clusters when stationary but at the

Table 3.VIII

Percent of samples in each zone by the two atypical females, F1 and F11

	Stationary:				Moving:					
	Edge	Middle	Clusters	n	Front	Side	Rear	Middle	Clusters	n
F1 mother:	7.5	7.5	85.0	(40)	0	2.8	0	13.9	83.3	(36)
F1 cycling:	6.5	4.4	89.1	(46)	7.1	0	0	14.3	78.6	(14)
F11 lactat:	52.0	8.0	40.0	(50)	7.4	22.2	25.9	18.5	25.9	(27)
F11 cycling:	56.4	10.3	33.3	(39)	8.7	26.1	34.8	4.4	26.1	(23)

front during progression. Thus the adults who travelled most at the edges were the two newcomers and the three post-prime males. The slight tendency for low-ranking males to the rear (Tab 3.VII) was not linear and was mainly due to A6 and the aged, slow-moving A8.

3.V d.(iii) Comparison of the adult males' spatial and social differences

Because the position of particular males has been disputed (refs. in Introduction), the amount of time each adult spent in clusters was compared with social parameters derived from the chapters that follow (Table 3.XIX). Adult males' ranks for time in clusters when stationary were correlated with those during progression (r_s 0.786, n 8, $p < 0.05$), and pooling both troop states it is clear that A3 spent most time in clusters, often with A7, A4, and A5. A1 and A8 spent about half the time in clusters, while A6 spent less and A2 very little. Their tendency to be in clusters was independent of their rank (r_s - 0.214, n 8, n.s.). Because the female classes had differed in the time they spent in clusters, it seemed likely that males' time there would reflect their association with females (Chapter 4), and this was indeed the case. The males seen most often in clusters were associated more with mothers (r_s 0.833, n 8, $p < 0.05$), and progressively less with lactating females (r_s 0.262, n 8, n.s.), and cycling females (r_s - 0.071, n 8, n.s.) and least with pregnant females (r_s - 0.643, n 8, n.s.). During travel females maintained proximity to males more than the reverse (except those females who were followed by their male consorts), which implies that the males with high clustering scores during travel were those whom the mothers followed, in this case A3, A4 and A5. The fact that A7 left the clusters for the front during progression was at least in part because the females did not move with him, and the increase in A5's cluster score at this time implies that the mothers preferred to travel with him instead.

Table 3.XIX

Comparison of adult males for spatial and social parameters. The scores in each column apply to the males listed in order of dominance rank on the left.

Rank:	Cluster:			Total neighbour-frequency with females			
	Static	Moving	Overall	Cycling	Pregnant	Mother	Lactating
1	57.3	38.1	48.8	57.9	4.5	1.6	8.7
2	22.3	27.5	24.4	20.2	19.4	5.4	4.7
3	73.6	63.8	70.5	24.4	5.3	27.5	15.3
4	64.1	63.2	60.0	16.8	6.9	21.4	17.6
5	58.4	53.8	59.8	12.4	5.4	27.1	19.4
6	50.7	35.7	45.0	7.0	11.4	17.6	15.8
7	71.1	37.5	60.8	6.9	1.5	46.6	13.0
8	58.1	37.2	51.2	9.8	6.8	15.0	20.3

Measures used: Cluster is the percent of the subject's samples for which he was in a cluster. Female neighbour-frequency is the percent of his association samples for which a female in each class was scored nearest female.

VI. Discussion

3.VI a) General points

It was striking that the troop spent so little time in fast, compact progression - only 5.3% of progression time, compared with 62% of all progressions reported by Rhine (1975). It suggests either that such a formation was not very important as an anti-predator device at Ruaha, or more likely that baboons only close ranks in places of danger. The commoner formation, of slow progression over a broad front, is more efficient during foraging (Altmann S. 1974).

Evidence of predation risk is notoriously hard to obtain. In the ten predator-sightings in this study (seven during the 445 observation-hours) the troop ignored three (lion once, jackal twice), showed vigilance and gave alarm calls in five (lion, leopard, hunting-dog, two unknown), and twice they chased leopards although these may have been avoiding the observers. Many animals, including juveniles and a pregnant female, joined in these chases, but only adult and subadult males confronted the leopard closely. Adult male 3 was reportedly killed by a leopard at night after the end of this study (Ngatwika, pers. comm.). Alarm calls were given by females and juveniles as often as by adult males. These findings, and the ability of males to survive on their own (Chapter 8) suggests that predation risk by day was slight, and unlikely to be an important proximal factor determining individual placement in the troop.

There was tentative evidence that individuals' involvement in initiating or directing troop travel may have determined their position in the troop. Mobility differences were also clearly important in some cases: the animals seen most at the rear included one female during pregnancy, both of those with very new infants, an undersized mother, the sick female and the oldest male. Mobility may also explain the tendency of some subadults and the young adults at the front.

3.VI b) The spatial pattern of females

(i) Reproductive class differences

Mothers were seen most often in clusters. The fact that this was decreasingly true of subsequent reproductive classes suggests that females spend progressively less time in clusters as their infants age. This results in a sharp contrast between mothers and pregnant females which is not easily explained theoretically.

Both these classes are likely to be more vulnerable to predation, being probably less mobile and having infants at stake. They both also have higher nutritional requirements than other females (Portman, 1970): in theory, the requirement is greatest for mothers (Altmann J. 1980, and references therein), and there is good field evidence that pregnant females spend more time feeding than most (Post et al., 1980). Therefore if predation risk is crucial, both classes might favour the safety of the clusters, but only mothers do this. Conversely, if feeding efficiency is crucial, they might move to the edge to avoid competition, but only pregnant females do this. The requirement for food might be expected to outweigh the risk of predation (Altmann and Altmann, 1970). However, the classes' only similarity is a tendency to the rear, perhaps caused by the weight of their infants.

It is not clear why their spatial pattern should differ when their requirements are so similar, but other evidence suggests that the proximal cause is a social one. Infants are particularly attractive to other troop members, (Rowell, Din and Omar, 1968; Altmann J. 1980), so that mothers are the focus of much attention and interaction (DeVore, 1963; Seyfarth, 1976). This may even be sufficient to stress the mother (Altmann J. ibid), but at the same time infants may gain valuable social experience, and they certainly gain protection from those adult males in the clusters (Hall, 1963). Safety in numbers would naturally follow. In contrast, pregnant females lack this attractiveness, and they tend to be lethargic and to initiate fewer interactions (Rowell, 1972; Saayman, 1971a, 1972), a pattern shown by three of the four in this study. These four also received relatively little agonism from other females, particularly supplants (Chapter 6). Such reclusiveness may conserve energy (Smith, 1977) and avoid social stress, which is particularly important during pregnancy (Myers, 1972; Holm, 1979). However, it is also very likely that they would have obtained more food at the sides. So that while it is not clear whether feeding or social factors were more responsible for the pregnant females' behaviour, it remains that their contrast with mothers is primarily a social one.

3.VI b.(ii) Agonistic rank differences

Spatial patterns in which high or low rankers are over-represented in any zone may provide evidence of competition, with low rankers excluded from food or favoured social partners. But such patterns might also result if high rankers are more attractive, as reported for females by Seyfarth (1976). The data here cannot distinguish these two factors.

High ranking females were seen more in clusters, both when stationary and during movement. If low rankers had moved out to avoid competition, they may have succeeded, because low-ranking females were not supplanted any more than high rankers (Chapter 6). Alternatively, this pattern may reflect the attractiveness of high rankers, since it was most obvious among mothers, the most attractive class, and because this pattern persisted during movement, when supplanting was comparatively less frequent (Oliver, pers. comm.).

The tendency of low ranking females to the rear may be explained by converse arguments to the above: but it might also be explained if weaker animals are both slow and of low rank. This pattern among mothers was discussed previously (V c.(iii)). The tendency for lower ranking pregnant females toward the side suggests the importance of feeding competition, since their food requirement is so high, but it is inconsistent with the tendency for higher ranking lactating females to spend more time at the side and the front. Such problems require detailed data on what baboons do, and how much competition they encounter, in each zone.

3.VI (c) The spatial pattern of males

The males' spatial patterns showed striking differences which were not directly related to dominance rank or class. The most peripheral ones overall were the two newcomers and the subadult who emigrated (all three of whom might be expected to be outsiders socially as well as spatially), and the post-prime adult 6. During progression, the presence of the two highest ranking adults at the front and the lowest ranker at the rear, illustrate a rank-related trend noted by other authors (e.g. Rhine, 1975); but the presence of A6 and especially A7 near the front detract from this. Similarly the tendency of subadults 1 and 4 to travel at the front exemplify the conclusion of Rhine *et al.* (1979) about subadults: but S2 and S3 tended more to the clusters, although when they were at the edge they also travelled more at the front.

The presence of the two newcomers, the three post-prime adults, and the oldest subadult at the edge during progression would originally have been explained in terms of their role as protectors to the troop (e.g. Washburn and DeVore, 1961). Apart from reasons of mobility and leadership already mentioned, there are a number of reasons why males might tend to the edge. By virtue of size and dentition they are best able to defend themselves, and both Rhine (1975) and Harding (1977) suggest they are 'bolder' than females. And they might certainly have had offspring to protect: the oldest A8 was subjectively the most active in giving predator alarms. Since males also migrate between troops, peripheral position may allow them to monitor other troops (Rhine et al., 1979), although during this study such troops were not visible for more than five percent of the time (Oliver pers. comm.). Males are also twice as heavy as females, and might frequent the edge to obtain more food, but field evidence suggests they do not spend more time feeding than do females (Dunbar, 1977; Rhine and Westlund, 1978; Post et al., 1980).

On the other hand, males may gain advantages within the clusters, notably in that they may protect females and young directly against aggressors within the troop, and they may obtain social buffering against other males either through association with females (e.g. Packer, 1978) or by using infants (Deag and Crook, 1971; Packer, 1980). These short-term benefits are less equivocal than those at the edge, and it is curious that some males, by being in the clusters, had access to them more than did others. These males were the prime adults A3, A4, A5 and the post-prime A7. These males will be referred to subsequently as the focal males, defined as those who spent most time with mothers. The fact that the non-focal adults were the young newcomers and the post-prime males suggest that adults are most likely to become focal in their prime. Since three of these focal males were the ones the mothers preferred to travel with, and the fourth (A7) interacted with mothers often (Chapter 4) it seems likely that males become focal by establishing affiliative relationships with females. The newcomers appeared not yet to have done so, and the females appeared no longer to prefer the ageing males. There was little evidence that aggression against non-focal males was sufficient to force them to the periphery (except for occasional 'gang-attacks' on newcomers: Chapter 6), but the possibility remains that the focal males were excluding them by subtler means.

CHAPTER 4

Affiliative relations

PART 1. INTRODUCTION

4.1.1 Baboon troops comprise a number of related females and their offspring, with a complement of breeding males born elsewhere (refs. in Chapter 1). The affiliative relationships that have been described reflect this pattern. Thus the mother-infant bond is strong, and persists through the adult-life of both mother and daughter (DeVore, 1963; Moore, 1978; Altmann, 1980). Bonds between female kin may therefore be the most stable in the whole troop. However females may establish relationships with those outside their immediate family (Strum, 1975), and Seyfarth (1976) has shown that high-ranking females and mothers with new infants are particularly attractive in this way.

Male offspring, on the other hand, do not develop such strong ties, but as subadults show greater interest in other troops and eventually transfer elsewhere to breed (Cheney and Seyfarth, 1977; Packer, 1979a). Perhaps because a troop's adult males are therefore immigrants, their affiliative relations are more transitory, but two are obvious and well documented. First, there is an attraction between males and cycling females which culminates in consortship and mating at midcycle (Hall, 1962 ; DeVore, 1965; Saayman, 1970; Hausfater, 1975). Secondly, mothers with young infants are often associated with some of the adult males (Hall and DeVore, 1965; Saayman, 1971b). In some cases relationships between male-female pairs may persist through both cycling and lactation (Ransom and Ransom, 1971; Seyfarth, 1978b; Altmann, 1980), although not all partnerships persist in this way (Seyfarth *ibid*.).

The adult males' relationships with one another are little documented, being usually characterised as antagonistic. However males often ally together during aggression (Hall and DeVore, 1965; Packer, 1977b).

The aim in this chapter is to describe the pattern of affiliative relations in the troop in terms of *association* and of *grooming*. A third behaviour which may be affiliative, namely alliance in aggression, is discussed in Chapter 6. These two are described in turn. Each is analysed first to look for differences due to sex and reproductive state as reported in the studies cited above. Secondly, individual differences in the frequencies of these behaviours are compared with dominance rank. This is to test the hypotheses that high rankers may attract more affiliative behaviour (Seyfarth, 1976; Stammbach, 1978), or may be more successful in gaining access to favoured partners. Thirdly, dyadic frequencies within each sex are compared with the distance in dominance rank between the participants. This is because among females competition may force close-rankers to groom more (Seyfarth, 1977), and because kin-based affiliation may coincide with closeness in rank (discussed further in 4.3.1). Association at each rank-difference among males is examined because competition may be more intense between close-rankers (Chapter 6). Finally, the patterns of dyadic relations are portrayed and discussed.

PART 2. ASSOCIATION

Association between pairs was estimated by the frequency with which each subject was the nearest neighbour of its sex to each other. There are drawbacks in this measure (described below), but it is assumed that proximity provided evidence of affinity. However, while established relationships may well be revealed by the distance between two animals (Carpenter, 1952), not all affinities need be apparent because of competition or inhibition (Vaitl, 1978). This is an argument that applies also to social interactions. Secondly, while it may be true that the distance between members of small primate groups is a compromise between attraction and repulsion (Kummer, 1969 p.222) yet Msembe troop was so large that troop-members were not constrained to be close at all. Therefore more emphasis is here placed on association than on lack of it.

4.2.1 Methods

The data presented here were derived from instantaneous samples on each subject, recording on the minute the identity of nearest male subject and nearest female subject within 15m (2 V-VIII). These data indicate the amount of time for which each was nearest neighbour of its sex to each subject, in terms of dyadic neighbour frequencies (2 XII b), using whole or part sample data, 2 XII a): from these were calculated each subject's mean dyadic neighbour frequency across all members of an associate class (as in 2 XII a).

4.2.2 Interpretation

In a high proportion of samples of both male and female neighbours, there was no neighbour at all within 15m. Therefore no single neighbour could have absolutely excluded any other from being nearest to any subject over the whole study. But the practice of recording only the nearest may have masked others who were not so close, because it measures relative rather than absolute proximity. This has two consequences. First, if F1 usually has A1 as nearest male, but F2 is usually even nearer to A1, then F1 will seldom appear in A1's records although A1 will regularly appear in F1's records. Thus the reciprocal cells of nearest neighbour records are not truly reciprocal, and for this reason they have not been pooled in analysis. Secondly, the extent to which the nearest neighbour masks other nearby associates of its sex depends on the number of potential neighbours in that sex: each associate's chances of being nearest decreased if there were more other potential associates. In this study such masking affects female neighbours (n=19) more than males (n=12), so that mean frequencies of female neighbours tend to be lower than those for male neighbours (Table 4.1). Since these measures of male neighbour frequency and female neighbour frequency are therefore not comparable, the following analyses are limited to comparisons within, but not between, these measures.

4.2.3 Overall neighbour frequency

Over 98% of all possible pairs were associated as subject and neighbour at least once, so there was much mixing. Pairs spent an average of 3.55% (s.d. 3.13) of the time as nearest neighbours: the mode was between 1.50 and 2.50%, and the range from nought to 44.44%.

4.2.4 Sex-differences in association

Mean neighbour frequencies within and between sex are compared in Table 4.1. There was no general tendency for females to have male neighbours more often than males did, but females had female neighbours more often than males did ($p < .05$). This was almost entirely due to the high female-neighbour scores of the mothers (4.2.5(b) below).

Table 4.I

Association within and between the sexes. Mean dyadic neighbour-frequencies of male and female subjects with (a) male neighbours, and (b) female neighbours. Data from F11 are excluded.

	Mean	s.d.	Mann-Whitney
(a) Male neighbours			
Male subjects	3.82%	.80	U=77. n 12,18
Female subjects	4.15%	.84	$p > .10$ n.s.
(b) Female neighbours			
Male subjects	3.15%	.61	U=57. n 12,18
Female subjects	3.59%	.47	$p < .05$

4.2.5 Class-differences in association

Mean neighbour frequencies between classes are listed in Tables 4.II and 4.III. There are several paradoxes in that the scores for association between any pair of classes vary depending which class is considered as subject. This is partly because of the masking effect described above (4.2.2), but also due to lack of uniformity within-class. Thus all mothers had male neighbours frequently, but not all males had mothers as frequent neighbours. Reciprocal scores are compared in Table 4.IV, but the differences only attain significance in the case just described.

4.2.5a) Association between male classes: Male pairs were associated as nearest neighbours for an average of 3.82% of the time. Table 4.IIa) shows some class variation from this, but no significant differences were found: Fig. 4.1 suggests that subadults spent slightly more time near males than did adults.

4.2.5b) Association between female classes: Female pairs were associated as nearest neighbours an average of 3.59% of the time, but reproductive classes differed significantly (Table 4.IIb: $p < .01$). Mothers had female neighbours most often (Fig. 4.2), and successive reproductive stages had fewer. The neighbours of each class were drawn randomly from the reproductive classes except those of mothers ($p < .01$), of whom all but one had other mothers as the most frequent neighbour class.

4.2.5c) Association between the sexes: Female classes did not have male neighbours equally often (Table 4.IIIa: $p < .01$). Cycling females, and mothers, had male neighbours relatively frequently (Fig. 4.2). These males tended to be adults more often than subadults, significantly so for mothers ($p < .02$), and over the whole study for most of the 18 females ($T=2$, $p < .01$).

The associations of male subjects reflect these findings (Table 4.IIIb). Adult males had female neighbours more often than did subadults ($p < .03$), but neither class showed consistently high association with females in particular reproductive states. However, a number of males had cycling female neighbours very often, and some had mothers (Fig. 4.1).

As noted above, all mothers had adult male neighbours comparatively frequently, (between 4.08% to 6.74%), but these did not include all of the adult males (range 0.22% to 8.89%).

Table 4.II Association within each sex

Mean dyadic neighbour-frequencies between classes within-sex. Standard-deviations in brackets. Results of statistical comparisons are listed at the foot of the relevant column, or at the end of the relevant row.

(a) Male-male

	Neighbours			
Subjects	All males	Adults	Subadults	Wilcoxon
Adults (8)	3.51 (.53)	3.18 (.59)	3.84 (1.00)	T=6.5 n.s.
Subadults (4)	4.44 (.97)	4.41 (1.05)	4.49 (.96)	no test
Mann-Whitney	U=6. n.s.			

(b) Female-female

	Neighbours					
Subjects	All females	Cycling	Pregnant	Mothers	Lactating	Friedman χ^2_r
Cycling (5)	3.18 (.38)	2.79 (1.43)	4.39 (3.11)	3.14 (.75)	3.31 (.65)	1.86 n.s.
Pregnant (4)	2.99 (.46)	2.63 (1.19)	3.60 (1.46)	2.71 (.84)	3.43 (.71)	2.70 n.s.
Mothers (8)	4.07 (.15)	2.93 (.90)	2.30 (1.17)	6.04 (1.17)	2.98 (1.08)	15.36 p .01
Lactating (7)	3.25 (.38)	2.54 (1.77)	3.03 (1.12)	3.88 (1.53)	3.30 (.58)	0.43 n.s.
Kruskal-Wallis	H=15.35 $p < .01$					

Table 4.III Association between the sexes

Legend as for Table 4.II. Mean percent, with standard deviations.

(a) Female subjects

	Neighbours All males	Adults	Subadults	Wilcoxon
Subjects				
Cycling (5)	5.37 (1.07)	6.35 (1.81)	3.18 (1.69)	no test
Pregnant (4)	3.19 (.89)	3.55 (1.20)	2.49 (.88)	no test
Mothers (8)	4.37 (.52)	5.13 (.91)	2.54 (1.38)	T=1 $p<.02$
Lactating (7)	3.51 (.75)	3.60 (.76)	3.15 (1.31)	T=8 n.s.
Kruskal-Wallis	H=11.89 $p < .01$			

(b) Male subjects

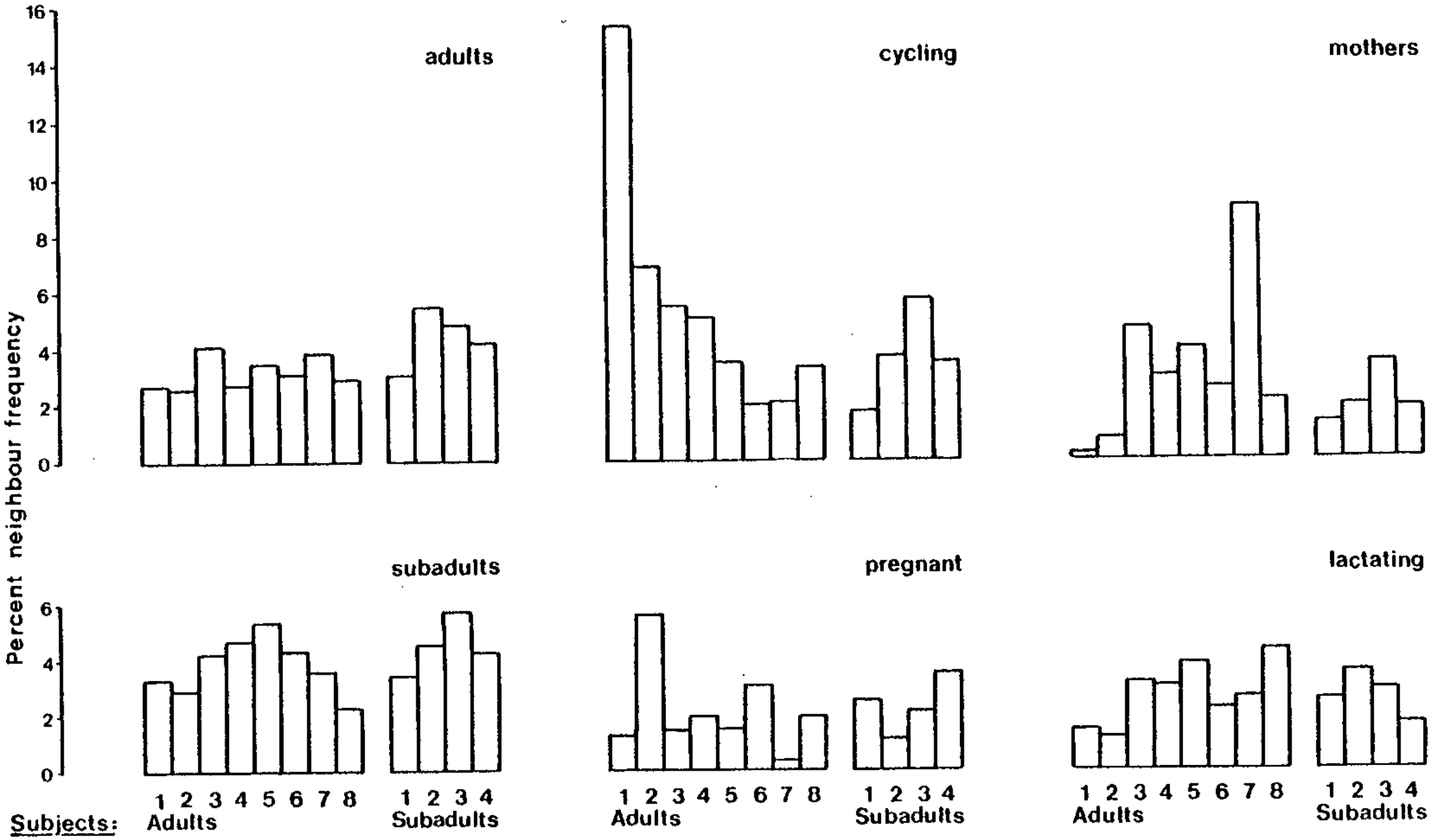
	Neighbours All females	Cycling	Pregnant	Mothers	Lactating	Friedman χ^2_r
Subjects						
Adults (8)	3.39 (.55)	5.45 (4.33)	2.14 (1.58)	3.21 (2.70)	2.22 (1.29)	5.06 n.s.
Subadults (4)	2.66 (.41)	3.76 (1.64)	2.33 (1.00)	2.14 (.92)	2.63 (.77)	2.50 n.s.
Mann-Whitney	U=3 p .028					

Table 4.IV

Results of Mann-Whitney U tests comparing the subjects' scores of dyadic mean neighbour-frequency between reciprocal class-pairs.

	Subadult males	Females:			
		Cycling	Pregnant	Mothers	Lactating (7)
Males:					
Adult (8)	11 p .46	11 p .46	6 p .11	10 p .02	14 p .12
Subadult (4)		7 p .56	7 p .89	12 p .57	10 p .53
Females:					
Cycling (5)			6 p .41	18 p .83	13 p .53
Pregnant (4)				11 p .46	8 p .32
Mothers (8)					21 p .46

FIG. 4.1



Neighbour-classes

Fig. 4.1. The associates of males. Male subjects' mean dyadic neighbour frequencies with members of each class. Each bloc contains histograms for 8 adult males (left) and 4 subadults (right), subjects in descending order of dominance rank within class from left to right. Male neighbours are divided into adults and subadults, females are divided according to reproductive state. The absolute frequencies with male neighbours cannot be compared with those with female neighbours (4.2.2).

FIG 4.2

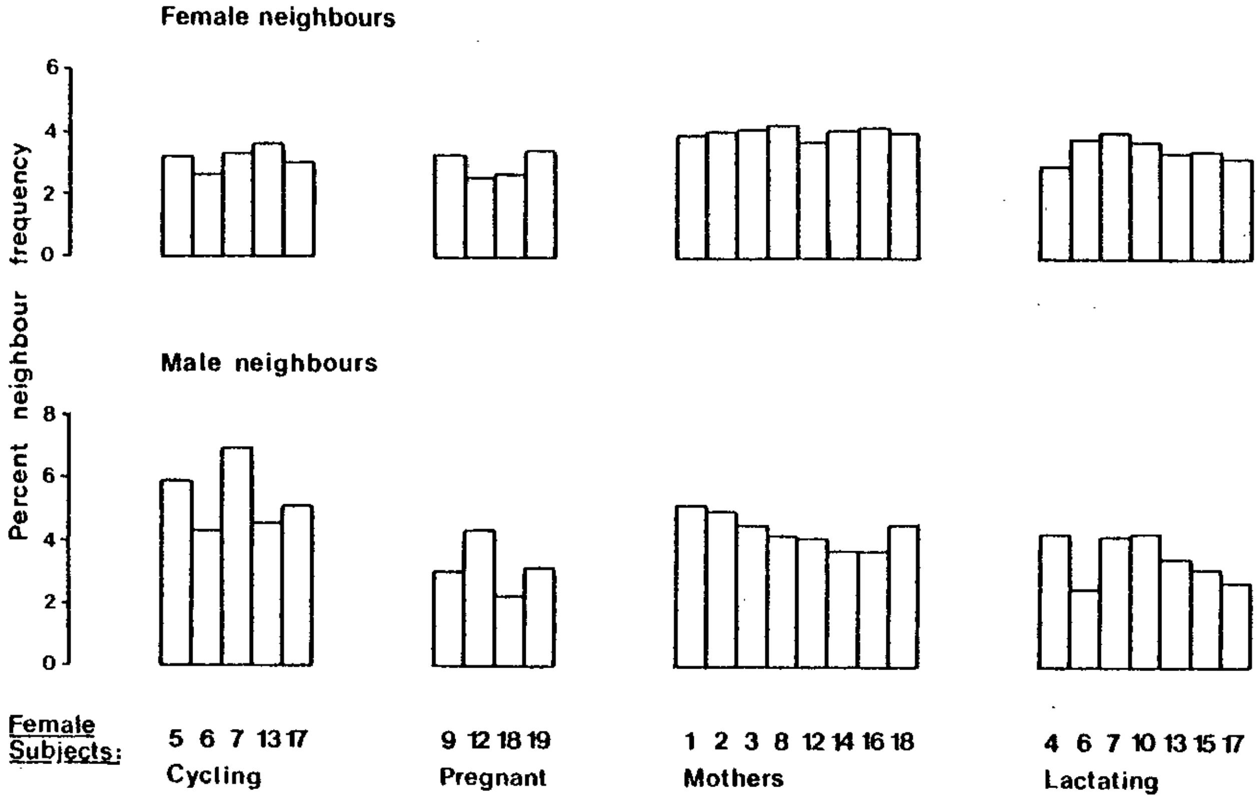


Fig. 4.2. The associates of females of each reproductive class. Mean dyadic neighbour frequencies with females and with males: part-sample data used for subjects who changed reproductive state. Class-members in descending order of dominance rank from left to right.

4.2.6 Mothers' association and infants' age

The data in Table 4.IIb) are consistent with previous reports that the attractiveness of mother-infant pairs declines as the infants age; the mothers' scores were further compared to see if the same trend was apparent during the infants' first six months. The mothers' rank-order for increasing age of the infant was unrelated to their ranks for association with males (r_s 0.190), females (r_s -0.357), or other mothers (r_s -0.143), with n=8 in all cases. It is clear in Fig. 4.2 that those with the newest infants, F12 and F18, did not differ markedly from the rest, except that F18 spent more time near males than expected from the dominance rank trend within her class. However the mean dyadic association frequency between these two females (11.51%) was far higher than their association with the six mothers of older infants (4.39%), whose mean association together was 6.70%.

4.2.7 Agonistic rank and association frequency

Class-members' rank-orders for dyadic neighbour frequency with other classes were compared with their agonistic ranks (Table 4.V). Of 38 coefficients, less than one are expected to exceed 1% significance by chance alone. It is concluded that higher-ranking adult males had cycling female neighbours more ($p < .01$, Fig. 4.1) and that higher ranking females had male neighbours more ($p < .01$, Fig. 4.3), a tendency also apparent among mothers.

4.2.8 Agonistic rank-difference and association frequency

The mean dyadic neighbour frequency within sex was compared for dyads at each rank-difference, as described in 2 XIII c. Fig. 4.4 shows that association frequency was independent of rank-difference among males (r_s -0.476, n=8, n.s.) and among females (r_s 0.191, n=14, n.s.). Furthermore, Table 4.VI shows no clear tendency for first neighbours to be within two places of rank, except weakly among males. The tendency for disparately ranked males to associate more is because subadults (of low rank) were associated with prime adults (above median rank; 4.2.9a).

Table 4.V Neighbour-frequency and dominance rank

Subjects' dominance ranks compared with their ranks for association with each neighbour-class by Spearman rank correlation coefficients. Subjects listed on left. $^{**}p < .01$

	Neighbours		Female neighbours			
	All males	All females	Cycling	Pregnant	Mothers	Lactating
Subjects						
Males:						
Adults (8)	-.405	.286	.905**	.048	-.429	-.595
Subadults (4)	-.100	-.400	-.400	-.400	-.400	.400
Females (18)	.752**	.121				

	All males	Adult males	Subadults	All females	Cycling	Pregnant	Mothers	Lactating
Females:								
Cycling (5)	.100	.500	-.700	-.200	.400	-.100	-.800	-.718
Pregnant (4)	.000	.000	.400	-.400	-.400	-.800	-.400	.949
Mothers (8)	.619	.238	.619	-.143	-.238	-.691	.071	.310
Lactating (7)	.378	.607	.321	.179	-.571	.143	.250	-.357

FIG. 4.3

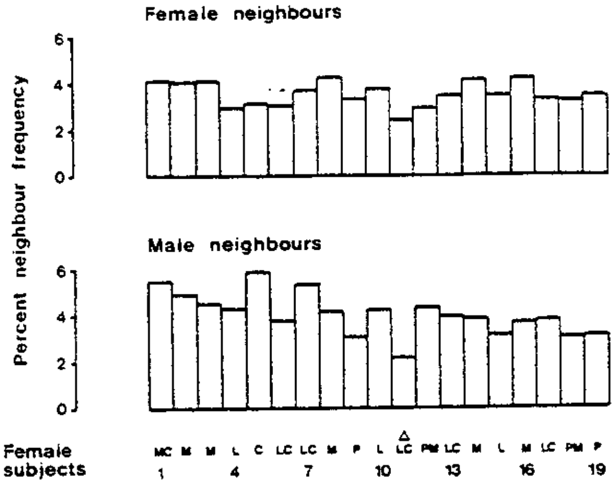


Fig. 4.3. The associates of females. Mean dyadic neighbour frequency with each sex, the subjects arranged in descending order of dominance rank from the left, and using whole-sample data for each subject. The two measures are not comparable (4.2.2). Females are C - cycling, P - pregnant, M - mothers, L - lactating. The sick female included △ .

FIG. 4.4

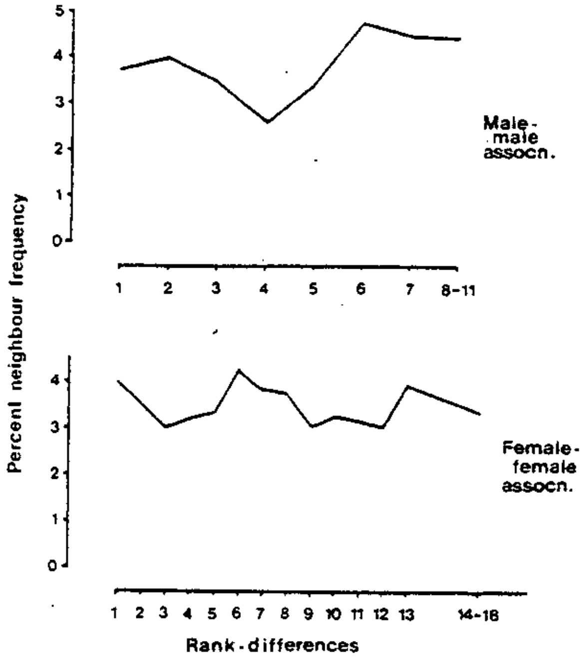


Fig. 4.4. Rank-difference and association frequency. Mean dyadic neighbour frequencies within sex for pairs at each rank-difference: adjacent rankers have rank-difference of 1; the more distant rank-differences have been pooled.

Table 4.VI

The numbers of first neighbours within and beyond two places of dominance rank compared with those expected from availability of partners.

(a) Association between males

	Rank-places	
	1-2	3+
observed	5	6
expected	3.5	7.5

binomial test: p .520

(b) Association between females

	Rank-places	
	1-2	3+
observed	3.8	14.2
expected	3.7	14.3

binomial test: $p \leq 1.00$

4.2.9 Dyadic relationships

The more frequent neighbour associations between pairs of animals are portrayed in Figs. 4.5, 4.6 and 4.7. Arrows run from subjects to those neighbours who were nearest in 5.50% of more of the subject's samples over the whole study. This critical value was the highest which would include all subjects in at least one sociogram, and it includes only the top 14.0% of associated dyads. Subjects have been placed to minimise line-crossing, so that the distance between them is of no import. The width and number of arrows reflect frequency and reciprocity of association

4.2.9a) Association between male pairs: Three associations are prominent in Fig. 4.5. Adults A3 and A5 were frequent neighbours, and each was associated with a subadult, respectively S2 and S3. Furthermore, one of these four males contributes to every link shown.

4.2.9b) Association between female pairs: Fig. 4.6 illustrates the frequent association among mothers. This is not apparent for F12 and F18 because they gave birth comparatively late in the study: however they both showed increased association with most other mothers after parturition. The mother with the least links to other mothers, F14, was the one with the oldest black infant. Three lactating females associated with particular mothers, namely F7, F10 and F15; while F13 increased her neighbour-frequency with F12 by 7.30% after the latter had given birth.

Some females who resumed cycling during the study showed increased association together which coincided with increasing association with a particular male. This was the case between F5 and F7 (both consorts of A1) and between F1 and F17 (both consorts of A3), although both associations were short-term.

4.2.9c) Association between the sexes: The most frequent dyadic associations in the whole study were between certain male-female pairs (Fig. 4.7). Males A1 and A3 give clear examples of partnerships with cycling females: that between A1 and F5 was the most persistent in the whole troop. Resumption of cycling brought a number of changes in females' association (Chapter 8): F1 changed first associate from A4 to A3; F7 changed from A3 to A1; F13 changed from A7 to A5; and F17 markedly increased association with A3.

FIG. 4.5

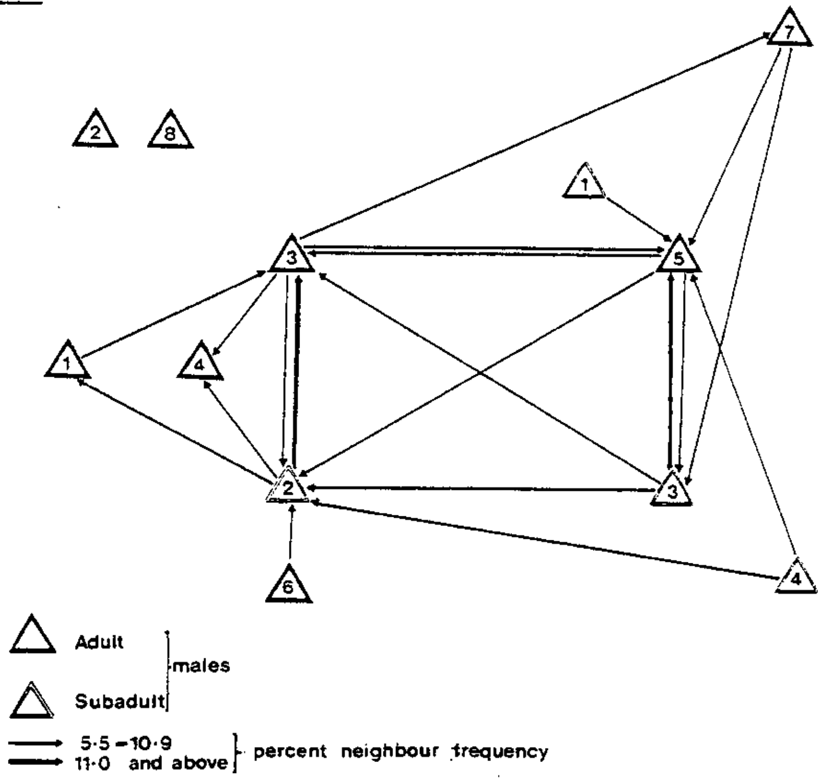
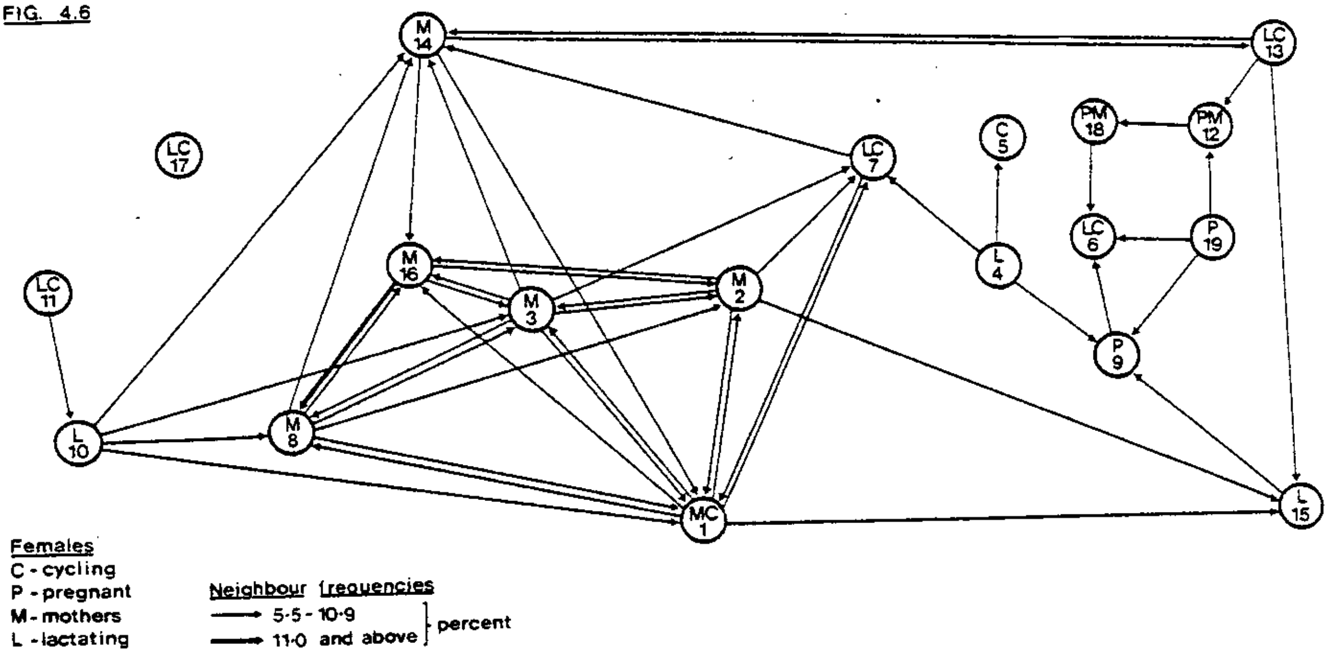


FIG. 4.6



Figs. 4.5 & 4.6. Dyadic association within each sex. Dyadic neighbour frequencies between males (4.5) and between females (4.6). Subjects identified by their dominance rank within class. Arrows run from subjects to those neighbours who were nearest in 5.5% or more of the subjects' samples.

FIG. 4.7

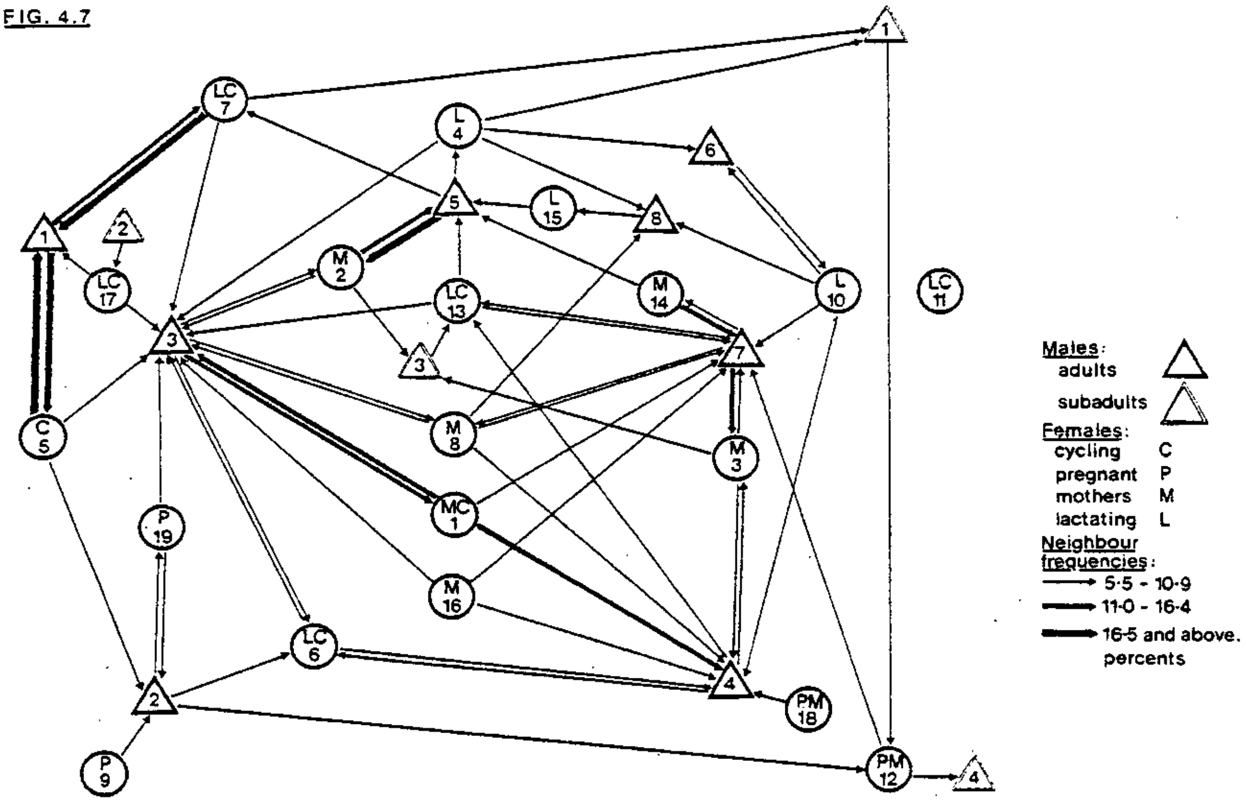


Fig. 4.7. Association between the sexes. Males (triangles) and females (circles) are identified by their dominance rank within class. Arrows run from subjects to neighbours nearest in 5.5% or more of subjects' samples.

Males A3, A4, A5 and A7 were characterised by their numerous links among mothers, which emphasises the focal position of these four compared with the newcomers A1 and A2, and the older A6 and A8.

Changes in association of the females who gave birth are not shown: F12's association with A2 ceased, and he was replaced by A7 (17.9%). Similarly, F18's prior associates, A2 and A4, decreased in favour of A7 (11.6%) and A3.

Finally, the fact that S3 and A5 shared association with F2 coincides with the frequent association between these two males (Fig. 4.5).

PART 3. GROOMING

4.3.1 Introduction

Grooming is one of the most frequent and time-consuming social behaviours of baboons. It is important in hygiene, since solitary animals become infested with ectoparasites (Hoogstraal, 1956; Struhsaker, 1967) which may carry disease (Kuntz and Myers, 1967), and because wounds which are not groomed may harbour fatal infections (Bramblett, 1967).

Grooming is clearly beneficial to the recipient, and, at cost merely of time and energy to the donor, appears to be altruistic (Kurland, 1977). It is not surprising therefore that it is distributed along patterns of kinship (Sade, 1965), dominance (Seyfarth, 1977), and alliance (Dunbar, 1980 ; Seyfarth, 1980), and has acquired social importance which some consider outweighs its hygiene function (e.g. Sparks, 1967).

Social grooming is usually a relaxed interaction. It was early characterised as an act of appeasement (Sade, 1965) and a means of reducing tension (Terry, 1970). In the long-term it evidently initiates or maintains social bonds of the sort described earlier (Part 1 above). Zuckerman (1932) considered its primary contribution was to mating relationships. While this is certainly true of short-term consortships (Saayman, 1971a) and long-term heterosexual bonds (Dunbar, 1978b; Seyfarth, 1978b), the majority of it cannot be construed as sexual at all, since it is especially prominent within matrilines (Sade, 1965; Strum, 1975; Cheney, 1978). Because adult females assume dominance ranks close to those of their mothers and sisters (Moore, 1978), much matrilineal grooming occurs between females close in rank. However, Seyfarth (1977) has proposed that grooming might be more frequent between close-rankers even without kinship, as a result of competition. He found that high-ranking females were more attractive as grooming partners, but that lower ranking females were unable to gain competitive access to them, and instead groomed the highest rankers available to them, to whit, those close in rank. Seyfarth's model proposes that this pattern is modified by kinship and by the attractiveness of newborn infants, and subsequent studies confirm most of its predictions (Seyfarth, 1980; Fairbanks, 1980). Partnership with high rankers may confer the benefits of increased affiliation and appeasement from others (Fairbanks *ibid.*) and alliance in aggression (Seyfarth, 1980, but cf. Fairbanks *ibid.*).

4.3.2 Methods

Because *ad libitum* observations were not continuous, it was impossible to reliably record the initiation and duration of most grooming interactions. Whenever a pair was seen grooming, their identity was recorded, and a subsequent record was only made if the direction of grooming had reversed or if 20 minutes had elapsed since the pair was last seen grooming. Even within bouts separated by more than 20 minutes, only the first instance of grooming by each partner was recorded, and subsequent reciprocations were ignored. The minimum interval was recommended from focal animal data by J.I. Oliver, and was probably conservative since Packer (1977a) calculated that bouts were independent if separated by intervals of two minutes or more.

The number of times any animal was recorded as grooming in this study was probably a compound of both the frequency and duration of its grooming. Self-grooming (autogrooming) was not recorded. In the initial analyses, subject-rates (2 XII c.(i)) of grooming are included, because the number of partners a subject could groom in a day is probably less than the number available in each sex in the study troop.

4.3.3 General observations

A total of 793 grooming interactions were recorded between adults, and 248 between adults and young. Simultaneous mutual grooming was never seen. All interactions were dyadic, except that on five occasions two animals simultaneously groomed a third (always a mother

Table 4.VII Sex-differences in grooming

Mean rates of grooming within and between each sex. Rates are expressed per hundred hours per subject (above), and per dyad (below), with standard deviations.

	Recipients			
Subject rates:	Males	s.d.	Females	s.d.
Groomers				
Males (12)	.07	(.20)	3.81	(2.97)
Females (18)	2.39	(1.71)	4.57	(2.76)

	Recipients			
Dyad-rates:	Males	s.d.	Females	s.d.
Groomers				
Males (12)	.01	(.02)	.20	(.16)
Females (18)	.20	(.15)	.25	(.15)

FIG. 4.8

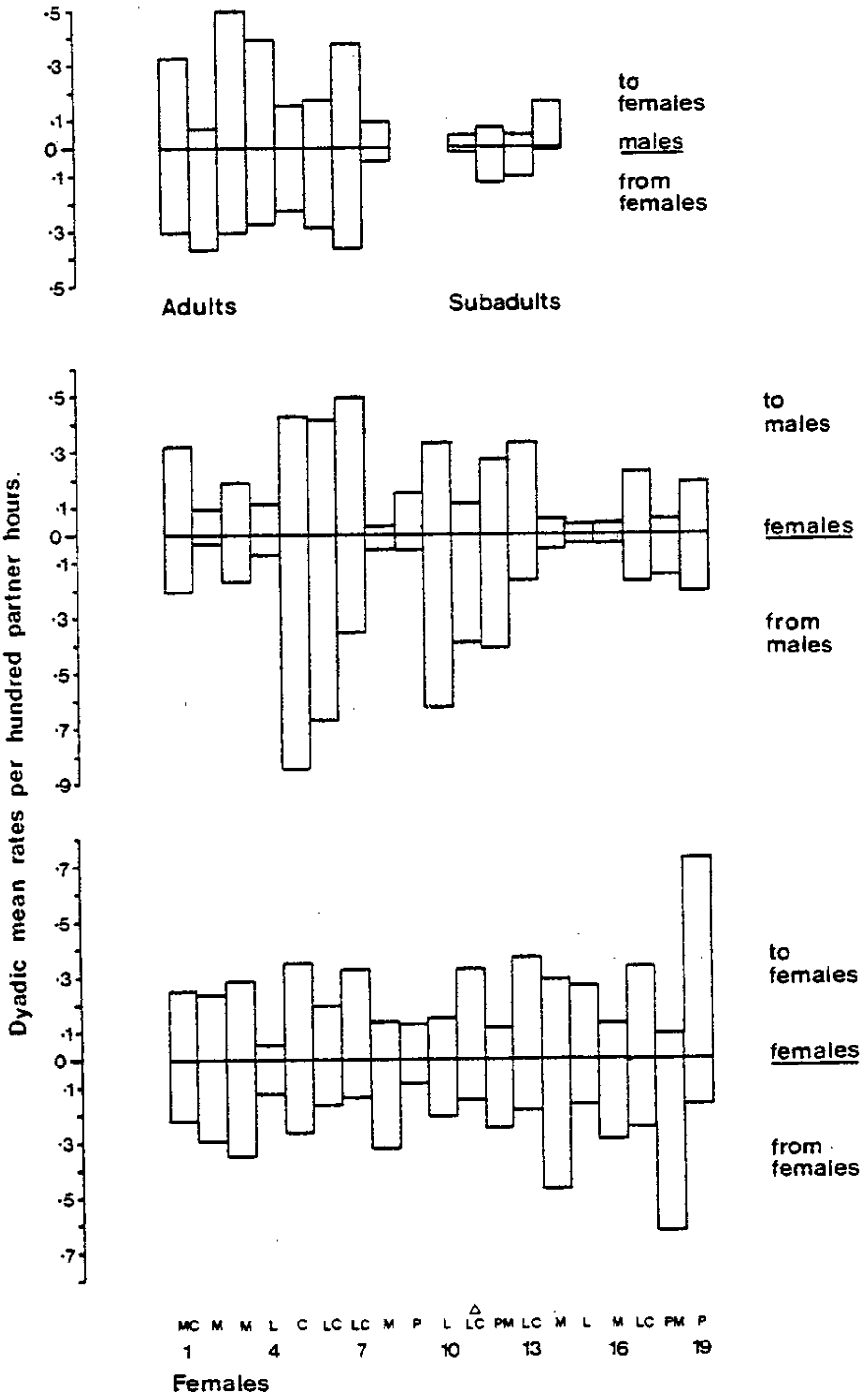


Fig 4.8. Grooming within and between sexes. Mean dyadic rates at which subjects of each sex gave grooming (above x-axis) and received it (below) with male and female partners. Subjects in descending dominance rank order from the left; females are C - cycling, P - pregnant, M - mothers, L - lactating, and the sick female Δ .

with a black infant), and twice a grooming chain of three animals was seen. It is likely that more grooming would have been recorded if more observations had been made in the earliest part of the day, and during the afternoon (2 XI d.(i)).

4.3.4 Sex-differences in grooming rates

Each female subject was seen grooming on average every 14.4 hours, each male every 24.7 hours. The rates of grooming within and between the sexes are compared in Table 4.VII (also Fig. 4.8). The most obvious finding was that males hardly ever groomed one another. The rate at which females groomed males per subject-hour was considerably less than the rate at which they groomed one another (T=19, ± obs. corr., n 17, $p < 0.01$), but the mean dyadic rates were about the same (T=70, ± obs. corr., n 18, n.s.). This was partly because more female partners were available, and partly because each female groomed an average of 50% of the other females, but only 32% of the males (T=22, n 18, $p < .01$).

There were no significant differences in the rates at which males and females groomed one another, in subject rates (U=79.55, corr. obs. 74, n 12, 18, n.s.) nor in dyadic rates (U=110, corr. obs. 120, n 12, 18, n.s.). On average, each male groomed 27% of the females, which is close to the reciprocal percentage noted above, so that the higher subject-rates by males are due to the greater availability of females.

In summary, there is little evidence that grooming rates were affected by sex except that males seldom groomed one another, and that females groomed a higher proportion of the other females than of the males.

4.3.5a) Grooming between male classes: Subadult males groomed adult males three times (rate = 0.08 per hundred dyad hours), and once an adult groomed a subadult (corresponding rate 0.01), but grooming within either class was not seen.

4.3.5b) Grooming between female classes: The highest mean grooming rates were found between females. The reproductive classes did not differ in the rates at which they groomed (Table 4.VIII), although cycling females tended to groom most, and pregnant females (excluding F19) least (Fig. 4.9). Cycling females and mothers did not groom other classes at random ($p < .05$ in both cases) chiefly in that both classes favoured mothers, and mothers rarely groomed pregnant females.

Table 4.VIII Grooming between female classes

Dyadic mean rates per hundred hours, with standard deviations

	Recipients					Freidman
	All females	Cycling	Pregnant	Mothers	Lactating	χ_r^2
Groomers						
Cycling (5)	.38 (.13)	.41 (.28)	.16 (.03)	.73 (.51)	.15 (.18)	8.46 $p < .05$
Pregnant (4)	.26 (.31)	.12 (.18)	.33 (.39)	.44 (.66)	.15 (.18)	5.48 n.s.
Mothers (8)	.17 (.09)	.21 (.18)	.00 (.02)	.37 (.27)	.22 (.25)	9.71 $p < .05$
Lactating (7)	.22 (.11)	.28 (.40)	.06 (.06)	.42 (.28)	.18 (.17)	7.36 n.s.
Kruskal-Wallis	H=6.77 (corr.obs. 7.33) n.s.					
All females groom		.24 (.09)	.10 (.02)	.55 (.47)	.15 (.08)	

FIG. 4.9

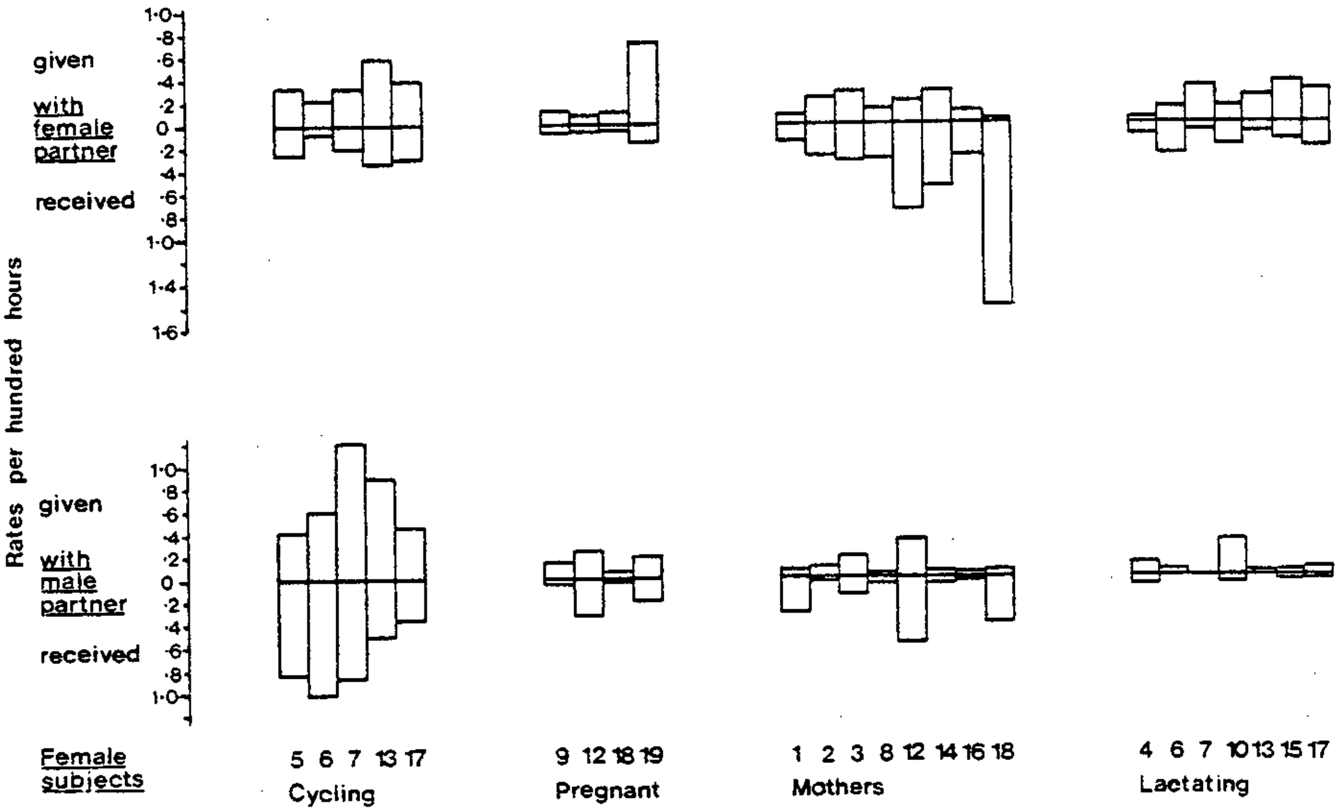


Fig. 4.9. Grooming rates of members of each female class with other females (upper figure) and with males (lower figure). Histograms show dyadic mean rates given (above) and received (below). Subject classes are named beneath, their class-members arranged in order of dominance ranks which are also listed. Part-sample data are used for those females who changed reproductive state. The mothers with the youngest infants were F12 and F18.

Although pregnant and lactating females groomed other classes at random both tended also to groom mothers more. The high mean rates by (and among) cycling females may be an effect of reproductive state, but may also be due to the increase in grooming in the wet season, since most of the dyads concerned were not cycling during the dry season.

4.3.5c) Class-differences in grooming between the sexes: The mean dyadic rates are compared in Table 4.IX. The female classes did not groom males at the same rates ($p < .01$), mainly because cycling females groomed males very much (Fig. 4.9). All female classes tended to groom adults more than subadults, significantly in the case of mothers, who never groomed subadults ($p < 0.01$); and over the whole study 15 of 18 females groomed adults more ($T=12$, n 18, $p < .01$).

Conversely, adult males groomed females more than did subadults (Table 4.IXb, $p < .05$), although neither class showed a uniform tendency to groom females in any reproductive state. Nevertheless, some males groomed cycling females particularly frequently, and one groomed mothers very often (Fig. 4.10).

4.3.6 Grooming between adults and young

Subjects differed markedly in their grooming rates with immatures (Fig. 4.11). Of the 29 that exchanged any grooming with immatures, 22 received more grooming than they gave (Sign test, $p < 0.01$). Mean subject-rates of grooming are listed for each class in Table 4.X. The rates are patterned, in that although classes did not differ consistently in grooming given, yet they received grooming at different rates ($p < .01$). Cycling females and mothers received the most, and data in Table 4.XI suggest that the cycling females were groomed mainly by young males.

4.3.7 Mothers' grooming and infants' age

The mothers rank-order for increasing age of their infants are compared with their rates of grooming exchanged with various classes by Spearman rank correlation in Table 4.XII. Variation between mothers was not linearly related to infant age, so that other factors may be more important. However it is clear in Fig. 4.9 that the females with the newest infants, F12 and F18, were groomed more by both males and females.

Table 4.IX   Grooming between the sexes

Legend as for Table 4.VIII.   Mean dyadic rates per hundred hours, with standard deviations in brackets

(a) Female subjects

	Recipients			Wilcoxon
	All males	Adults	Subadults	
Groomers				
Cycling (5)	.71 (.33)	.94 (.41)	.22 (.32)	no test
Pregnant (4)	.16 (.08)	.18 (.08)	.13 (.15)	no test
Mothers (8)	.11 (.10)	.16 (.14)	.00 -	T=0. p<.01
Lactating (7)	.09 (.11)	.11 (.17)	.05 (.09)	T=7. n.s.
Kruskal-Wallis	H=12.95 (corr.obs. 13.50) p < .01			
All females groom		.27 (.21)	.07 (.10)	

(b) Male subjects

	Recipients					Freidman
	All females	Cycling	Pregnant	Mother	Lactating	χ^2_r
Groomers						
Adults (8)	.26 (.16)	.93 (.83)	.17 (.22)	.23 (.50)	.13 (.36)	6.68 n.s.
Subadults (4)	.08 (.06)	.29 (.37)	.12 (.09)	.02 (.03)	.05 (.07)	2.78 n.s.
Mann-Whitney	U=4 (corr.obs.3) p < .05					

FIG. 4.10

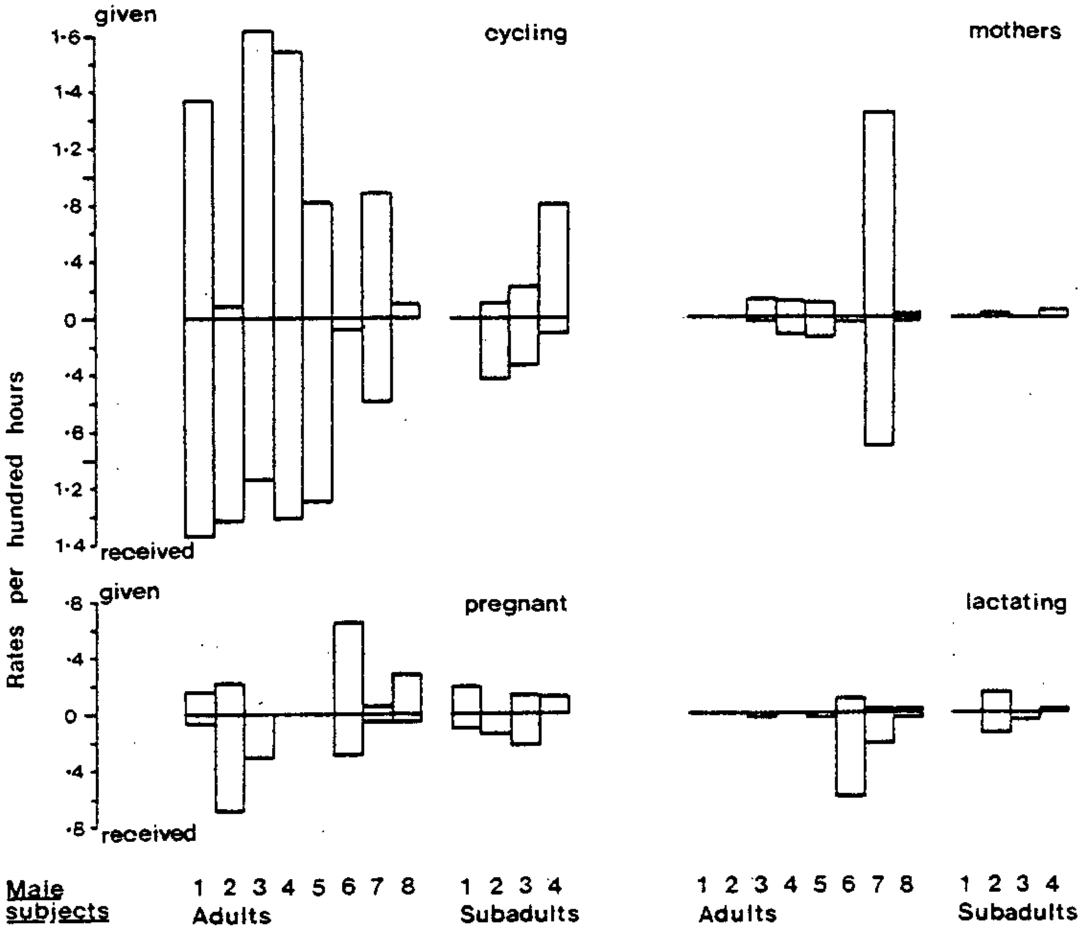


Fig. 4.10. Male subjects' grooming rates with females of each class. Histograms show dyadic mean rates per hundred hours, with grooming given (above x-axis) and received (below). Males arranged in order of dominance rank within class.

FIG. 4.11

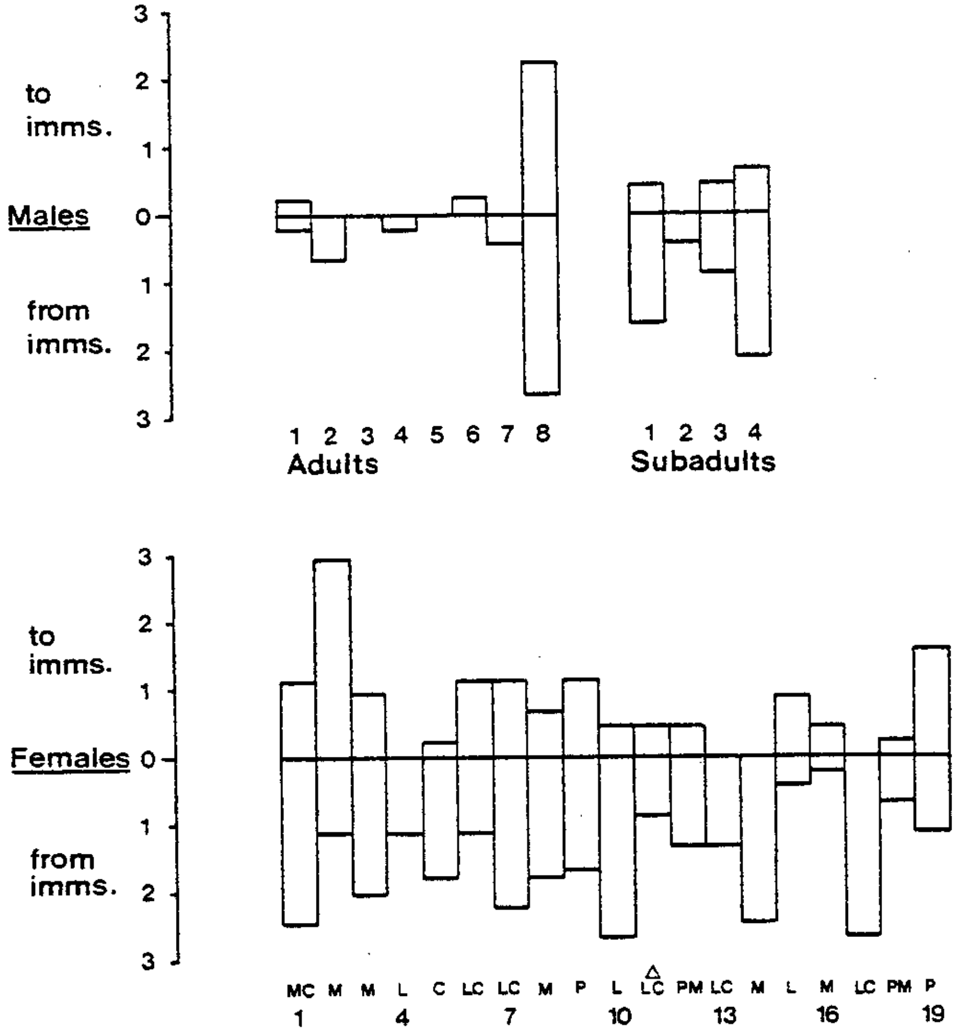


Fig. 4.11. Subjects' grooming rates with immature partners. Grooming given is above the x-axis, grooming received is below it. Rates expressed per hundred hours per subject (cf. Figs 4.8 to 4.10). Subjects in descending order of dominance rank from the left, with females C - cycling, P - pregnant, M - mothers, L - lactating, and the sick female △ .

Table 4.X

Class mean rates of grooming to and from immatures, expressed per hundred subject hours. Standard deviations in brackets.

Subjects	Grooming given	Grooming received
Adult males (8)	.34 (.78)	.53 (.90)
Subadult males (4)	.38 (.28)	1.30 (.79)
Cycling females (5)	.82 (1.05)	3.28 (1.59)
Pregnant females (4)	.85 (.69)	.77 (.74)
Mothers (8)	.66 (.97)	2.03 (1.02)
Lactating females (7)	.25 (.35)	.84 (.96)
Kruskal Wallis	H=4.04 (corr.obs. 3.86) n.s.	H=15.91 (corr.obs. 15.20) $p < .01$

Table 4.XI

Incidents of grooming to females by immatures: all cases in which the sex of the immature was known.

	Recipients			
Groomers	Cycling females	Other females		
Imm. males	12	2	χ^2	22.06
Imm. females	4	25	df 1.	$p < .001$

Table 4.XII   Infant's age and mother's grooming

Mothers' ranks in order of increasing age of their infants (rank 1 for youngest infant) compared with their rank-orders for rates of grooming given and received.   N = 8 mothers.

Grooming	Spearman	Corr. obs.
to males	.595 n.s.	.714 ($p < .05$)
from males	.542	.476
to females	-.084	-.167
from females	.575	.548
to mothers	-.214	-.357
from mothers	.578	.405
to immatures	-.146	-.024
from immatures	.238	.381

4.3.8 Reciprocity in grooming pairs

Of the 793 adult grooming interactions, 11.1% were first reciprocations within 20 minutes (4.3.2), but as many as 84.3% were between partners who reciprocated at some time during the study. Grooming pairs could therefore be divided into one-way and reciprocal pairs. The hypothesis was tested that baboons would tend to groom partners which in turn groomed them - i.e. that more pairs than expected would be reciprocal. In grooming from one class to another, the proportion of dyads in which grooming was seen at all was related to the dyadic mean rate of grooming in that direction (comparing these measures over 33 class-pairs yields r_s 0.818, $p < .01$). Thus the proportion of dyads in which grooming occurred was a reasonable measure of the grooming tendency between classes.

If there were no relation between grooming given and grooming received, the proportion of dyads in which grooming was reciprocal in any class-pair was expected to be merely the product of the proportions of pairs that groomed at all in each direction. Thus if class A groomed in 50% of its dyads with class B, but class B groomed only 25% of its dyads with class A, reciprocal grooming would be expected in 12.5% of dyads.

4.3.8a) Reciprocity according to sex: Fig. 4.12 shows that over 70% of female-female dyads groomed at least once, but that far fewer than expected groomed reciprocally (Table 4.XIII, $p < .001$). In contrast, less than 40% of male-female dyads groomed at all, but far more of them than expected groomed reciprocally (Table 4.XIII, $p < .001$). Females gave proportionately more one-way grooming to males than males did to females.

4.3.8b) Class-differences in reciprocity: Table 4.XIV shows the number of dyads between each pair of classes in which neither, one, or both partners groomed. Because the expected number of reciprocating pairs is calculated from the proportion groomed by each class as subjects in each case, the expected scores account for variation in grooming tendency between classes. Among females, reciprocation was more frequent than expected in seven of the ten class-pairs, suggesting that the lack of reciprocation among females as a whole may be attributed to variation in affinity between classes. Conversely, the high levels of reciprocation between male and female may be traced especially to pairs of adult males and cycling females, and pairs of adult males and

FIG. 4.12

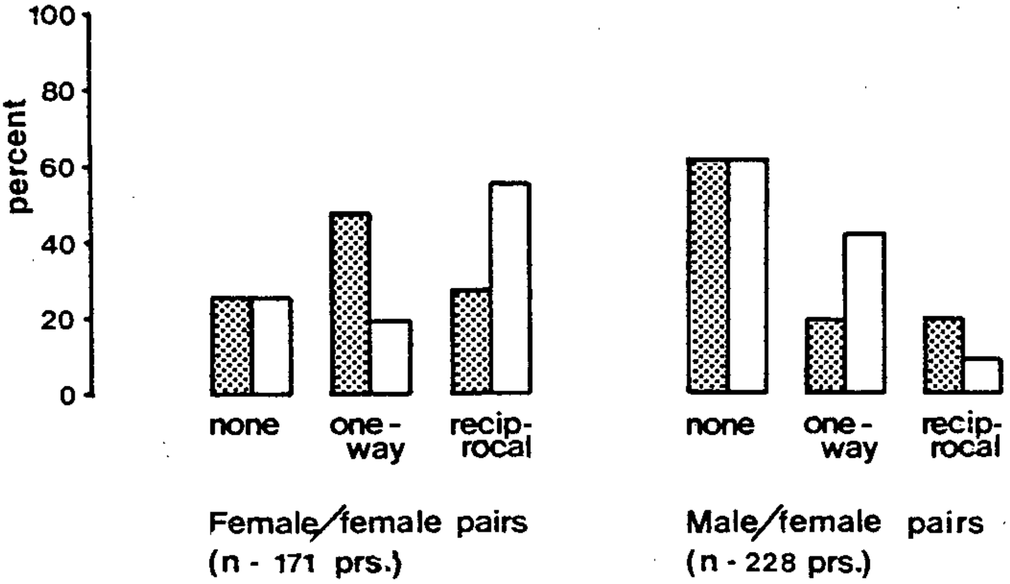


Fig. 4.12. Reciprocity in grooming, among females (left) and between males and females (right). The shaded bars of the histograms show the percentage of all pairs in which neither animal groomed, in which one groomed, and in which both groomed. The open bars represent the percentages expected from the nul hypotheses described in 4.3.8.

Table 4.XIII Reciprocity in grooming pairs

Comparisons of the numbers of pairs in which neither, one, or both partners groomed, in relation to the numbers expected. Expectations derived as explained in the text.

(a) Grooming between females

	Grooming			
	Neither	One-way	Reciprocal	Chi square
Observed	44	81	46	χ^2 96.67
Expected	(44)	32.6	94.4	df.1. $p < .001$

Chi square goodness of fit compares one-way and reciprocal pairs only.

(b) Grooming between male and female

	by males		
by females	No grooming	Grooming	
No grooming	139 (113.5)	15 (40.5)	chi square contingency χ^2 67.25
Grooming	29 (54.5)	45 (19.5)	df.1. $p < .001$

Table 4.XIV Reciprocity in grooming between classes

The proportion of dyads between each pair of classes in which grooming was seen in either direction. For each class as subject – indicates the number of dyads in which the subject-class did not groom, + indicates the number in which the subject-class groomed. Thus the lower-right cell of each 2 x 2 matrix is the number of reciprocating pairs, and the expected number is immediately to its right. Those with more reciprocal pairs than expected are emphasised by boxes.

		Adult ♂			Subad. ♂			Cycling ♀			Pregnant ♀			Mother ♀			Lactating ♀		
		–	+	e	–	+	e	–	+	e	–	+	e	–	+	e	–	+	e
Adult ♂	–	0	0		28	3		17	5		18	6		50	4		47	6	
	+		0	=	1	0	.09	1	$\boxed{17}$	9.9	3	$\boxed{5}$	2.8	1	$\boxed{9}$	2.0	0	$\boxed{3}$	.5
Subad. ♂	–				0	0		12	1		8	3		27	0		24	1	
	+					0	=	3	$\boxed{3}$	1.3	3	$\boxed{2}$	1.6	3	0=0		2	$\boxed{1}$	.2
Cycling ♀	–							3	4		11	1		13	3		16	3	
	+								3	4.9	4	$\boxed{3}$	1.5	15	$\boxed{6}$	5.1	2	$\boxed{3}$	1.3
Pregnant ♀	–										4	1		14	1		18	3	
	+											$\boxed{1}$	.7	14	0	.5	5	$\boxed{2}$	1.3
Mother ♀	–													7	6		21	13	
	+													7	6=6		5	$\boxed{9}$	6.4
Lactating ♀	–																14	4	
	+																	$\boxed{3}$	2.3

mothers.

4.3.9a) Grooming and dominance rank

Previous studies disagree as to how dominance rank affects grooming. Sparks (1967) concluded that allogrooming was more frequent in species with a pronounced dominance hierarchy (e.g. Defler, 1978, but cf. Rosenblum *et al.*, 1966), and Lindburg (1973) suggested that grooming might counteract any fragmenting effects of dominance relationships. Where grooming is more frequent from dominant to subordinate, the high rankers groom more (Rowell, 1968; Bramblett, 1978). But in the majority of studies, grooming is more frequent from subordinate to dominant (Bernstein and Sharpe, 1966; Rowell, 1971; Wade, 1977; Stammbach, 1978), especially outside kin-groups (Oki and Maeda, 1973; Hinde and Proctor, 1977). Thus high-rankers often receive more grooming (Seyfarth, 1976, 1980; Bramblett *ibid*; Fairbanks, 1980). However there are studies that report no clear relation between rank and grooming (e.g. Simonds, 1965; Bernstein, 1970).

In comparing these studies it is important to consider the differences between age/sex classes. In *Papio* adult males are always dominant to females; thus high ranking females might *receive* more grooming from their own sex, but *give* more grooming to males because they can monopolise access to them (Hall and DeVore, 1965; Kummer, 1968).

4.3.9b) *Rank correlations*: Table 4.XV compares subjects' dominance rank-orders with their rank orders for rates of grooming with male, female, and immature partners. There is no obvious relation between the two variables, as is also apparent in Figs. 4.8 and 4.11. In case the conspicuous class-differences among females were obscuring any lesser tendencies due to dominance rank, the same variables are compared for grooming between particular classes in Tables 4.XVI and 4.XVII. In 40 comparisons, two are likely to exceed 5% significance by chance alone, so that the only clear finding is that higher-ranking adult males are groomed more by cycling females ($p < .01$). This is shown in Fig. 4.10, which also suggests that except for A2 the higher-ranking adult males also groomed cycling females more (for the other seven adults, $r_s = 0.714$, corr. obs. 0.790). Apart from this there is little evidence that high rankers attract more grooming or achieve

Table 4.XV

Grooming and dominance rank: I: Overall comparisons. Spearman rank correlation coefficients between subjects' dominance ranks and rates of grooming given and received with the partners indicated. In brackets are the results of the comparisons repeated on scores corrected for observability: if they are the same, they are written (=)

	Grooming given			Grooming received		
	Partners			Partners		
	All males	All females	Immatures	All males	All females	Immatures
Subjects						
Males						
Adult (8)	-	.143 (=)	-.266 (=)	-	.476 (.357)	-.171 (=)
Subad. (4)	-	-.800 (-.200)	-.800 (-.400)	-	.400 (=)	-.400 (=)
Females (18)	.330 (.139)	-.129 (-.189)	.318 (.282)	.161 (.088)	-.092 (-.164)	.253 (.178)

Table 4.XVI

Grooming and dominance rank: II: Females' dominance rank compared with their grooming rates with other females, and with immatures. Tabulated as in Table 4.XV. $^{*} = p < .05$

	Grooming given		Grooming received	
	Partners		Partners	
Subjects	All females	Immatures	All females	Immatures
Cycling (5)	-.600 (=)	.564 (=)	-.600 (=)	-.600 (-.900)
Pregnant (4)	-.400 (=)	-.200 (=)	-.200 (=)	.400 (=)
Mothers (8)	.252 (.143)	.586 (=)	-.659 (-.738)	-.238 (=)
Lactating (7)	-.714 (-.857)*	-.256 (=)	-.143 (-.036)	-.126 (=)

Table 4.XVII

Grooming and dominance rank: III: Grooming between male and female. Subjects' dominance rank compared with their rank orders for rate of grooming given and received with partners of the opposite sex. Spearman coefficients with (in brackets) and without observability corrections.

$^{*}p < .05$ $^{**}p < .01$

	Grooming given			Grooming received		
	Partners			Partners		
	All males	Adult males	Subadults	All males	Adult males	Subadults
Female subjects						
Cycling (5)	-.300 (=)	.100 (=)	-	.700 (=)	.900 (=)	-.600 (=)
Pregnant (4)	.000 (=)	.600 (=)	-	.000 (=)	.000 (=)	-
Mothers (8)	.381 (=)	.429 (.095)	-	-.084 (-.167)	-.287 (-.262)	-
Lactating (7)	.143 (=)	.234 (=)	-	.111 (=)	-	-

	Partners (females)				Partners (females)			
	Cycling	Pregnant	Mothers	Lactating	Cycling	Pregnant	Mothers	Lactating
Male subjects								
Adults (8)	.500 (.571)	-.268 (-.095)	-.342 (=)	-	.905** (.857)**	.434 (.347)	-.627 (-.683)	-.726* (-.830)*
Subadults (4)	-1.000	-	-	-	-	-	-	-

more access to grooming partners.

4.3.10 Dominance and direction of grooming among females

Data in Table 4.XVIII compare the distribution of grooming up and down hierarchy in terms of (a) total grooming interactions, and (b) the number of dyads in which grooming occurred, among females. In neither case is there any evidence that dominance affected the predominant direction of grooming, as summarised in that rates uprank and downrank were almost the same.

4.3.11 Dominance rank-difference and grooming among females

The distribution of grooming at each rank-difference was analysed as described in 2.XIII c). Fig. 4.13a shows that the highest mean rates of grooming occurred at adjacent rank. Although the dyadic mean rate did not decrease linearly at more distant ranks (r_s 0.508, n=14 rank-places, n.s.) yet there was a significant tendency for first partners to be within two places of rank ($p < .001$, Table 4.XIX, Fig. 4.13b). The number of first partners is less than 18 because mutual first partners were counted only as one, and F11 was excluded as a partner. There was also a tendency that proportionately more of the grooming pairs groomed reciprocally at closer ranks (r_s 0.610, n 14, $p < .05$, Fig. 4.13c).

4.3.12 Dyadic grooming relationships

The distribution of grooming between pairs of subjects is summarised in Figs. 4.14 and 4.15.

4.3.12a) Grooming between females: Female subjects have been positioned in descending order of dominance rank, anti-clockwise from the top (Fig. 4.14). There are 51 links portrayed: their distribution among classes differs from that expected had they been formed at random, illustrating a number of the conclusions drawn above. Thus, grooming among mothers was not especially frequent (9 links, 8.7 expected): but mothers were groomed by non-mothers far more than expected (24 links, 13 expected). In turn, mothers groomed others very little (8 links, 13 expected). The females who cycled have 23 links, more than the 16.1 expected. Finally, grooming was frequent between pairs of adjacent rank (16 links, 5.4 expected).

Table XVIII

Comparison of the proportion of grooming among females given to dominant and to subordinate partners

		to dominant	to subordinate	
1. The amount observed in each direction compared with the amount expected from a 50:50 distribution, in terms of:				
(a) Interactions:	observed:	206	181	χ^2 1.615
	expected:	193.5	193.5	df.1. n.s.
(b) Number of dyads in which any grooming observed in each direction	observed:	87	86	χ^2 0.006
	expected:	86.5	86.5	df.1. n.s.
2. Mean dyadic rate in each direction:		.32	.33	Wilcoxon: over 16 females (minus F1, F11,F19), T=60, n.s.
s.d.		(.31)	(.35)	

Table 4.XIX Rank-difference and grooming

The number of first grooming partners among females within and beyond two places of dominance rank

	Rank-differences		
	1-2	3+	
Observed	10.4	5.6	binomial test $p < .001$
Expected	3.4	12.6	

FIG. 4.13

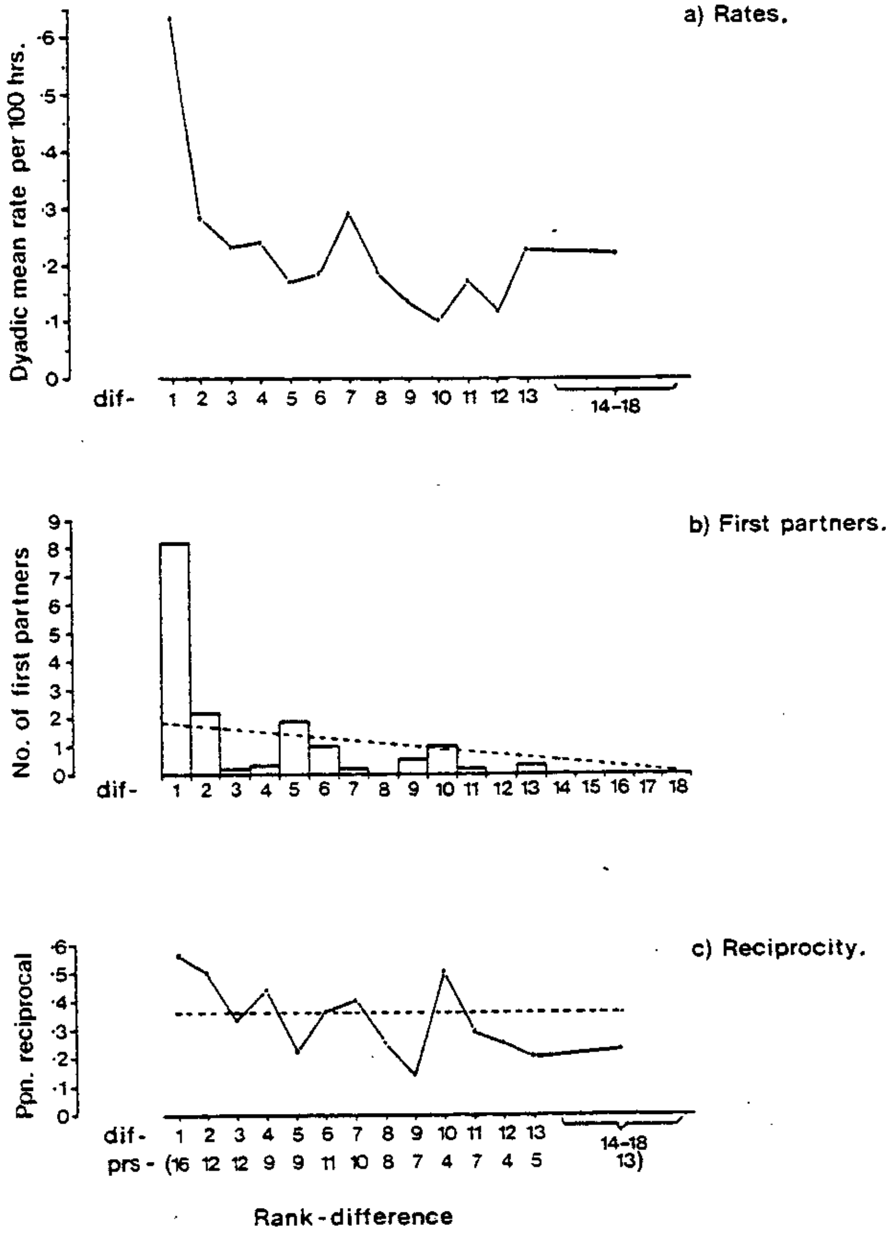


Fig. 4.13. Three estimates of grooming frequency at each rank-difference among females. Rank-differences increase from left to right; a) shows dyadic mean rates at each one; b) shows the distribution of first grooming partners as described in the text, with the dotted line being the distribution expected if first partners had been chosen at random. Graph c) shows the proportion of all grooming pairs in which both members were seen to groom; the dotted line is the proportion overall; the figures beneath show the number of grooming pairs, from which the proportions were calculated.

FIG. 4.14

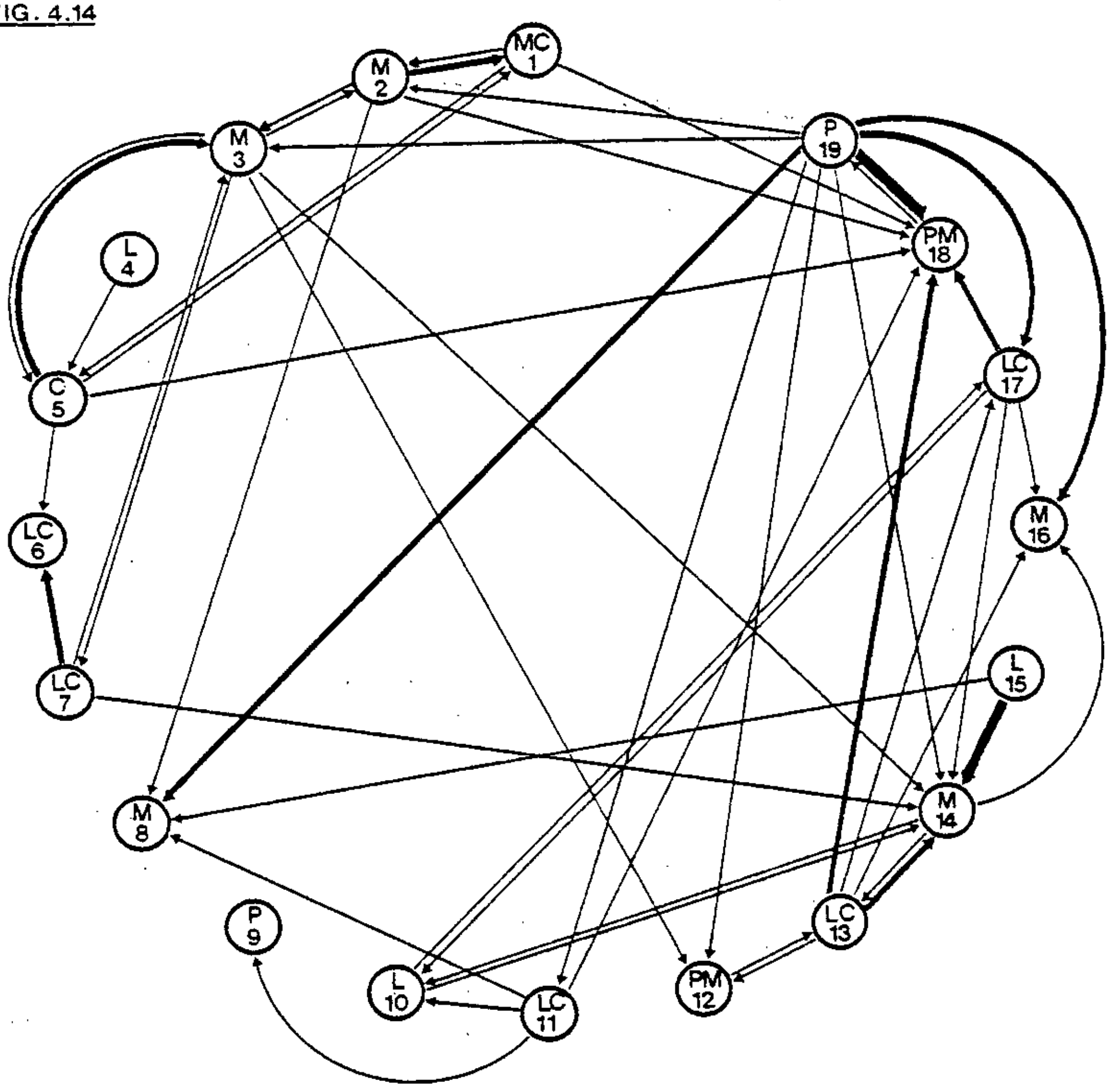


Fig. 4.14. Grooming between female pairs. All partnerships with a rate equal to or greater than 0.67 times per hundred hours are indicated by arrows from groomers to recipients, derived from whole-sample data only. Females identified by dominance rank, with reproductive states indicated. The arrows account for 57% of the 387 interactions recorded.

Other conspicuous features reflect individual differences. Some females groomed almost at random (e.g. F6), but the majority were more selective. The one who groomed least was apparently the oldest (F4), while the one who groomed most was the lowest ranker, F19, who groomed extraordinarily often and to many partners. The mother of the oldest black-infant, F14, was groomed by many females. Of the two who gave birth, F18 gained more partners thereafter (13 who had not groomed her before) than did F12, who gained only four partners but lost one.

4.3.12b) Grooming between male and female: In Fig. 4.15, subjects have been positioned to emphasise the grooming of cycling females, which are arrayed down the centre (except for F17 and F11 at the top left).

In comparison with grooming among females, the greater reciprocity of male-female grooming is obvious. While some females groomed males very little (Fig. 4.8), the partnerships between adult males and cycling females were conspicuous. Most included consortship, and became prominent only after cycling had begun, except those between F1 and A4, and between F13 and A7, which had been apparent before. The males most involved were A1, A3 and A4.

There were comparatively fewer and weaker partnerships between males and mothers. Adults A3, A4 and A5 are linked to two mothers each. A7 had the most conspicuous partnership, with F3, and he also groomed often with the two females who had given birth, resulting in his exceptionally high score with mothers (Fig. 4.10). His relationship with them had not been apparent during pregnancy, because F12 had shared a mutual first partnership with A6 (±A2), and F18 had exchanged little grooming with any male during pregnancy. Thus A6 and A2 were the main partners of pregnant females (the latter especially with F9). A6 also groomed often with lactating F10.

Grooming between subadult males and non-cycling females was not prominent, except for the mutual first partnership between S2 and F4.

FIG. 4.15

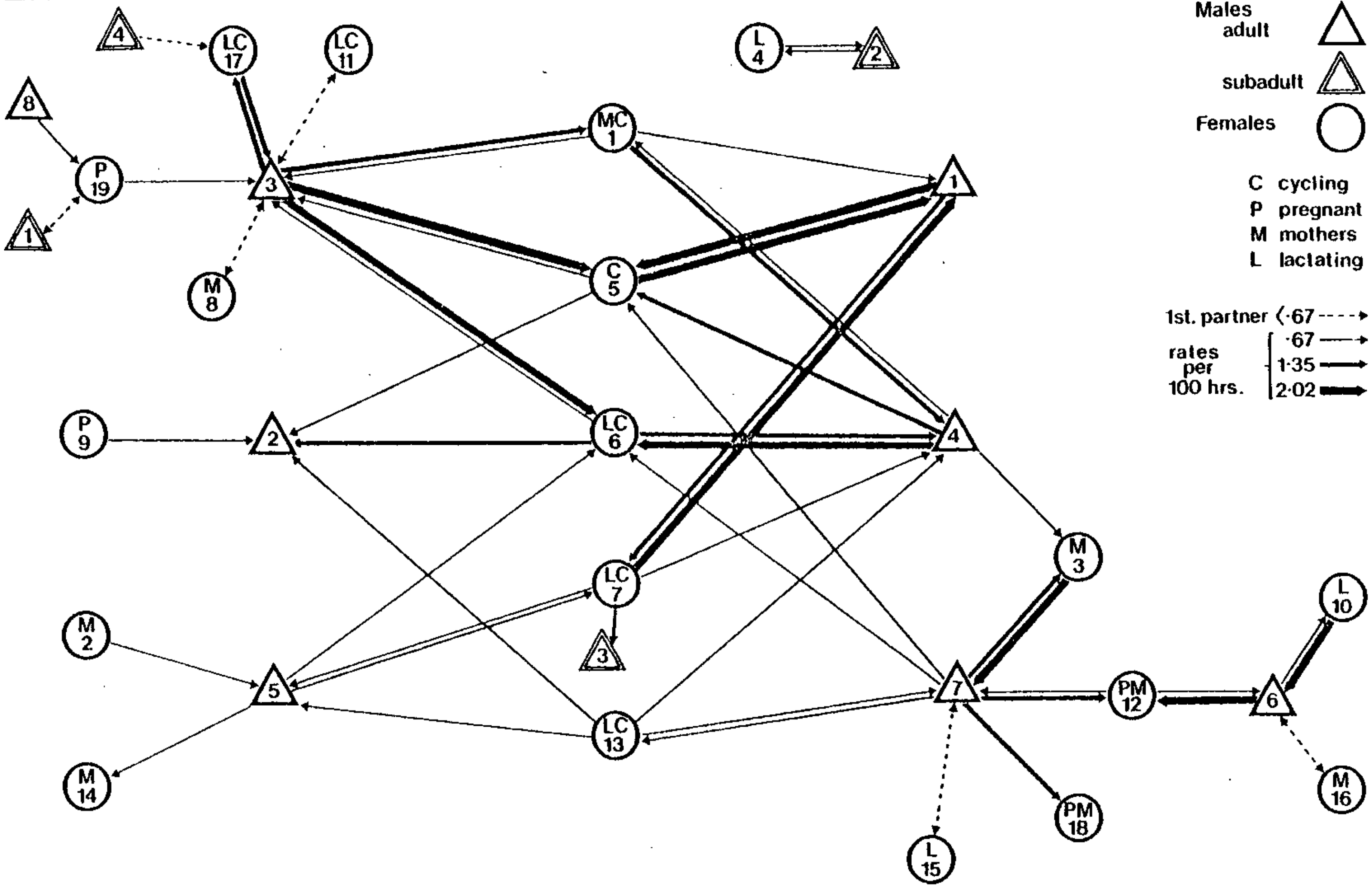


Fig. 4.15. Grooming between male and female. All partnerships with a rate equal to or greater than 0.67 times per hundred hours indicated by arrows from groomers to recipients. For subjects without any such partnerships, dotted lines indicate their most frequent recipient below this rate. Rates from whole-sample data only: subjects identified by dominance rank, female reproductive states as indicated; cycling females down centre and at top left. The arrows account for 73% of 202 cases of grooming by females and 79% of 200 by males.

PART 4. GROOMING AND ASSOCIATION COMPARED

4.4.1 Analysis

The hypothesis was tested that subjects would groom more those partners who were near them more often. For each subject was calculated a rank-order across all other subjects firstly in order of their neighbour frequency and secondly in order of the rate at which the subject groomed them. The data were independent since grooming partners had not been included as nearest neighbours. Although the grooming ranks were often based on small numbers of interactions, with a number of animals who were not groomed at all tied at the lowest ranks, yet if the measures were related the ranks should have been positively correlated. Table 4.XX compares these measures for each subject, and lists also the neighbour-frequency of the first grooming partner(s) as a proportion of the subject's mean neighbour frequency with that sex. For the latter, any value greater than 1.0 indicates that the first grooming partner was also a neighbour more than average.

4.4.2 Results

The majority of correlation coefficients were positive, and for nine to be significant is more than expected by chance alone (2.5). This suggests that there was an underlying trend for subjects to groom their more frequent neighbours more often, illustrated by the fact that 76% of first grooming partners were above-average neighbours.

The strength of correlation between association and grooming with female partners was higher for the higher-ranking subjects in both sexes (Table 4.XX, columns A and B). Comparison between degree of positive correlation (in terms of Spearman coefficients) and subjects' dominance rank yielded r_s 0.657 for male subjects ($n=12$, $p < .05$) and 0.588 for female subjects ($n=19$, $p < .01$). However this tendency was not apparent in females' tendency to groom male associates (column C, r_s 0.374, n 19, n.s.). This suggests that higher ranking males and females had more consistent relationships among the females of the troop, but more detailed data would be required to explain why.

Table 4.XX Association and Grooming compared

Spearman rank correlation coefficients between each subject's partner-ranks for neighbour-frequency, and rate of grooming to, each partner. The right-hand column in each case lists the neighbour-frequency of the first grooming partner as a proportion of the subject's mean dyadic neighbour-frequency with that sex.

Male subjects

A. with 19 female partners

Males	r_s	1st partner
A1	.401	10.96
A2	.428	1.88
A3	.564*	1.32
A4	.639**	2.06
A5	.320	1.33
S1	.339	2.02
A6	.324	.94
A7	.165	1.40
A8	.267	.53
S2	.394	1.44
S3	.363	1.61
S4	.053	.89

Female subjects

	B. with 18 female partners		C. with 12 male partners	
Females	r_s	1st partner	r_s	1st partner
F1	.224	1.57	.453	3.19
F2	.548*	1.89	.409	4.90
F3	.449	2.21	.674*	3.06
F4	.416	1.86	.364	.91
F5	.089	.44	.762**	7.07
F6	.271	.99	.427	1.16
F7	-.031	.57	.634*	3.76
F8	.277	.73	.675*	2.02
F9	.340	1.06	.618*	2.09
F10	-.210	.40	.459	1.81
F11	.276	2.42	.406	1.66
F12	.340	1.74	.091	.92
F13	.089	2.08	.432	.99
F14	.237	1.51	.676*	3.25
F15	.236	1.37	.337	1.48
F16	.218	1.29	.318	1.19
F17	-.075	1.28	-.060	2.61
F18	-.257	.90	.584	1.51
F19	-.232	1.33	.387	1.94

PART 5. OVERVIEW AND DISCUSSION

4.5.1 Association and grooming

Individuals clearly differed in their choice of, or access to, particular companions and in some cases overtly competed over them. Overall, females appeared to maintain proximity to males, especially during travel, except that adult males predictably followed their oestrus female consorts.

The patterns of association and grooming were not always concordant, suggesting they might provide slightly different benefits. Thus to be near a particular animal, especially a potential ally, might favourably alter relations with other animals at the time: but to groom another might provide less immediate advantage, yet contribute to longer-term beneficial relationships (e.g. Cheney, 1978). In other cases, however, proximity without interaction may be the result of inhibition. Other discordancies between the measures reflect differences in the way the data were collected. Because association was sampled regularly, at intervals, data are likely to reflect tendencies that were consistent over the whole study. In contrast, grooming was recorded more opportunistically whenever it was seen, and the data are more likely to include intense short-term relationships as well.

4.5.2 Affiliation and the spatial pattern

The affiliative relations described above coincided generally with the spatial pattern of the troop. The males who had mothers as neighbours more often also spent more time in the clusters (3.5 d.(iii)), and a similar correlation was found for females (r_s 0.740, n 19, $p < .01$). A number of examples are given below which support this conclusion. The exceptions are in some grooming relationships: thus F19 groomed mothers very often, but spent little time in the clusters; and sick F11 also had normal grooming rates despite being exceptionally peripheral.

4.5.3 Initiation and context of grooming

Most grooming was relaxed interaction during periods of rest, and appeared to be affiliative behaviour by the groomer, except that a number of interactions were actually initiated by the groomee

(Simpson, 1973). Grooming often began in response to groom-presents or rear-presents: some animals would groom briefly before groom-presenting, particularly when adult males solicited females' grooming (also Rowell, 1972; Packer, 1977a).

Mounting occasionally led to grooming by the mountee. After aggression, the recipient sometimes groomed the aggressor, which might represent conciliation although occasionally the aggression itself seemed directed to elicit grooming. Grooming also occurred between recent allies in aggression (as reported for female grooming of males, Packer, 1977a) and animals under attack sometimes took refuge by grooming an adult male (as in Kummer, 1967, and Kurland, 1977).

Direct competition over grooming partners was not frequent, but obvious when a third animal supplanted or chased one of a grooming pair and then groomed or solicited grooming from the other. Adult males regularly groomed their female consorts, but there was no indication this was instrumental to successful copulation (cf. Saayman, 1970, 1971a). Both consort grooming, and males' grooming of mothers with new infants, was sometimes possessive against nearby males.

Thus although grooming may have originated as a utilitarian behaviour concerned with hygiene (Hutchins and Barash, 1976), it has clearly acquired a variety of social uses, so that its patterning between different individuals may reveal underlying social relationships.

4.5.4 Affiliative relationships: review

The patterns of association and grooming were influenced more by the participants' sex and reproductive class than by dominance rank.

4.5.4a) Relations between males: Association between males was not especially infrequent, but grooming between them was extremely rare, as in other troops (Rowell, 1967a; Saayman, 1971a). While this may reflect lack of kinship between transferred males, it is more likely to reflect the competitiveness of their relations (Chapter 6). Thus in hamadryas and gelada baboons, grooming occurs between males who do not have access to females, but is rare among those who do (Kummer, 1968; Dunbar and Dunbar, 1975). However, other factors may be involved, since male macaques sometimes groom together

(Sugiyama, 1971; Sade, 1972).

Packer (1979a) concluded that transferred (adult) males tolerated the proximity of natal (subadult) males more than of other transferred males. Six of the eight adults here also had subadults as more frequent neighbours (Fig. 4.1), and the mean frequency of association among adults was the lowest among any male class. The conspicuous association between A3 and A5 clearly reflected their frequent alliance (Chapters 6 and 8). The more frequent proximity between S3 and A5 was at least in part a shared association with F2, but there was no obvious common associate in the partnership of S2 and A3. These subadults' proximity to the adults did not often confer the benefit of alliance (Chapter 6), and there is no evidence to support the idea that they were 'identifying' with the roles of leader males, as suggested by Imanishi (1963).

4.5.4b) Relations between females: The high mean frequency of association between females was mainly due to the mothers. Females groomed more often than did males, primarily because the former groomed all classes while the latter only groomed females very often. Females groomed one another most, especially in that they groomed a high proportion of female partners. These data agree with other reports that the most frequent grooming is between females (Hall and DeVore, 1965; Rowell, 1967b, 1968) in contrast with hamadryas (Kummer, 1968).

i) Female dominance rank. High ranking females did not attract more association or grooming from other females (cf. Seyfarth, 1976). Furthermore, association was not more frequent between close rankers, but grooming clearly was, and tended to be more reciprocal. More frequent grooming at close ranks is widely reported (Rowell, 1966b, 1971; Seyfarth, 1976, 1980; Lindburg, 1973; Oki and Maeda, 1973). Without data on kinship between females, it is not possible to determine whether this represented grooming between close-ranking kin, or the resolution of attractiveness and competition proposed by Seyfarth (1977). Overt competition was not common, but evidence for more subtle competition is that partnerships of association and grooming were more concordant for higher-ranking females. Similarly J. Altmann (1980) found that low-ranking females appeared frequently near attractive individuals (in this case mothers rather than high-rankers), but that high-rankers were more prominent in interacting with them.

The discrepancy between association and grooming in this result suggests that close rankers do not spend more time together, but that when they do they are especially likely to groom. Alternatively, sampling of association within a radius as great as 15m might have failed to detect any effect of rank-difference on closer associates.

ii) Female reproductive state. Females' reproductive state affected their association with other females; and it affected the amount of grooming received more than grooming given (also Rowell, 1968). Consistently, mothers were associated with other females more, and received more grooming from them, while pregnant females associated and were groomed the least. In detail, all female classes groomed mothers the most, and both mothers and lactating females had mothers as most frequent neighbours, although the associations of cycling and pregnant females were less consistent with their grooming. Mothers gave little grooming, least to pregnant females, and all of them received more grooming than they gave (Saayman, 1971a; Altmann, 1980) whereas most other females gave more than they received (Fig. 4.9). Cycling females groomed more than most (perhaps a seasonal bias in observation, 2 XI d).

The attractiveness of mothers is common to baboons (e.g. Rowell, 1968; Seyfarth, 1976), except for hamadryas (Nagel, 1971), and is largely due to the attractiveness of the infant (Rowell et al., 1968) which declines as the infants age (DeVore, 1963; Nash, 1978a; Altmann, 1980). The affiliative and spatial patterns of females in Msembe Troop appeared to be determined largely by this fact (also Chapter 3). The interest in infants among mothers and by their associates such as F7 and F10, may represent maternal behaviour generalised to include the infants of other females (Nash, 1974). However, nulliparous females in Presbytis are reported to learn infant-handling in this way (Hrdy, 1976, 1978). While mother and infant may gain safety in numbers from the attentions of others, and the infants may gain valuable social experience, yet their attentions are not entirely beneficial since they may become so frequent as to cause distress to the mothers (Altmann, 1980).

The four pregnant females' low levels of association and (with one exception) grooming reflect previous reports that they are socially inactive (Saayman, 1971a; Rowell, 1972). This, and their spatial pattern, differ greatly from those of mothers (Chapter 3).

The data on association and grooming contrasted markedly in that the former emphasised relations among mothers (Fig. 4.6) while the latter emphasised relations between other females and mothers (Fig. 4.14). This is partly because mothers groomed so infrequently, since when they did so they still groomed one another the most. The reason that they groom so infrequently may partly be that they are preoccupied with their infants (Altmann, 1980), but perhaps also they receive so much interaction that they are little motivated to increase it. Conversely, other females groomed them more than expected from association, especially cycling and pregnant females who associated comparatively little.

Four females require further comment. Mother F14 was groomed by many females (Fig. 4.14) perhaps because her associations with mothers were less intense (Fig. 4.6). She may therefore have been more accessible, also in that her infant was the oldest and her rank relatively low. Secondly, although the two females who gave birth showed sharply increased association and received more grooming thereafter, yet F18 showed the greatest increase in grooming, perhaps because she was the lower ranking of the two (also Rowell, 1972; Seyfarth, 1976). The frequent association between these two females exemplifies the 'maternity bonds' described by Ransom and Ransom (1971; also Nash, 1976; Altmann, 1980).

Finally, the pattern of relationships in Fig. 4.14 is much influenced by the grooming of F19 who groomed more than any female, and encompassed 15 of the other 18 females, including all the mothers, as groomees. It is possible that as the lowest ranker she was least attractive, and so may have been attempting to establish bonds with others, inevitably higher rankers; but she attracted far less grooming than she gave.

4.5.4c) Relations between males and females: Association and grooming between males and females was more frequent than that between males, but less frequent than that between females. However the most conspicuous dyadic relationships were between some males and females. Higher ranking females had male neighbours more often (Fig. 4.2), which suggests that they were more successful in gaining access to males, or (as implied by Ransom and Rowell, 1972) more attractive to them. Male-female grooming was more reciprocal than that between females, and relations between the sexes were much affected by male class and female reproductive state.

Subadult males showed less involvement with females than did adult males. Both Saayman (1971a) and Packer (1977a) found that females groomed the subadults less, but in the latter case this was because the adults solicited grooming more: although in other behaviours the females also preferred the adults (Packer, 1979a). Three subadults tended to associate and groom with cycling females, and they were evidently more attracted to these than to other females, especially mothers (also Altmann, 1980).

Two subadults had partnerships with females involving frequent association but little grooming, S4 with F12, and S3 with F2; the latter pair shared strong physical resemblance, and may have been siblings. In contrast, S2 and the old F4 were one another's first grooming partners of that sex, but associated little: from other details of their relationship, and from Cheney's (1978) finding that females rarely groom subadults who are not their sons, it is likely that F4 was his mother.

In relations between adult males and females, data on association emphasise the adults' partnerships with cycling females _and_ with mothers, while data on grooming emphasise mainly the former. This was in part because relations with cycling females were more transitory, but also because they involved a conspicuous amount of grooming. The adult males differed individually in their involvement with each female class.

The partnerships between adult males and cycling females were directly concerned with mating, as described elsewhere (Hall, 1962; DeVore, 1965; Saayman, 1970; Hausfater, 1975; Seyfarth, 1978a), and are discussed in Chapters 7 and 8. High-ranking adults spent more time with cycling females, were groomed more by them, and (except for A2) groomed them more. This pattern reflects both the competitive ability of high rankers and the preferences of the females (Chapter 8).

Adult males less frequently groomed or associated with pregnant females, except for A2 (notably with F9), and A6 who groomed often with F12. Such grooming was also noted by Rowell (1968) and Saayman (1971a). These partnerships might have been imposed by the males to obtain grooming, since pregnant females were more accessible to these two peripheral males. However, A2's pregnant partners included at least two females with whom he had mated beforehand: such partnerships may therefore continue relationships established in mating, and might coincide with paternity. Finally, they might represent male investment towards access to the infant, of use in agonistic buffering (Chapter 6). Although A6 did not gain access to F12's infant, yet A2 was the first of the newcomers to gain access to any infant, that of his associate F9 (Ngatwika, pers. comm.).

Adults A7, A3, A4 and A5 shared partnerships with mothers. It is often reported that mothers maintain proximity to adult males, often favouring particular ones (Stoltz, 1972; Seyfarth, 1978b; Altmann, 1980), and that the males often seek out mothers (DeVore, 1963; Hall, 1963; Ransom and Ransom, 1971) so that their affinity appears to be mutual. A3 and A7 competed over access to the new mothers F12 and F18. Both mother and infant gain protection from such males, both passively and actively since males are quick to defend them (DeVore, 1963; Hall, 1963; and especially Altmann, 1980). A general protectiveness to infants may be adaptive behaviour in males, especially males who have fathered a high proportion of them. However, because male-female partnerships may persist through both mating and lactation (Ransom and Ransom, 1971; Seyfarth, 1978b), males may give more protectiveness to those infants that are more likely to be their offspring (Altmann, 1980). Yet in this study the partnerships between the new mothers and A7 could not have been predicted during pregnancy (and no data on their mating are available): and Packer (1980) found no correlation between probable fatherhood and protectiveness to infants. Because not all male-female partnerships persist in this way (Seyfarth, 1978b) it seems likely that some male/mother relationships may coincide with paternity, others may not.

Adult males' relationships with mothers may also allow the male to carry the infants, which as Packer (1980) has shown gives them advantage in agonistic interaction with other males ('agonistic buffering': Deag and Crook, 1971). This is further discussed in Chapter 6.9 Males manipulating infants would groom them, more in restraint than in care (also Nash, 1973; Packer, 1980).

Adult males showed less affiliation with lactating females than with mothers, but from the frequency of their association, and the identity of the males involved, it is likely that many of the partnerships may have waned from more intense relations during motherhood. The most prominent relationship was between A6 and F10.

4.5.5 Grooming between adults and young

Immatures gave most grooming to mothers (also Saayman, 1971a) and cycling females, most of the latter being by young males (Ransom, 1971; Cheney, 1978). Many of the immature female groomers were daughters of the groomees (Lee, pers. comm.). Many of the differences between females may reflect mother-offspring relations: thus F2's frequent grooming was largely to her juvenile son (Lee, pers. comm.).

4.5.6 A comparison of the males

The males showed a full range in apparent age from young subadult (S4) to aged adult (A8). If the behaviour of each may be taken as representative of its age, the data suggest a hypothetical life-history of male affiliative relations.

1) Subadults: The three younger subadults associated mainly with one another, and with the focal adult males; and with cycling females, with whom they exchanged grooming. They associated less with other female classes, and groomed least with mothers. They groomed with immatures more than did adult males - perhaps because of kinship - and two had partnerships with females who may have been kin. The older S1 spent less time with either sex, and did not groom with cycling females despite his higher rank.

Given the peripherality of S1, these data suggest that subadults have few bonds with females other than cycling females, and their kin, and that both these and their partnerships with males may wane as they near adulthood and emigration (Packer, 1979a).

2) Young adult/newcomer males: A1 and A2 spent as much time near males as did longer-term residents. Their two salient features are the rarity of their association with mothers and lactating females (they groomed with neither); and their conspicuously frequent association and grooming with cycling females. A2 was often involved with pregnant females also.

It is by no means usual for newcomers to assume the highest dominance ranks as they did here (Hausfater, 1975; Packer, 1979a), so that it may not be typical for them to interact so much with cycling females, unless preferred by them. However their lack of involvement with mothers is probably typical. They also tended to be peripheral during travel, and association with pregnant females (as for A2) may be a consequence of this.

3) Prime adults: A3, A4 and A5 shared the following features. They tended to have subadult male neighbours, and they were near mothers much more than were the newcomers. They groomed mothers a little, and pregnant females least, but their main association and grooming was with cycling females.

These prime adults had been in the troop at least a year, and their behaviour suggests that familiar prime adult males become the focus of groups of mothers, but that they interact with cycling females in accordance with their dominance rank.

4) Older adults: A6, A7 and A8 differed individually, and will be discussed in turn.

A6 did not associate unusually with any class, except that he had notable partnerships with one pregnant and one lactating female.

A7 was involved most with cycling females and mothers, least with pregnant females. In this he therefore resembled the three prime adults; except that females tended not to travel with him (Chapter 3). But his frequent involvement with mothers was unique. He monopolised access to the two with newest infants (despite competition from higher-ranking A3), he groomed them more than they groomed him, and was the first to have access to their infants (Chapter 6). Packer (1977a,1979b) also found that old males groomed females more, echoing Seyfarth's (1978b) description of a male grooming females who no longer preferred him (paralleled also in Kummer and Kurt, 1965, pp.74-75, and Nagel, 1971, p.54). In the light of this, A7 may have been attempting to strengthen relationships with these mothers, perhaps because they were likely to prefer the prime adults (Chapter 3). The short-term benefit of access to their infants for agonistic buffering would have been especially valuable for a male of advancing age and presumably declining rank.

The aged A8 appeared further advanced in such changes. His main associates were lactating females, but he was seldom groomed by females at all - he groomed them more than the reverse. But he groomed conspicuously often with immatures (Fig. 4.11), mainly brown-phase infants, and occasionally carried them against other males. He therefore appeared to have lost most bonds with females, but to be cultivating relationships with immatures, for the observed benefits of grooming returned and some agonistic buffering.

These data suggest that ageing males lose their affiliative bonds among females, but that they may counter this by investing more grooming in particular partners, in this case mothers or immatures. An alternative interpretation for A7 and A8 would be that they were establishing protective relationships with infants that may have been their offspring: there are no data on paternity to assess this likelihood, but such behaviour might be expected in older males of lower reproductive value (Kurland, 1977; Packer, 1980).

CHAPTER 5

Sociosexual Behaviours

5.1 This chapter describes the distribution of two behaviours, presenting and mounting (defined in Appendix I.c). Because these two patterns are integral to copulation, but yet occur in wider contexts including between members of the same sex, they are classified as sociosexual behaviours (Hanby, 1976).

Presenting is also described as an act of subordinance, and mounting an assertion of dominance, so there has been confusion as to whether they are motivated sexually or agonistically. The view that they are primarily sexual assumes that because females present to males, and males mount, and yet males are dominant to females in most species, the two behaviours have secondarily come to express dominance relations. An extreme form of this view is that the present undercuts the agonistic impulses of the partner because it is a sexual invitation and elicits instead a sexual response ("prostitution", Kempf, in Maslow, 1936).

The alternative proposition, that mounting is primarily an act of dominance and presenting of submission, so that mating is only possible if the male is dominant (Maslow, 1936), has received little support. Instead Rowell (1974) emphasises that within a range of species there is no universal context of mounting (or presenting) except for copulation itself, so that 'sexual' patterns grade into agonistic and friendly patterns in different ways in different species.

The situation in any one species can best be understood from the ontogeny of the behaviours. Hanby (1976) considers that in Old World primates, 'sociosexual' behaviours develop in two contexts: contacting and copulation. The preliminary evidence in baboons is that they first arise in contexts neither sexual nor agonistic. Mounting appears to be derived from the infant's climbing to ride dorsally on the mother: the mother's invitation to the infant to do so is often indistinguishable from a present (Owens, 1976). Presenting is related to the fact that adults often inspect the ano-genital region of infants, sometimes lifting the rear to do so. Older infants initiate such interactions themselves, even by backing into the adults; presenting appears to develop from this pattern (Ransom and Rowell, 1972), and it may therefore be important in individual recognition (Hinde, 1974).

The data presented here portray the distribution of these behaviours with respect to the sex, class, and rank of the participants. Dyadic partnerships are described, and the contributions of presenting and mounting to the social relations of the adults are discussed.

PART 2. METHODS AND CATEGORIES

5.2.1 Because of the ad libitum method of recording behaviour, fine distinctions were not made between different types of present and mount (cf. Kummer and Kurt, 1965; Struhsaker, 1975). Secondly the distinction between sexual and sociosexual behaviour was an arbitrary one: non-intromitted mounts are considered here, intromitted mounts in Chapters 7 and 8, although many of the former were clearly failed attempts at the latter.

A third problem is that presents and mounts were not entirely independent. Of 184 presents to adult and subadult males for which the response was seen, 10.3% elicited mounting. This accounts for about 8.9% of these males' unintromitted mounts analysed here: possibly more of these mounts had been preceded by presents, since mounts were more conspicuous. Because the measures overlapped by so little, all interactions have been retained in analysis.

Presents were only recorded if made by adult females to males or immatures. This was because they were to be used in analysis primarily as an index of female preference for males, but it was not felt they would provide a useful index of rank within either sex (mainly from personal observations of olive baboons at Gombe). This proved to be an error, because the few presents which were incidentally recorded within-sex were mainly by subordinates; Stammbach (1978) found this also among female hamadryas.

Analysis of mounting between males is presented more fully in Chapter 6, as part of a description of male-male relationships.

Fig. 2.2 suggested that more presents might have been recorded if observations had continued later in the day, but there is no evidence that this applies to mounting. Table 2.6 also showed that individual differences in present-rates were not closely paralleled by observability differences, but that rates of mounting given by both males and females were.

PART 3. SEX AND CLASS DIFFERENCES

5.3.1 Females' present-rates are known to change with reproductive state (Rowell, 1967a; Saayman, 1970), in part following hormonal changes but in macaques also influenced by recent sexual experience (Zumpe and Michael, 1977) and social context (Slob et al., 1978). The rate at which males mount females varies in the same way, being highest for cycling females at full swelling (Rowell ibid: Hausfater, 1975). Males are commonly reported to mount one another, but female-female mounting is less common.

Because all males were dominant to all females, heterosexual mounts by males were inevitably downrank, while presents by females were uprank. Even within sex, however, most mounts were downrank (5.4.2). Rates of mounting by male and female are therefore only compared if calculated in the same rank-direction, and class-rates within sex are analysed separately downrank and uprank (Ch.2 XIII a.2).

5.3.2 Sex differences

Each male mounted on average every 17½ hours, while each female did so only every 105½ hours. Mean dyadic rates within and between sex are listed in Table 5.1. No female was ever seen to mount an adult or subadult male. There was no clear indication that males mounted females more than one another (T=21, corr. obs. 19, n 12, n.s.), nor more than they mounted males of lower rank (T=18, corr. obs. 21, n 11, n.s.). However, mounting among males was more frequent than that among females (U=46, corr. obs. 42, n 12, 18, $p < .02$), which as Table 5.II shows was in part because males mounted uprank consistently more than females did.

5.3.3 Class differences

5.3.3a) Mounting between males: Data presented in the next chapter (6.8.3) show that male classes differed only in that adults mounted lower ranking adults at particularly high rates, significantly more than they mounted subadults ($p < .05$).

Table 5.1 Mounting within and between each sex

Mean dyadic rates per 100 hours, standard deviation in brackets. (n = 350 mounts)

	Recipients	
	Males	Females
Mounters		
Males (12)	.15 (.14)	.22 (.14)
Females (18)	-	.04 (.05)

Table 5.II Mounting within each sex

Mean dyadic rates per 100 hours, to dominants (uprank) and to subordinates (downrank)

	Between males (11)	Between females (17)	Mann-Whitney
Uprank	.06 (.08)	.02 (.03)	U=23.5 ± obs. corr. $p < .002$
Downrank	.15 (.19)	.08 (.09)	U=68, corr. obs. 67, $p > .1$

FIG. 5.1

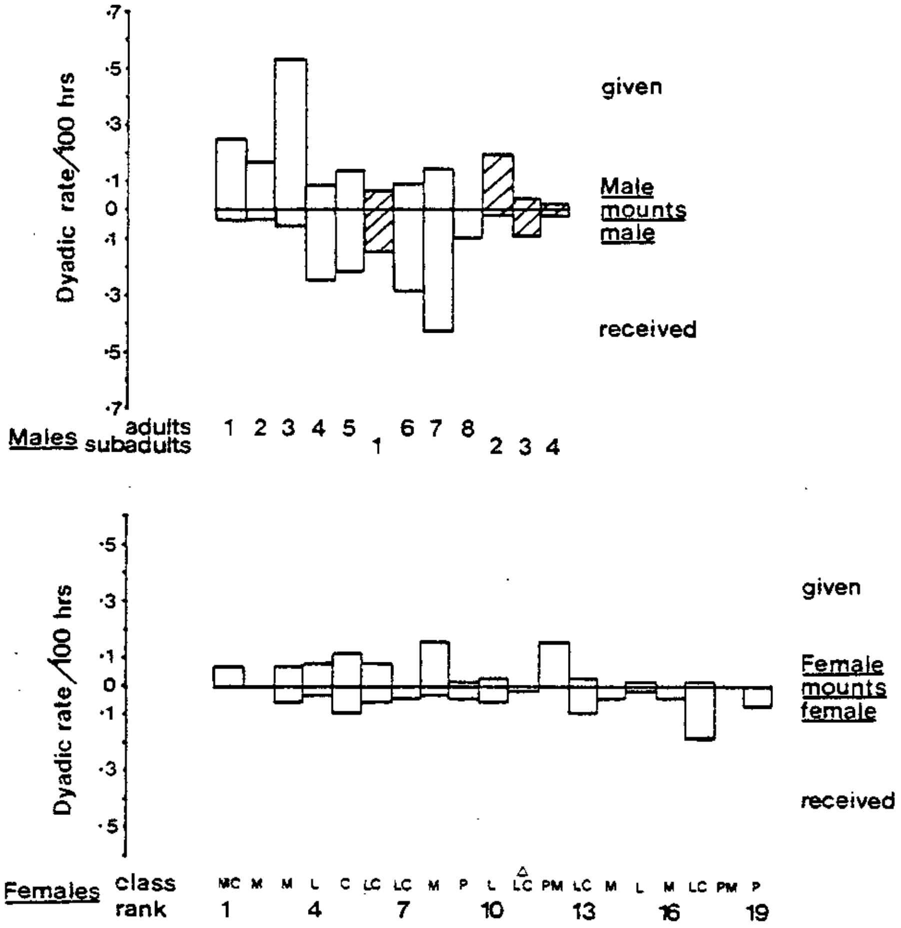


Fig. 5.1. Mounting rates between males (upper figure) and between females (lower figure). Mean dyadic rates per hundred hours, of mounts given (above x-axis) and received (below it). Subjects arranged in descending order of dominance rank from the left; females are C - cycling, P - pregnant, M - mothers, L - lactating, with the sick female △ .

5.3.3b) Mounting between females: Mounts uprank were too infrequent for analysis, but comparisons of rates downrank in Table 5.III show that reproductive state did not affect females' rates of mounting one another, but did affect how often they were mounted. Cycling females were mounted conspicuously often.

5.3.3c) Females present to males: Female classes presented to males at different rates (Table 5.IV: $p < .01$), with cycling females presenting most, and mothers least of all. All classes tended to present more to adults than to subadults, significantly so for those females who presented often enough over the whole study to compare ($p < .01$). Thus the rates from cycling females to adults were particularly high (Figs. 5.2 and 5.3).

5.3.3d) Males mount females: Adult and subadult did not differ consistently in their rates of mounting females (Table 5.V). Subadults did not mount females at random ($p = .02$), all favouring cycling females (Fig. 5.2). Adult males were not consistent in their preference for particular classes, but some mounted cycling females very often (also Fig. 5.2).

5.3.4 Interactions between adults and immatures

The scant data on females' presents to immatures show that classes differed (Table 5.VI: $p < .05$) with cycling females presenting most and again mothers the least. Classes did not differ in the rates at which they mounted immatures, but differed in their receipt of mounts (Table 5.VI: $p < .01$), with cycling females receiving most, and the two male classes the least. The sex of the immature partners was not usually identified, but in 52 mounts on females in which it was, 47 were by young males: yet in the eight mounts by adult females on identified immatures, all were on females.

PART 4. DOMINANCE RANK AND SOCIOSEXUAL INTERACTION

5.4.1 The ideas that presenting is an act of subordinance, and mounting an act of dominance, are supported by those studies of whole groups which show that high rankers mount more and present less (Hall and DeVore, 1965; Rowell, 1966b; Richards, 1974; Deag, 1977). However such correlations may be spurious (Rowell, 1974): in any pair, mounting may be more likely from male to female, and presenting from

Table 5.III Mounts between females

Mean dyadic rates per 100 hours, downrank only (i.e. from dominant to subordinate). Standard deviations in brackets. n = 62.

	Female classes				Kruskal-Wallis
	Cycling	Pregnant	Mothers	Lactating	
Mounts given	.09 (.11)	.06 (.09)	.16 (.27)	.06 (.05)	H = .03, corr.obs. .04 p c 1.0
Mounts received	.26 (.14)	.04 (.04)	.02 (.03)	.07 (.06)	H = 12.15,corr.obs. 11.71 p < .01

Table 5.IV Females present to males

Mean dyadic rates per 100 hours (s.d. in brackets), calculated over all females using whole-sample data, and for each class including part-sample data. (N = 194).

	Recipients			Wilcoxon
	All males (12)	Adults (8)	Subadults (4)	
Presenters				
All females (18)	.19 (.19)	.27 (.27)	.03 (.05)	T=0 (± obs. corr.) n 13. p<.01
Classes:				
Cycling (5)	.77 (.37)	1.08 (.54)	.12 (.10)	no test
Pregnant (4)	.11 (.04)	.16 (.05)	.01 (.03)	"
Mothers (8)	.03 (.03)	.05 (.04)	.01 (.02)	"
Lactating (7)	.14 (.10)	.19 (.13)	.05 (.07)	"
Kruskal-Wallis	H=16.25 corr. obs. 16.70 p. <.01			

FIG. 5.2

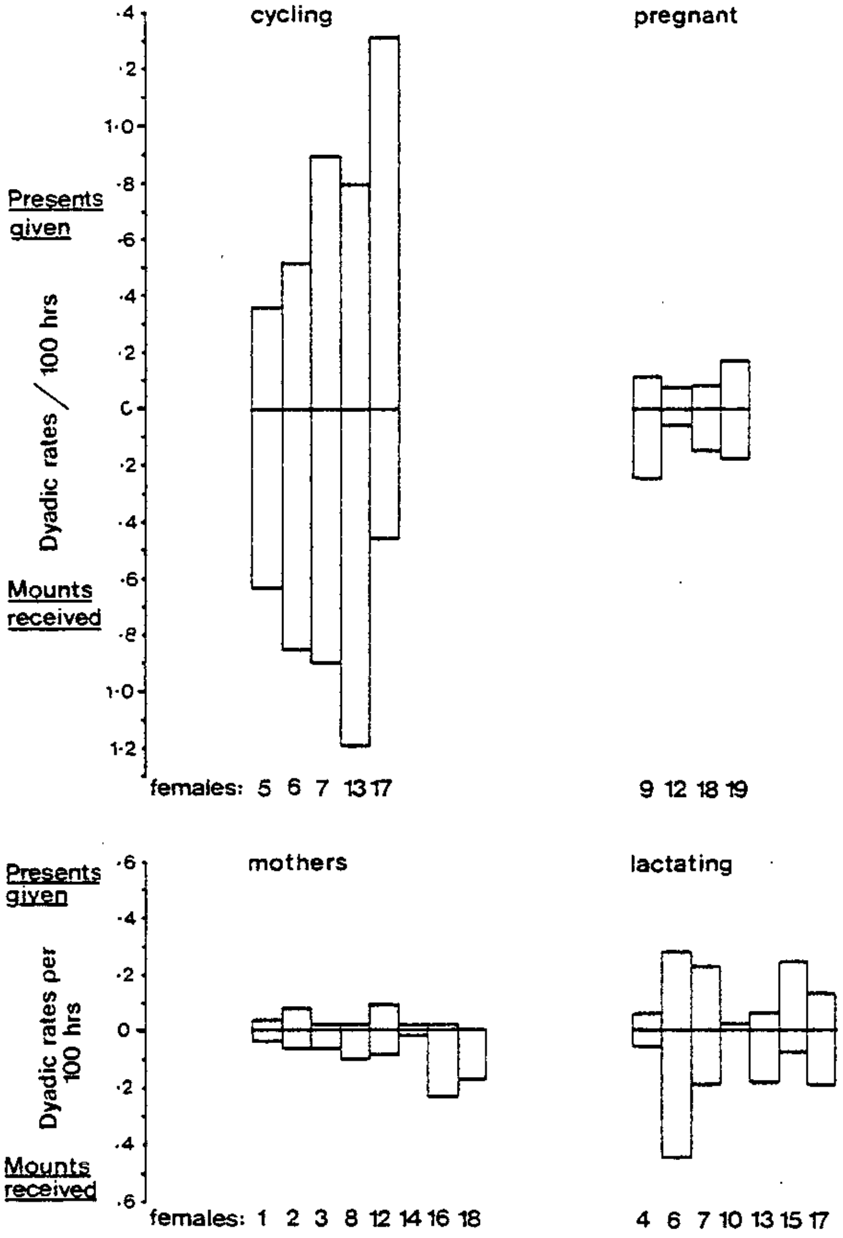


Fig. 5.2. Female class-members' rates of presenting to males (above x-axis), of being mounted by them (below it). Layout and scale as in Fig. 5.1; females identified by their dominance rank numbers below each histogram.

FIG. 5.3

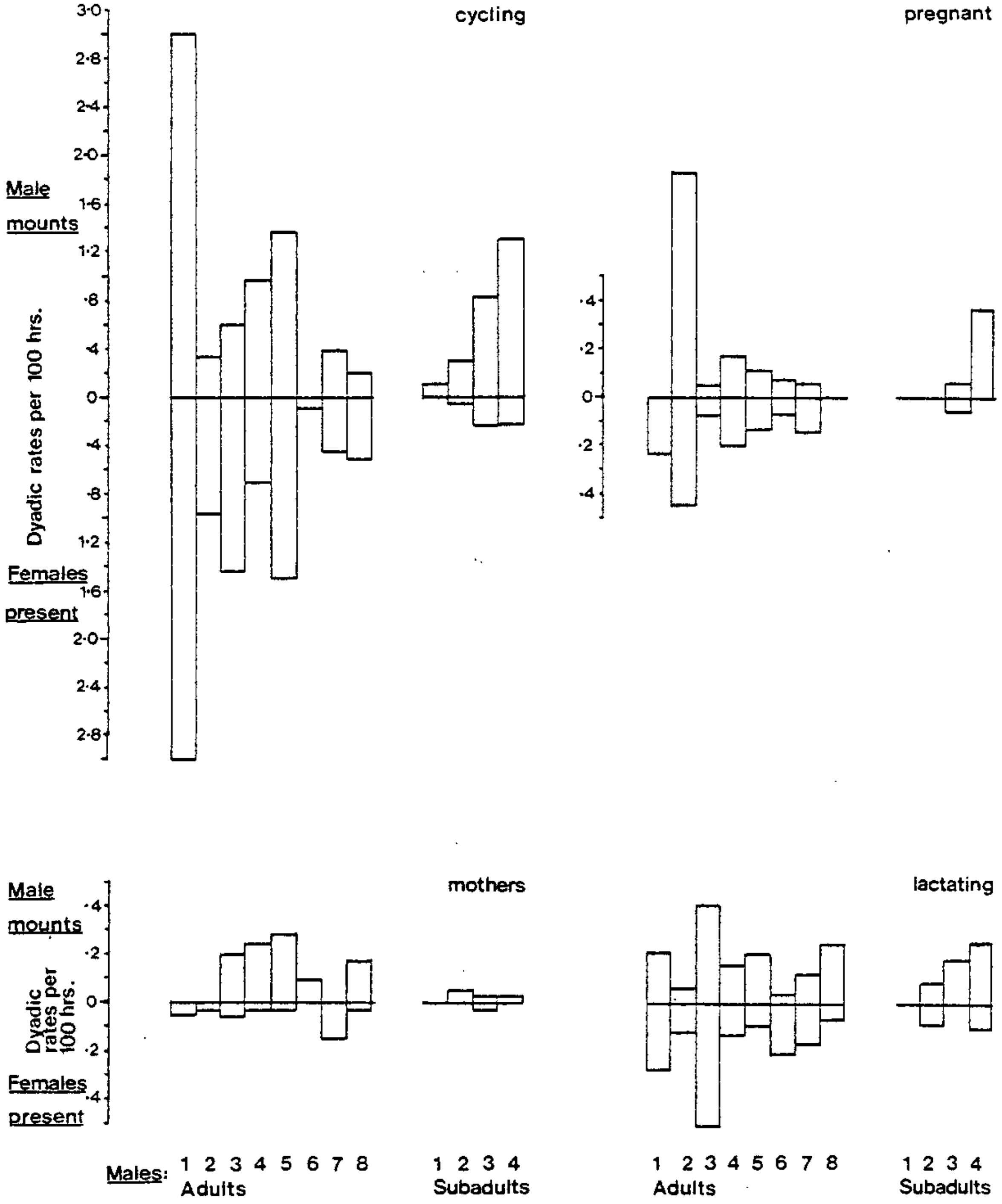


Fig. 5.3. Males' rates of mounting females in each class (above x-axis) and of receiving presents from them (below it): this is therefore the inverse of Fig. 5.2. Layout as in the preceding two tables, but the scale of the top left histograms (with cycling females) are reduced to half those of the rest.

Table 5.V Males mount females

Mean dyadic rates per hundred hours (s.d. in brackets). n = 210.

	Female recipients					Freidman
	All (18)	Cycling	Pregnant	Mothers	Lactating	χ_r^2
Mounters						
Adults (8)	.25 (.14)	.86 (.98)	.17 (.31)	.12 (.12)	.17 (.12)	5.66, df 3 $p < .2$
Subadults (4)	.15 (.12)	.63 (.54)	.11 (.18)	.03 (.02)	.13 (.11)	8.40, df 3 $p = .02$
Mann-Whitney	U = 9 (± obs.corr.) $p = .28$					

Table 5.VI Interactions between adults and young

Mean subject rates per 100 hours (s.d. in brackets)

	Behaviours by adult subjects		
	Presents given (n=17)	Mounts given (n=25)	Mounts received (n=152)
Classes			
Ad. males (8)	-	.17 (.27)	.17 (.26)
Sub. males (4)	-	.33 (.12)	.22 (.32)
Cycling (5)	.69 (.59)	.65 (.65)	7.54 (5.17)
Pregnant (4)	.17 (.21)	.06 (.11)	.79 (.79)
Mothers (8)	.03 (.08)	.08 (.24)	.35 (.41)
Lactating (7)	.19 (.27)	.14 (.29)	.97 (.89)
Kruskal-Wallis	H = 9.17 (corr.obs.8.40) $p < .05$	H = 9.13 (8.69) n.s.	H = 17.85 (18.14) $p < .01$

female to male, but since males are often higher ranking such correlations become an inevitable result of sex-differences. Similar arguments apply to size if the larger of any pair is more likely to mount and to be dominant. The importance of rank per se can only be assessed by examining interactions between animals of similar sex and size.

Accordingly in this section the rates of mounting within sex are examined for evidence of any effect of dominance. Some studies report also that mounting is more frequent between partners closer in rank (Tokuda et al., 1968; Owens, 1976). Secondly, the distribution of presents and mounts between the sexes are analysed for evidence that rank affects them through competition or attractiveness.

5.4.2 Rank-direction of mounting within each sex

Data in Table 5.VII indicate that most mounts were from dominant to subordinate ($p < .001$ in both sexes). A higher proportion were downrank among females than among males ($p < .05$). Most females showed higher dyadic mean rates of mounting to subordinates than to dominants (T=2 ± obs. corr. n 11, $p < .01$), but this tendency was not general among males (T=16, corr. obs. 13, n 9, n.s.).

5.4.3 Dominance rank and interaction rates

5.4.3a) Mounting among males: Correlation coefficients between males' ranks and their rates of mounting are listed in Chapter 6 (6.8.4). They show that higher ranking males mounted more overall ($p < .05$: also Fig. 5.1a): this was partly because subadults, who mounted less, were of lower rank, but the tendency was also apparent within each class. Secondly, lower-ranking males did not receive more mounts, reflecting the fact that the highest rates were downrank among adults, so that lower ranking adults received more ($p < .05$: Fig. 5.1a). It is also shown that high ranking adults mounted more downrank ($p < .01$), i.e. more than expected merely from the availability of subordinates to each.

5.4.3b) Mounting among females: Females' dominance ranks are compared with mounting rates in Table 5.VIII: although mount-rates were not proportional to dominance rank (also in Fig. 5.1b) yet the coefficients for mounts given were all positive, and for mounts received, negative. The weakness of the linear correlation probably reflects paucity of data and conspicuous individual differences, since the direction

Table 5.VII Rank direction of mounting within each sex
Number of mounts given to dominants (uprank) and to subordinates (downrank) in each sex. Chi square goodness-of-fit compares with 50:50 expectation: chi square 2 x 2 compares males with females.

	Uprank	Downrank	% down	χ^2 goodness of fit
Between males	20	58	74.4%	18.57. $p < .001$
Between females	7	55	88.7%	37.16. $p < .001$

2 x 2 χ^2 4.34, $p < .05$

Table 5.VIII Dominance rank and mounting between females
Spearman rank correlation coefficients between females' dominance rank and ranks for rates of interaction with all other females. Results of tests repeated on scores corrected for observability are shown in brackets, (=) if unchanged $^{*}p < .05$

	Mounts given		Mounts received	
Subjects (N)				
All females (18)	$.469^{*}$	$(.453)^{n.s.}$	-.291	(-.251)
Cycling (5)	.667	(=)	-.600	(-.500)
Pregnant (4)	.738	(=)	-.316	(=)
Mothers (8)	.343	(=)	-.166	(-.152)
Lactating (7)	.649	(=)	-.036	(=)

constancy was so high (5.4.2).

5.4.3c) Presenting: The rates at which females presented were independent of their dominance rank (Table 5.IXa) except possibly among cycling females (Fig. 5.3a). High ranking males received more presents (Table 5.IXb), again in part because subadults received less but also because higher ranking adults received more ($p < .05$). The four female classes did not present most to the same adults: Kendall coefficient of concordance comparing the eight adults' rank-orders for presents received from each class yields W=0.45, corr. obs. 0.40, $p > .1$. Therefore the high rates to high-ranking adults were mainly due to the cycling females ($p < .05$), and possibly the pregnant ones, (as evident in Fig. 5.2).

5.4.3d) Mounting between classes: Rates of mounting with partners other than adults of the same sex are compared with dominance rank in Tables 5.X and 5.XI. There was no relation between them except that high ranking adult males mounted females more ($p < .05$). The adults' rank-order for mounting was not the same to all female classes (Kendall W, as above, 0.28, corr. obs. 0.27, $p > .3$), and their overall result seems determined primarily by their mounting of cycling and pregnant females (Fig. 5.2). In contrast, subadults of lower rank tended to mount females more, especially cycling females.

5.4.4 Mounting and dominance-rank differences

The mean dyadic rates of mounting at each rank-difference were calculated within each sex, uprank and downrank separately, and analysed as in 2.XIII c). Among females, mounting tended to become less frequent at more distant ranks (Fig. 5.4a: r_s .566, n 14, $p < .05$), not apparently because they mounted partners within two rank places, but all first partners were within seven places of rank (Table 5.XII: Fig. 5.4b). Females' mounts uprank were too few to analyse.

Among males, however, there was no relation between rank-difference and mount rates (Chapter 6.8.5). In both sexes, mounting was most frequent to partners five rank places away, due to two pairs within each sex and presumably a chance result.

Table 5.IX Dominance rank and presenting by females

Spearman rank correlation coefficients between subjects rank-orders for rates of presents given or received compared with their dominance ranks. Coefficients derived from scores corrected for observability, in brackets; (=) if unchanged. *p <.05 **p <.01; d means insufficient data.

(a) Females present

Female subjects (n)	to males	to immatures
All (18)	.029 (-.007)	.031 (-.107)
Cycling (5)	-.900 (-1.000)*	d.
Pregnant (4)	-.400 (=)	d.
Mothers (8)	d.	d.
Lactating (7)	.536 (=)	d.

(b) Males receive presents

Male subjects (n)	from: All females	Classes Cycling	Pregnant	Mothers	Lactating
All males (12)	.778** (.776)**				
Adults (8)	.810* (.833)*	.738* (.762)*	.738* (.667)$^{n.s.}$	d.	.476 (.405)
Subadults (4)	-.633 (-.800)	d.	d.	d.	d.

Table 5.X Dominance rank and mounts between the sexes
Spearman rank correlation coefficients between subjects' rank order for rates of mounting given or received compared with dominance rank. Coefficients with observability corrections in brackets.
(=) if unchanged; d = insufficient data; *p < .05, **p < .01

(a) Males mount females

	Recipients				
	All females	Classes:			
Mounters		Cycling	Pregnant	Mothers	Lactating
All males (12)	.448 (.497)				
Adults (8)	.714* (.857)**	.571 (.691)	.180 (=)	-.195 (-.317)	.024 (=)
Subadults (4)	-1.000 (=)	-1.000 (=)	d.	d.	d.

(b) Females receive mounts from males

		r_s	corr. obs.
Subjects:	All females (18)	-.127	(-.133)
	Cycling (5)	.000	(.100)
	Pregnant (4)	.200	(=)
	Mothers (8)	-.587	(-.595)
	Lactating (7)	-.107	(-.179)

Table 5.XI Adults' dominance rank and rates of mounting with immatures

Spearman rank correlation coefficients, presented as in the preceding tables, between subjects' dominance ranks and their ranks for rates of interaction with immature partners

Subjects (n)		Mount immatures		Receive mounts from immatures	
All males (12)		.026	(.138)	-.175	(-.108)
All females (18)		.050	(.065)	.179	(.106)
Females:	Cycling (5)	.616	(.308)	-.900	(-.700)
	Pregnant (4)	d.		.200	(-.400)
	Mothers (8)	d.		.100	(.000)
	Lactating (7)	d.		-.018	(.071)

Table 5.XII Dominance rank-difference and mounts between females

The number of first partners within two and within seven places of rank compared with that expected from partner availability

	Rank-places			
	1-2 :	3+	1-7	8+
Obs:	4	8	12	0
exp:	2.26	9.74	7.08	4.92
binomial prob:	.260		.002	

FIG. 5.4

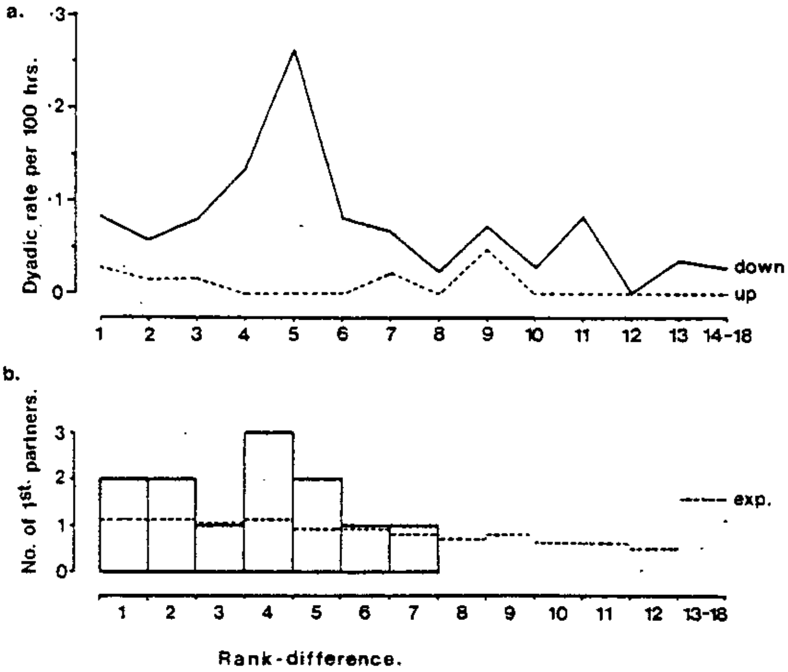


Fig. 5.4. Dominance-rank difference compared with rates of mounting between females. The upper figure shows the dyadic mean rate of mounting for pairs at each rank-difference, calculated separately uprank (dotted line) and downrank. The lower figure shows the distribution of first mounting partners, compared with that expected had such partnerships occurred at random; the expected line is not straight because some subjects were not seen to mount at all.

FIG. 5.5

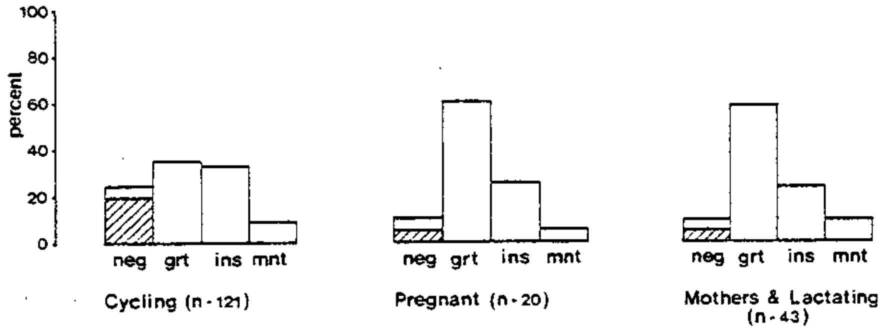


Fig. 5.5. Males' responses to the presents of three subsets of females, all subjects pooled. Categorised as negative responses (neg, of which the shaded part is the minimum proportion in which the male looked away), greets rear (grt), inspects (ins), and mounts (mnt).

PART 5. QUALITY OF INTERACTIONS

5.5.1 Response to presents

For those 210 presents for which the males' response could be seen, females were greeted in 40.5%, inspected in 30.0% and mounted in 11.9%: only 1.4% led to intromitted mounts, and as many as 17.6% received negative response. Fig. 5.5 shows that adult males responded in the same way to pregnant females, mothers, and lactating females, but that these pooled responses differed from those to cycling females (χ^2 11.08, d.f. 3, $p < .02$), chiefly in that the latter received fewer greetings and more negative responses, especially by males looking away.

The male classes' pooled responses are shown in Table 5.XIII: there was some heterogeneity within classes, but in general adult males showed fewest mounts and more negative response, and newcomers looked away the most.

5.5.2 Quality of mountings

a) There were insufficient data to separate the data from each individual, but Table 5.XIV compares the quality of mounts between different classes of partner. Chi-square tests revealed significant differences between classes in terms of (a) the proportion of all mounts (including half- and attempt-mounts) in which the full mounted position was attained, and (b) the proportions of these full mounts with and without pelvic thrusting (definitions: Appendix I: XVI).

Mounts between males were usually full mounts, and thrusting occurred in about half of them. Mounts by females were usually full mounts, but females seldom thrusted. When males or immatures mounted females, they were less likely to attain full mounts, but when they did so thrusting was frequent.

5.5.2b) Quality of mounts within sex: The data gave no indication that the likelihood of attaining full mounts, or of thrusting, was affected by reproductive state among females nor by dominance or class-differences among males.

5.5.2c) Mounts upon females: All classes attained proportionately fewer full mounts upon cycling females than upon other females (Table 5.XVa), apparently because cycling females avoided more (described below). Adult males showed proportionately less thrusting on non-cycling females ($p < .01$; Table 5.XVb).

Table 5.XIII Responses to females' presents by different subsets of partners. The percent scores compared: that in brackets is the minimum percent in which the male looked away. Immatures include both sexes.

	Responses					
	Negative (Looks away)		Greets rear	Inspects	Mounts	Total
Newcomers (2)	24	(21)	42	30	5	82
Resident adults (6)	16	(9)	46	27	11	102
Subadults (4)	10	-	20	30	40	10
Immatures (40)	0	-	13	50	37	16

Table 5.XIV Differences in the quality of unintromitted mounts between various classes. On the left is shown the percent of all mounts (including half- and attempt-mounts) which were full mounts. On the right is shown the percent of those full mounts in which pelvic thrusting was seen.

χ^2 in each case compares the proportions of the two types of mount.

	% full	N	% thrust	N
Partners:				
Male to male	95.4	65	56.5	62
Male to female	74.5	196	62.3	146
Female to female	92.0	50	8.7	46
Female to young	92.3	13	0	12
Young to female	75.9	141	71.0	107
	χ^2 20.71 $p < .001$		χ^2 68.90 $p < .001$	

Table 5.XV Quality of mounts

Mounts given to cycling females compared with mounts to other females: for (a) the proportion of the total which were full mounts, and (b) the proportion of the full mounts which included pelvic thrusting, as in Table 5.XIV.

(a) Percent which were full mounts

	Recipients					
	Cycling females		Non-cycling females		χ^2	p
Mounters	%	N	%	N		
Adult males	67.4	(86)	88.5	(61)	7.62	$<.01$
Subadults	61.5	(26)	94.7	(19)	4.87	$<.05$
Immatures	69.6	(102)	92.3	(39)	6.75	$<.01$

(b) Percent full mounts including thrusting

	Cycling females		Non-cycling females		χ^2	p
Mounters	%	N	%	N		
Adult males	72.4	(58)	40.7	(54)	10.20	$<.01$
Subadult males	81.3	(16)	77.7	(18)	no test	
Immatures	73.2	(71)	66.7	(36)	no test	

5.5.2d) Females' avoidance of mounts: Females would sometimes move out from under a male mounter, usually before (but sometimes after) he had attained the full mount position. (This avoidance of mounting is distinct from agonistic avoidance and from the locomotory response to intromitted mounts, defined in Appendix I: (VI and (XII.c) respectively). Table 5.XVI shows that cycling females avoided a higher proportion of mounts than did other females (χ^2 12.18, d.f. 1, $p < .001$), a tendency apparent with all classes of mounter. Non-cycling females also avoided adult males' mounts comparatively often. The fact that cycling females avoided adults and subadults more was probably because these males mounted so much at full swelling (including with intromission) that avoidance increased also (7.5.3c). Cycling females' avoidance was the cause of 82% of the incomplete mounts by adult and subadult males, but only 22.5% of those by immatures.

5.5.2e) Wrongly oriented mounts: The mounts of adult and subadult males were all correctly oriented from the rear (Table 5.XVII), but females and especially immatures tended to mount at other angles.

5.5.2f) The timing of mounts between females: Mounts between females tended to be clumped in time, in that some days were characterised by frequent female mounting. Although such mounts were seen on average only once in every seven hours, yet nearly 18% of them took place in four periods of under 30 minutes (n=62). This appeared to be because a participant in the mounting would then give or receive mounts with another, and heterosexual mounts were sometimes involved as well.

In the longer term the incidence of such mounting was associated with mating. When the average rate of intromitted mounts was calculated over the 83 days of observations, 29 days had rates above average, and were designated mating-days. Of the 62 mounts between females, 35 occurred on mating days, which is a significantly higher proportion than the expected (21.7 mounts) had they occurred at random over all study days (χ^2 12.54, d.f. 1, $p < .001$). Female-female mounting was therefore related to mating in some way. However, 21% of such mounts, including some clumped in time, occurred on days when no mating was seen at all, so that other factors were also involved.

Table 5.XVI Avoidance of mounts

The proportion of mounts by adult and subadult males, and by immatures that were avoided by cycling and non-cycling females.

	Mountees			
	Cycling females		Non-cycling females	
	% avoid	N	% avoid	N
Mounters				
Adult males	35.4	96	19.1	68
Subadult males	39.3	28	0.0	21
Immatures	15.5	103	2.4	42
Overall	26.9	227	10.7	131

Table 5.XVII Wrongly oriented mounts

The percent of full mounts by each class which were wrongly oriented

Mounter:	Adult male	Subadult male	Female	Immature
Total:	191	50	72	124
% wrong:	0%	0%	4.3%	14.5%

PART 6. DYADIC RELATIONS

5.6.1 Interactions between males

Mounting between males is further examined in Chapter 6. There is little to add to the individual differences apparent in Fig. 5.1a, except that A3 was responsible for all the conspicuous dyadic partnerships: he mounted most A7, then A5, then A4, that is, the other focal males. A7 and S2 tended to mount higher rankers.

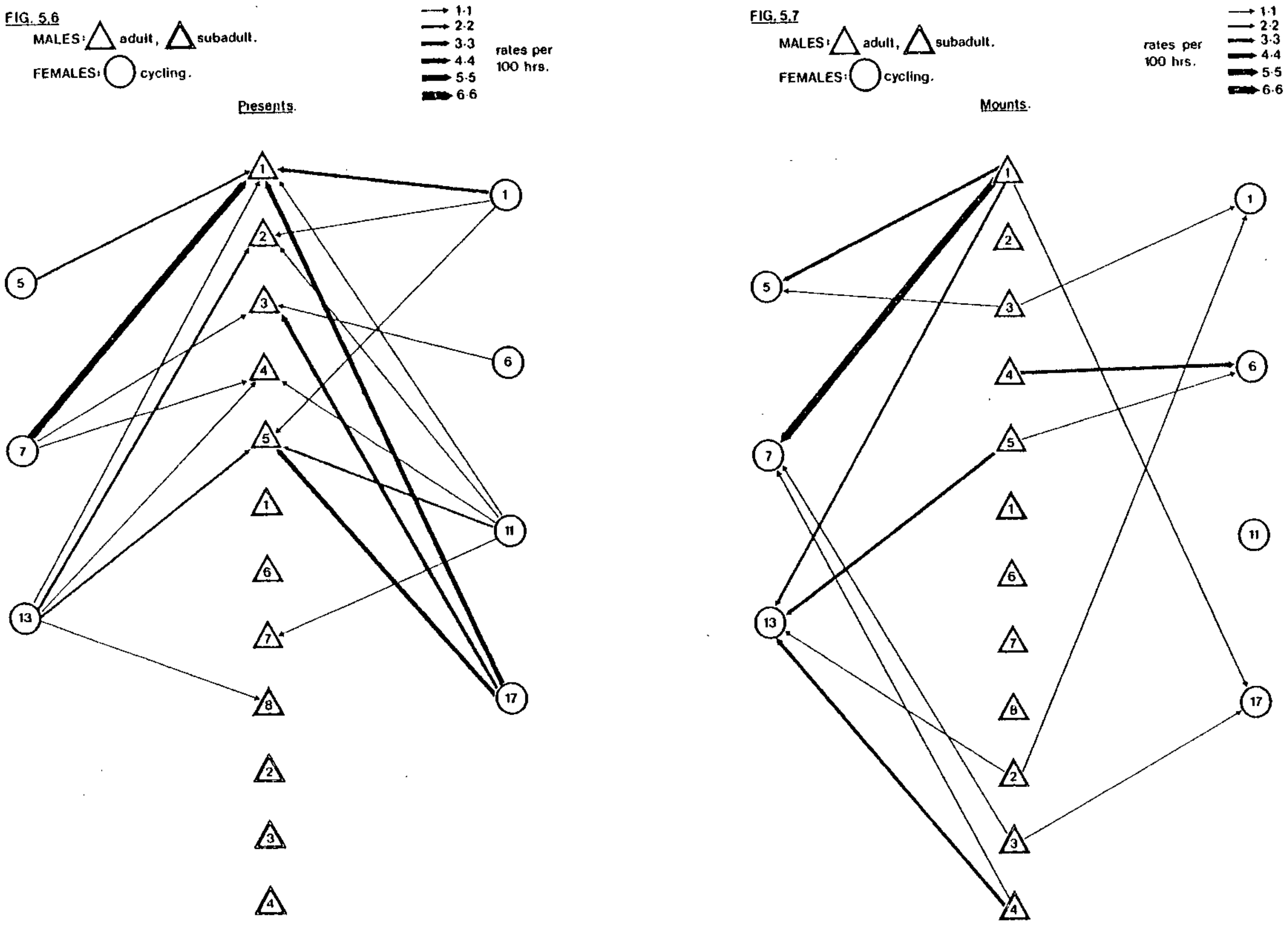
5.6.2 Interactions between females

Mounting was seen in 22.8% of all pairs of females (n=171). Three females gave 53% of the 62 mounts, namely F12, F8, and F5. Three females received 45% of all mounts, and all cycled during the study; F17, F13, and F5. Neither of the two most frequent mounting pairs was ever seen grooming together. F12 and F17 seldom associated, and F12 mounted F17 mainly at the end of the study when she was a mother and F17 was cycling. F8 and F13 became more frequent associates after the latter resumed cycling, which was when mounting occurred.

5.6.3 Interactions between the sexes

Rates at which cycling females presented to particular males are shown in Fig. 5.6. The pattern illustrates how females presented more to high ranking adults than to subadults or to older adults A6, A7 and A8. Three females presented most to A1, namely F1, F5, and F7. There were no other conspicuous partnerships between the sexes except that F9 presented to A2.

In Fig. 5.7 is shown the comparable pattern for males' mounting. This contrasts from presenting in that the high-ranking adults were less obviously involved (although their mount rates were still high), while the subadults were more so. Two pairs were one anothers' first partners on both measures, namely A1 and F7, and A5 and F13, although all of their mounts were independent of their presents. Otherwise the pattern corresponds only from A1 to F5 and F13. The sick female F11 received few mounts despite presenting to several males.



Figs. 5.6 & 5.7. Rates at which cycling females presented to males (5.6) and were mounted by them (5.7). Dyadic rates per hundred hours, using part-sample data. Males in order of dominance rank descending from the top. Females also named by dominance rank, the higher rankers nearer the top. These figures illustrate 73% of the 128 presents, and 69% of the 121 mounts, between these animals.

PART 7. OVERVIEW AND DISCUSSION

5.7.1 Contexts of sociosexual behaviours

Most presents by non-cycling females appeared simply to be affiliative, with an element of appeasement or deference as characterised elsewhere (Hanby, 1976; Seyfarth, 1976). Presenting was never seen to be used to inhibit an aggressor (reported by Zuckerman, 1932; Hall, 1962; Lorenz, 1966, p.117; but not by Rowell, 1967a, nor Stoltz and Saayman, 1970), although it was seen as a response to an assertive approach. Presenting during 'protected threat' (Kummer, 1967) was only once seen. On another occasion a male under threat from a dominant was seen to evade it by presenting to a male of even higher rank.

The tendency for mounting to occur downrank in both sexes suggests that it may be assertive or agonistic. However a large number of mounts, including between the sexes, occurred in relaxed contexts and sometimes preceded grooming. At other times they occurred during social excitement (also in Bertrand, 1969; Hanby, 1974b; Hall and DeVore, 1965): thus mounting was on occasion associated with aggression, aggressive alliance (as in Massey, 1977) and possessiveness (see also Ch.7). It appeared to function to achieve non-aggressive contact, sometimes to reassure, sometimes to establish a bond between two animals with respect to others.

5.7.2 Sex-differences

Males mounted more often than did females, and this was partly because they mounted all classes while females did not mount males, but also because males mounted one another more than females mounted one another. The fact that males mounted males about as often as they mounted females (also Rowell, 1967b) may not be true of other troops: the rate of male-male mounting is reportedly higher if male dominance relations are unstable (Hall and DeVore, 1965): and the rate of male-female mounting probably depends on the number of cycling females present, since males' highest mount-rates were with that class.

5.7.3 Class-differences

5.7.3a) Mounting between males: Most mounts between males were from dominant to subordinate (i.e. 74%), the highest rates being downrank among adults. Mounting by dominants has been reported in baboons (Evans, 1974; Sugawara, 1979), and other genera (Carpenter, 1942b; Jay, 1965), and the proportion downrank was close to that of agonistic mounts among male macaques, 73%, found by Hanby (1974 b). This pattern accords with that of agonistic behaviours described in Chapter 6; and male-male mounts often appeared tense, once causing the mountee to turn and attack the mounter, or more often to show redirected aggression to an animal nearby. Although such mounts seemed assertive, they were not more frequent at close rank. The pattern was much determined by A3: the fact that his frequent mounting was concentrated on the other three focal males coincides with the distribution of his solo aggression.

5.7.3b) Mounting between females: Females mount one another in a number of primate species (Bernstein, 1970), perhaps more in captivity (Kummer and Kurt, 1965: also Akers and Conaway, 1979, cf. Lindburg, 1971). The high proportion of such mounts which were downrank at Ruaha, 89%, is almost exactly that found for yellow baboons at Mikumi (87% of 56 mounts; K. Rasmussen pers. comm.), and a similar tendency is found in captive baboons (Bramblett, 1978; Stammbach, 1978), macaques (Hinde and Rowell, 1962) and in langurs (Hrdy, 1977). The fact that they were more often downrank than among males is also characteristic of agonistic behaviours (Chapter 6), and again suggests an agonistic component to mounting. Some mounts occurred with supplanting or aggression; although they might have represented reassurance rather than antagonism. However most mounts appeared more relaxed than those between males, sometimes grading into embraces which are a form of greeting. It is not clear whether the tendency to mount partners closer in dominance rank reflected intensity of competition or affiliation between closer rankers. The two pairs who mounted most did not share strong affiliative bonds, in contrast to those observed by Hinde and Rowell (1962), Chevalier-Skolnikoff (1976) and Akers and Conaway (1979).

Mounting between females is often linked with oestrus (Carpenter, 1942b; Kummer, 1968, p.40; Hrdy, 1977), but the fact that cycling females here received, rather than gave, more mounts contrasts with the findings of Bopp (1953), Bolwig (1959) and Maxim and Buettner-Janusch (1963). The concentration of such mounts on days when mating was frequent was also suggested by Maxim and Buettner-Janusch (ibid.). Female macaques mount and consort together in the breeding season

(Carpenter *ibid.*; Fedigan and Gouzoules, 1978) and females who are *not* in oestrus may mount more when others *are* (Chevalier-Skolnikoff, 1976), also in patas monkeys (Rowell and Hartwell, 1978). The high rate of female mounts at Ruaha (discussed below) was therefore partly due to the increased mating activity as females resumed cycling at the start of the wet season. The fact that mounts were often clumped in time, and were more frequent when mating was frequent, suggests social facilitation (Rowell and Hartwell, *ibid.*): and the fact that more mounts were on cycling females suggests the influence of sexual attractiveness or motivation.

The rate of mounts between females was higher than reported elsewhere. In chacma baboons they are reported as occasional (Bolwig, 1959) or not mentioned at all (Saayman, 1970; Seyfarth, 1976). Among olive baboons, they were not seen at Ishasha (Rowell, 1967b), and observers at Gombe saw them rarely (Ransom, 1971; Nash, 1974; pers. obs.) or not at all (Owens, 1976). Ransom's data suggest a rate of about 0.07 mounts per female per hundred hours, considerably less than the comparable subject-rate of 0.78 in this study. It is not clear why this difference exists. The high rate may have been due to competition: because most mounts were downrank, even the most relaxed of them were likely to reaffirm dominance relations. Feeding competition was more intense at Ruaha than at Gombe (Oliver and Lee, 1978), suggesting greater advantage of asserting dominance at Ruaha, even though females' *ranks* may not be very changeable (Hausfater, 1975). Alternatively, they may have been in competition over access to adult males: a number of mounts occurred during such competition, mostly from mothers to cycling females, the two classes who were most often near males.

Whether these mounts were sexual, competitive, or affiliative, there are three ways in which the difference in mount-rate between this and other troops may have arisen. First, mounting might be a direct response to local conditions: for example, feeding competition might encourage assertive mounting. Secondly, it might represent a difference of tradition: for example, Bertrand (1969) found that female-female mounting arose in only one of her six groups of captive macaques, and it spread within that group from the high-ranking females. This is supported at Ruaha by the marked *individual* differences in mount-rate (also noted by Hanby and Brown, 1974). Stephenson (1973) also found that macaque troops differed in the frequency and patterning of mounting by females.

Thirdly, it may be an inherited difference in behaviour. It is infrequent in chacma baboons (refs. above) and olive baboons (refs. above; and at Gilgil, B.B. Smuts, pers. comm.), in contrast to its comparative frequency in yellow baboons at Ruaha and Mikumi (K. Rasmussen, pers. comm.): and it was seen by Maxim and Buettner-Janusch (1963) at Darajani (also yellow baboons, Maples and McKern, 1967).

5.7.3c) Sociosexual interaction between the sexes: The distribution of presenting and mounting between the male and female classes were very similar, and coincided in most respects with those of grooming. Their patterns were also much as reported elsewhere, in that cycling females gave most presents (Hall and DeVore, 1965; Rowell, 1967a; Saayman, 1970; Seyfarth, 1978a) and received most mounts (Rowell, ibid.; Saayman, ibid.; Owens, 1976), not only with mature males but also with immature partners. Mothers presented least (also Saayman, 1971b; Seyfarth, 1978b), and were mounted seldom. As with grooming, the higher-ranking (and probably older) subadults interacted less with females: the oldest received no presents at all. This is probably a result both of female preferences, and subadult males' becoming peripheral with age. Among adults, the higher rankers interacted most with females: as with grooming, this probably reflects both male competitive ability and female preference (see below). The fact that sociosexual behaviours less often involved non-cycling females suggests that the sexual component of such interaction between male and female is quite high, although both behaviours were obviously part of the general currency of interaction. Thus A2 showed frequent interaction with F9, as he did in grooming. However in contrast with grooming, A7 interacted little with mothers, nor did A6 with females F10 and F12.

It was conspicuous that so few presents elicited mounting: in Chapters 7 and 8 it is proposed that they function to solicit male possessiveness more than copulation. The males' responsiveness to presents (80%), was greater than reported by Hall (1962), 45.6%; Rowell (1967a), 56-77%; or Seyfarth (1978a), 12-38%; chiefly in that greeting and inspecting were more frequent.

Although two studies found that females' reproductive state had little effect on the males' response to presents (Hall, 1962; Rowell, 1967a), yet both Saayman (1970) and Seyfarth (1978a) found that males responded to cycling females with proportionately more mounting. The effect of reproductive state at Ruaha was not so much upon mounting as that cycling females were greeted less, inspected more, and received more negative responses. This last has been noted for mangabeys at full swelling (Chalmers and Rowell, 1971), and for female macaques in the breeding season (Hanby and Brown, 1974). The possibility that their present-rates were too high to sustain the males' interest is countered by the higher proportion of inspects they received. In part, the lesser response was because cycling females were presenting more to males who responded less - the prime-age and newcomer adults. The fact that much of these males' response included looking away suggests that they may have been inhibited from responding, perhaps by the presence of other males nearby. Both Boese (1975) and Dunbar and Dunbar (1975) describe males ignoring presents from females who were members of other males' subgroups or units; which is particularly relevant here because the newcomers looked away most.

It is not clear why cycling females avoided a higher proportion of their mounts. This may be an endogenous feature of the behaviour of cycling females, but it may also be that females will not tolerate being mounted very often. Their avoidance was sufficient to cause a large number of mounts by adult and subadult males to be incomplete. Females avoided the mounts of immatures rather less, as reported by Rowell (1967a), but cycling females still avoided most.

Whether cycling females' presenting solicits copulation or consortship, it is thought to express choice of mates (Saayman, 1970; Seyfarth, 1978a; Packer, 1979a). Apart from favouring adults over subadults (also Rowell, 1967a; Saayman, ibid.; Packer, ibid.), cycling females appeared to prefer high ranking adults (as in Seyfarth, ibid.; but cf. Saayman, 1971b), especially the α-male. This male was also a newcomer, and a number of studies suggest that females willingly present to unfamiliar males (Nash, 1976; for oestrus females, Cheney and Seyfarth, 1977; Packer, ibid.), although the fact that they presented to newcomer A2 so much less suggests that dominance rank was more important. These statements about 'preference' are conditional on the fact that a number of presents occurred in response to the approach of a male (also in Packer, 1979a), and so may have been 'initiated' by the male, but the proportion was not recorded.

5.7.4 Interactions between adults and immatures

The behaviour of immatures was characterised firstly by the number of wrongly oriented mounts, suggesting that they must learn how to mount (Owens, 1976). Also they were more responsive to presents (also Rowell, 1967a; Saayman, 1970), notably by inspecting which suggests the importance of olfactory cues.

CHAPTER 6

Agonistic Behaviour, and Dominance

1. INTRODUCTION

6.1.1 The term 'agonistic' refers here to specific interactions involving conflict between animals with and without aggression (Scott and Fredericson, 1951). This chapter describes the distribution of such interactions, and analyses the pattern of dominance relationships between the subjects of this study.

Baboons are often described as aggressive animals (Jolly, 1972), and this has been linked perhaps unjustifiably to their necessity for defence against predators (e.g. Hall, 1964). The conspicuous aggressiveness of the large males led Hall and DeVore in 1965 to conclude that baboon society was organised around the dominance hierarchy of the adult males (also Zuckerman, 1932), a view which is no longer tenable (1.1). At that time there was already much confusion about dominance and its relation to other behaviours and Gartlan (1964) questioned whether hierarchies existed in the wild at all. He proposed that they occurred in captivity as a response to stress, and that behaviour in the wild was better analysed in terms of roles (Gartlan, 1968). Hierarchies certainly exist in captivity (Bernstein, 1970), and they affect the expression of agonistic behaviours. The patterning of such behaviours led Rowell (1966b and esp. 1974) to conclude first that hierarchies are a response to stress and secondly that they are maintained by the behaviour of subordinate animals rather than dominants. The confusion has been resolved by three authors. Deag (1977) showed conclusively that agonistic hierarchies occur in the wild and that they are produced by the behaviour of both dominants and subordinates. Hinde (1978) and Wade (1978) stressed the importance of distinguishing between the relationships of pairs of animals, in terms of the asymmetry in behaviour between dominant and subordinate partners, and the patterning of such relationships, which may or may not constitute a hierarchy. Hinde (*ibid.*) also emphasised that there is no *a priori* link between an animal's dominance and its performance of particular roles in the group, since the two differ conceptually. Finally, the application of game theory to agonistic behaviours has allowed prediction of their outcomes in terms of costs and benefits to antagonists (Maynard Smith & Parker, 1976). The relevance of such theory to primates has been discussed by Clutton-Brock and Harvey (1976) and Popp and DeVore (1979), although tests of their predictions on behavioural data have not been many (e.g. Packer, 1977a, Appendix B). Game theory identifies the selective advantage in particular patterns of behaviour, but does not explain the details of their evolution or control.

The following analysis concentrates first on identifying the dominance relationships of all subjects. Dominance is important to the individual because rank-differences have been shown to reflect a number of social differences such as attractiveness (Seyfarth, 1976), and mothering style (Altmann, 1980) and a number of longer-term variables such as female reproductive success (e.g. Drickamer, 1974b; Dittus, 1979), sex of offspring (Altmann, 1980), mortality rates (Dittus ibid.), mating success in males (Chapter 8), and feeding-efficiency (Dittus ibid; Post et al., 1980).

Thereafter are analysed the effects of dominance rank on rates of behaviour, both agonistic (in this chapter) and affiliative (Chapters 4 & 5). Finally, specific topics including alliances, agonistic buffering, and relations between males, are discussed in detail.

2. BEHAVIOURS : ANALYSES : CONTEXTS

6.2.1 The observation-methods have already been described (2.X) and the behaviours discussed here are more fully defined in Appendix 1B (vi-x). The main analyses are of avoidance, supplanting, and aggression. Avoidance was recorded whenever one animal moved out of the line of travel of another before the latter approached within arm's reach. So defined it probably includes some apparent avoidances which were merely fortuitous movements of both animals: otherwise responsibility could be assigned to the avoider, or to both partners. Supplants were recorded when one animal approached another within arm's reach and the latter left almost immediately, but without exchange of threat. Very few of these are likely to have been fortuitous, because these interactions require purposive approach by one and departure by the other.

In terms of the direction of approach-retreat interactions (Rowell, 1966b) a supplant given parallels an avoidance received, which explains why the terms given and received are transposed between these behaviours in the data tables (e.g. Table 6.V).

Aggression was recorded whenever one animal gave threat, chase, or contact aggression to another. An analysis of the intensity of aggression has been made but will be presented elsewhere. Aggression often occurred in prolonged exchanges of gestures, as in the 'bouts' of Hausfater (1975). Such exchanges were recorded here as separate interactions if: (i) there was a break in continuity of all aggressive gestures (Owens, 1975, used a break of one second as criterion); (ii) the direction of aggression was reversed: thus A chased B, then B chased A, comprised two interactions; and (iii) an ally joined in: thus A threatened C, then A and B threatened C, were recorded as one dyadic and one triadic interaction. Unlike Hausfater (1975) the outcome was not judged at the time except as implied by the direction of the behaviour: thus "counterchases" (in which the chaser shows gestures of fear, e.g. screaming, with tail up) were not distinguished from other chases. These data differ from those of Hausfater in that aggression was here quantified as exchanges of actions rather than whole bouts, so that interaction rates may appear relatively higher: also because interaction outcomes were not judged, proportionately more of the aggression in this study may run from subordinate to dominant, whereas it would be subsumed under 'counterchase' in his.

Finally, the method of ad libitum sampling may have relatively overestimated the frequency of polyadic aggression because it was more conspicuous (Walters, 1980).

6.2.2 Analysis of interactions

6.2.2a) Interactions excluded. Particular interactions have been retained in or excluded from different analyses depending on the question being asked. Previous studies, and qualitative observations during this study, suggest that the likelihood one animal will initiate interaction with another, and the rate and outcome of such interactions, may be affected by three factors:

1. Any animal acting in alliance with another may be more likely to win an encounter (Kawai, 1958).
2. A male may become temporarily dominant over a second male to whom he is usually subordinate if the first is (a) in the consort with a female (Packer, 1979b; Kummer et al., 1974), or (b) carrying an infant

(Packer, 1980).

Therefore, in detailed analysis of dominance relationships within pairs, such interactions are excluded. But in calculation of rates of interaction, they are retained. Finally, most analyses of this chapter separate dyadic from polyadic (allied) interactions, because only the former can reveal the exact relationships between individuals and the importance of dominance rank.

6.2.2b) Analysis of polyadic interactions According to the question underlying each analysis, polyadic interactions have been quantified in two different ways. In calculation of rates per hour per subject, each interactions is considered as one incident: thus A and B threaten C amounts to one incident given by each of A and B, and only one received by C. In contrast, for analysis of dyadic rates, the incident is broken down to its constituent dyads, so that the same interaction becomes one interaction given by each of A and B, but two received by C; and also one interaction of alliance between A and B.

Cases of redirected aggression, of the type A threatens B who threatens C, have been considered in analysis as two dyadic interactions.

6.2.3 Contexts

No attempt was made to classify all agonistic interactions according to detailed context, such as whether a supplant had occurred over a feeding or nesting site, or from a grooming-partner. Such details were not always apparent during *ad libitum* observation. However, a large proportion of supplants, and some low-key aggression, occurred over feeding-sites. Supplanting and aggression were also evident in competition for social (e.g. grooming) partners, and a large number of aggressive incidents represented overt competition between males to gain consortship of swollen females (8.3). Allied aggression between males appeared in some cases to be attempts to generate polyadic aggression and then direct it against consort pairs. Some other incidents were offshoots of such competition, as when consort and rival male would chase a nearby female rather than confront one another; and in some cases female aggression to a consort female appeared to be possessiveness over access to the male. Table 6.I estimates the contribution of such consort-related aggression to overall aggression, comparing the percent of all instances which involved animals in consort or were judged directly related to the presence of a consort pair. Most consort-related

Table 6.I Aggression and consortship. The percentage of all instances of dyadic and polyadic aggression which were judged to be related to the presence of consort pairs (6.2.3). (n = no. of instances).

Dyadic

Donors & recipients (n)	%
Male-male (459)	25.5
Female-female (116)	9.5
Male-female (283)	8.5
Female-male (27)	3.7
Male-immatures (110)	10.9
Imm.-male (17)	0
Female-imm. (70)	10.0
Imm.-female (85)	7.1

Polyadic

Participants (n)	%
Males only (112)	42.9
Females only (6)	16.7
Males and females (54)	33.3
Males and immatures (15)	0
Females and immatures (56)	7.1
Males, females immatures (13)	7.7
Not classifiable (26)	11.5

aggression was between males, especially in polyadic interaction, and it seldom comprised more than 15% of the aggression of other classes.

Agonistic interactions are here analysed as separate events, but they often occurred close together in time and were related in cause also. For example, an animal would sometimes respond to being supplanted by threatening another nearby. Or an aggressor would be thwarted when the victim sheltered close to an adult male, but would resume aggression when the male departed. Aggressive interactions often became very complex, as the following summary from the check sheet data illustrates:

Dec. 24th, 9.04: An adult male moves towards another, who avoids: both initiate interaction with black infants. The mother of one infant screams at the male, the other male leaves his infant and attacks the first male, and is joined in attack by a third. The first male redirects aggression at the α-male, and the two original males chase the α, who then shows aggression eight times to four of the resident adult males. Two of these withdraw and interact with black infants: another male intervenes possessively between one of these and the mother-infant pair ...

Finally, although aggression often appeared to be very intense, with the victims screaming and showing abject fear, yet when it ended they would often just walk away with no outward sign of injury nor even distress. Very few injuries were seen, mostly on adult males.

3. DETERMINATION OF DOMINANCE : HIERARCHY

6.3.1 Several studies of wild baboons have detected linear dominance hierarchies among adults: notably at Amboseli (Hausfater, 1975), Nairobi (Altmann, S. 1965, ref. Hall & DeVore, 1965), Gombe (Owens, 1975; Moore, 1978; Nowell & Heidrich, 1978; Packer, 1979b) and in South Africa (Seyfarth, 1976). Some initial studies did not recognise female hierarchies (e.g. Stoltz & Saayman, 1970), but the findings of Hausfater, Moore, Owens and Seyfarth (above) all confirm their existence.

The following section identifies dominance relations within each pair of subjects, and examines the patterning of such relationships for evidence of hierarchy. The term 'dominance' is used in a restricted sense, referring only to the imbalance of non-aggressive agonistic interaction in any pair, and does not refer to aggressiveness nor to the performance of any roles such as leadership, troop-defence, or mating activity. It is assumed that such imbalances may reflect competitive ability, mediated through size-differences (Lee & Oliver, 1979) and alliances (Cheney, 1977); and by kinship, especially among females and young (Walters, 1980). Such imbalances may change as animals mature and age, possibly reflecting reproductive value (Hrdy & Hrdy, 1976; Moore, 1978; Schulman & Chapais, 1980), and the relationships at any time probably represent the current state of a continuous learning process (Rowell, 1974).

Several authors suggest that low-intensity approach-retreat interactions provide clearer indications of dominance than do more intense aggressive behaviours, (Rowell, 1966b; Lindburg, 1971; Cheney, 1977; Packer, 1979b) and the outcomes of low-key interactions were certainly more predictable during this study. Therefore they were used to assign dominance. The use of threat may exaggerate an animals probability of attack and so increase its likelihood of winning (Popp & DeVore, 1979). Despite this, a number of authors have relied on overt aggression to indicate dominance (e.g. Sade, 1967; Poirier, 1970), or have not separated low-key and intense interactions (Hausfater, 1975).

6.3.2 Avoidance and supplants

Within each dyad was determined the prevailing direction of avoidance and supplants, excluding those interactions described in 6.2.2. Among females, directional data for both behaviours were available in 54 of the 171 pairs, but equating A supplants B with B avoids A the directions coincided in 53 of them ($p < .001$, Sign test). Among males, directional data for both behaviours were available in 49 of the 66 pairs but the directions coincided in 48 of them ($p < .001$, Sign test). Therefore, as indicators of asymmetry within each pair, the two behaviours were pooled.

6.3.3 Observed dominance

In any pair, the dominant was the partner whose total of supplants given and avoidances received was the greater. This allowed dominance to be assigned in all 66 pairs of males, but in only 143 of the 171 pairs of females and 187 of the 228 male-female pairs.

6.3.4 Probable dominance

For those pairs of females for whom data were not available, probable dominance was assigned to the female who was observed to be dominant to more, or subordinate to fewer, other females, by the method just described. Probable dominance was assigned in 26 pairs of females, and for those 15 for which J.I. Oliver had obtained data, all had been correctly assigned. When these probable dominance relationships were known, the remaining two pairs of ambiguous dominance were assigned probable dominance by including probable as well as observed pairs in their known relationships.

6.3.5 The pattern of dominance relationships

Because the male was dominant to the female in all 187 male-female pairs for whom data were available, and because males never avoided and were only twice supplanted by females, it was inferred that adult and subadult males were dominant to all females.

The directions of dominance for different pairs within each sex were highly interdependent. This was shown by testing the prediction that if A is dominant to B, and B is dominant to C, then A will be dominant to C. Considering only the pairs with observed dominance relationships, this prediction was correct in all 220 triads of males and 541 triads of females. It was concluded that dominance relationships were transitive, and so the subjects in each sex were arranged into linear hierarchies in which each subject was dominant to all those lower down. The data are given in Tables 6.II and 6.III.

6.3.6 Terminology

Because a linear hierarchy was found, the definitions of terms relating to it may be briefly summarised. The words dominant and subordinate refer only to the relationship of a pair of animals, determined as above (6.3.3, 6.3.4). Behaviours directed from dominant to subordinate are referred to as downrank, while those from subordinate to dominant are uprank (the latter equivalent to the reversals of other authors). The hierarchy is referred to as the dominance hierarchy, and a subject's dominance rank is its position in that hierarchy, with for example the highest-ranking femaled ranked 1, the lowest 19, so that a positive correlation between dominance rank and the rate of any behaviour indicates that high-ranking subjects interacted more. The terms higher- and lower-

Table 6.II Dominance relations among females. The number of times each donor (on left) supplanted or received avoidance from each partner (at top). Excludes 22 interactions involving females in consort with males. n = 90 avoidances, 355 supplants.

		Females: as avoiders/supplantees																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Females:	1	-	4	6	1	3	2	6	4	2				2		3	3		2	1
as	2	1	-	8		1	3	6	3	1			3		3	3	3	1	1	2
donors	3			-	3		4	3	5		2	1	1	2	1	1	1	2	1	2
	4				-	1	4		4	7	3		4	1	6	3			1	1
	5					-	2	3	1	5	2	2	2	5	1	5	3	2	4	1
	6						-	5	4	5	3	1	2	2	7	4	7	1	2	4
	7							-	1	2	1	1	1	3		4	3	3	1	3
	8			1				1	-	1	3	3	1	1	3	1	5			2
	9	1								-	4	2	2	3	5	5	3	4		4
	10										-	2	3	12	2	2	13	2		3
	11											-	2	1			3	2	2	1
	12												-	2	7	2	3	2	4	1
	13													-	11	4	6	4	6	3
	14			1											-	2	2	1	5	
	15														1	-	4	7	1	1
	16																-	3	1	1
	17																	-	1	3
	18		1														1		-	
	19																			-

Table 6.III Dominance relations among males. The number of times each male named on the left supplanted or received avoidance from each male listed along the top. Excluding 51 interactions by males in consort/allied/carrying infants: n = 134 avoidances, 512 supplants.

		Males as avoiders, supplantees											
		A1	A2	A3	A4	A5	S1	A6	A7	A8	S2	S3	S4
Males	A1	-	24	15	15	23	6	10	5	4	12	9	10
as	A2	4	-	5	3	4	2	5	5	5	8	11	6
donors	A3		1	-	22	33	7	12	16	10	11	9	3
	A4	1	1	1	-	11	8	7	8	9	22	7	7
	A5	1	2	1		-	10	19	25	7	25	22	8
	S1					1	-	3	1	2	16	3	4
	A6				1		1	-	2	6	8	3	5
	A7		1			1			-	4	2	2	1
	A8		1		1					-	10	3	2
	S2	1	1		1						-	15	12
	S3											-	14
	S4			1									-

ranking refer to relative positions in the hierarchy.

6.3.7 Rank-direction of agonistic behaviours

As dominance is usually defined, agonistic behaviour more often is given by dominant to subordinate, and submissive behaviour the reverse. The rank-direction of agonistic behaviours within each sex are listed in Table 6.IV pooling the interactions of all individuals. The distribution was compared with 50 : 50 expectation by chi squared, and the generality of the trend among all subjects estimated by comparing subjects' dyadic mean rates of interaction uprank and downrank by Wilcoxon matched-pairs test.

Although both avoidance and supplant were expected to be predominantly downrank because dominance was assigned by these behaviours, yet their direction constancy was particularly high in both sexes, a pattern common to nearly all subjects. Among females, both types of aggression were predominantly downrank: but taken together they were significantly more often uprank than their combined avoidance and supplants (χ^2 4.93, d.f. 1, $p < .05$). Among males, solo aggression was predominantly downrank although not all males showed this pattern (notably in that A7 directed more uprank). In contrast, allied aggression by most males was predominantly uprank. Both types of aggression were significantly more uprank than were avoidance and supplants (comparing these pooled with solo aggression yields χ^2 153.0, with allied aggression 493.6: at d.f. 1, $p < .001$ for both).

The sexes did not differ in the distribution of their avoidance and supplant (again both pooled, χ^2 3.1, d.f. 1, n.s.). However, aggression (solo and allied pooled) was significantly more often uprank among males than among females (χ^2 76.1, d.f. 1, $p < .001$).

6.3.8 Conclusion

These data reveal linear hierarchies within each sex, with adult and subadult males dominant to adult females, consistent with the findings of Hausfater (1975), Owens (1975), and Packer (1979b). Adult males were dominant to subadults, except that the subadult who was of full adult size ranked sixth among the adult males. Similar high-ranking subadult or natal males are also reported by Packer (1979a) and Altmann (1980).

Table 6.IV Rank-direction of agonistic interactions within each sex. The percentage downrank (i.e. by the dominant in each pair) is indicated. Calculated from all dyadic interactions, including animals in consort and males carrying infants: allied aggression is broken down into its constituent dyadic interactions. Wilcoxon tests examine individual tendencies.

	Male to male						Female to female					
	n	% downrank	χ^2	p	Wilcoxon	p	n	% downrank	χ^2	p	Wilcoxon	p
Avoidance	146	93.8	112.2	<.001	T=1, n 10	<.01	99	98.9	104.1	<.001	T=1,n 16	<.01
Supplant	539	97.0	476.9	<.001	T=1, n 10	<.01	370	98.1	342.5	<.001	T=1,n 16	<.01
Solo aggression	459	70.2	74.6	<.001	T=10,n 10	n.s.	116	95.7	96.9	<.001	T=1,n 15	<.01
Allied aggression	244	27.9	47.8	<.001	T=5, n 9	<.05	29	89.7	18.2	<.001	T=2,n 9	=.01

The adult male dominance hierarchy coincided closely with apparent age and with seniority. The age-groups of adults, named by their dominance rank, ran from young (A1, A2) through prime (A3, A4, A5) to ageing (A6, A7) and aged (A8). Thus adult male dominance was correlated with apparent age (r_s - .945, n 8, p <.01). Therefore any conclusions about adult male dominance rank remain inseparable from the effects of age, as suggested by Rowell (1974). Further, because the two newcomers occupied the highest ranks, any relationship between male dominance rank and behaviour may be emphasised or masked if there are behavioural contrasts between newcomers and residents. The seniority order among the latter was not known.

The direction constancy of avoidance and supplant was so high that they provide clear evidence of asymmetry within pairs. Although the nature of the resource disputed is predicted to affect the outcome of encounters (Popp & DeVore, 1979), it cannot have caused many temporary reversals in these behaviours. The finding that dominance predicted the direction of nearly *all* agonistic exchange between adult females seems general among baboons (also Rowell, 1966b; Hausfater, 1975; Owens, 1975; Moore, 1978), and in this case provides strong confirmation that female rank does not change with reproductive state (also Rowell, 1968 ; Hausfater *ibid*; Nowell & Heidrich, 1978). However the most striking finding was that substantially more aggression between males was given uprank, especially in alliance. This result differs from that of Hausfater (ibid.) who recorded few decided bouts of agonism uprank. The difference may in part be because any uprank aggression accompanied by submissive gestures in his study would have been discounted as counterchases, and temporary aggression uprank might also have been subsumed within 'bouts' won by the dominant (6.2.1). However, these caveats cannot apply to allied aggression, which in his troop was rare (less than 2% of all agonistic bouts) and not predominantly uprank. The rank-direction here was no doubt in part because much aggression was against the newcomers, and inevitably uprank because they were the highest rankers. However, there was sufficient uprank aggression to resident males, especially in alliance (Fig. 6.20) to imply that such behaviour was a feature of this troop, and that males were more likely to aggress uprank when in alliance.

Hausfater (1975) recorded dominance-changes between adult males once every 528 days per adult male pair. If changes had occurred at the same rate in this study, four or five would have been seen in the 2352 adult male pair-days. The data in Table 6.III suggest that they were not so frequent. The reversals between A1 and A2 were not consistently patterned in time. The most ambiguous relationship was between A6 and A7, and if aggression had been included in dominance assignments at least two short-term changes would have been found for this pair. However, there are no grounds for attributing the high proportion of uprank aggression to short-term dominance changes through this study.

4. SEX AND CLASS DIFFERENCES

6.4.1 Introduction

The fact that adult and subadult males are dominant to females suggests that agonistic interaction is not equally likely within and between the sexes, and this has been found in several studies. Males give agonistic interaction to females more frequently than the reverse (Hall, 1962; Rowell, 1967b; Saayman, 1972). Males are often found to be more aggressive in general than are females (Saayman ibid; Bramblett, 1978), and particularly so to their own sex (Evans, 1974; Seyfarth, 1976). While their high rank may give males more opportunity to show aggression, it does not however predict that they should be more aggressive to each other. Females' reproductive state also affects their agonistic rates, without altering their dominance rank. Thus cycling females reportedly are involved in much aggression (Hall ibid; Saayman ibid.) while mothers with young infants have to avoid others frequently (Rowell, 1969b; Altmann, 1980) although they may exchange less aggression (Seyfarth, 1976). The following section therefore examines the effect of sex and class upon rates of agonistic behaviour.

The earlier statement that dominance rank may affect a number of long-term factors such as reproductive rate and mortality (6.1.1) depends especially on two factors, feeding efficiency, and stress (e.g. Dittus, 1979; Dunbar, 1980a). The amount of agonism an animal gives and receives per hour may be related to both of these. The first analysis is therefore of the rates at which subjects gave and received agonism, per hour, irrespective of the identity of the opponents. The behaviour most relevant to feeding efficiency was probably supplanting (Oliver & Lee, 1978).

Thereafter, in order to investigate the underlying mechanisms, there follows a detailed analysis of the distribution of agonism according to class which accounts both for availability of partners and for the rank-direction of the behaviour concerned. Thus partner-availability within-sex was 50% uprank, 50% down, whereas between the sexes it was 100% downrank for males but 100% uprank for females. As far as possible, comparisons have been limited to rates calculated in the same rank-direction.

6.4.2 Sex-differences in subjects' rates of behaviour

Fig. 6.I shows the rates at which each subject gave and received the three types of agonistic behaviour, per hour, as subject-rates with all partners. Polyadic interactions were not broken down into constituent dyads but included as one incident per participant. Comparisons of the mean rates of each sex in Table 6.V show that (i) males were avoided more, and gave more supplants and aggression, than did females; (ii) the sexes did not differ in how often they avoided, or received supplants, but males received more aggression than did females: (iii) considering the ratio between each subject's agonism given and received, males were proportionately more 'successful' than females in all behaviours, especially some males in supplanting and being avoided (Fig. 6.1).

6.4.3 Sex- and class-differences in dyadic rates

Mean dyadic rates of behaviour within and between sex are compared in Tables 6.VI and 6.VII. The former compares rates to all partners irrespective of rank-direction: the latter is restricted to comparisons in the same rank-direction. The following pattern emerges:
(i) agonistic interactions were more frequent between males than between females, significantly so for all except avoidance. When rates downrank only were compared, significant differences were found for all behaviours (Table 6.VII).

FIG. 6.1

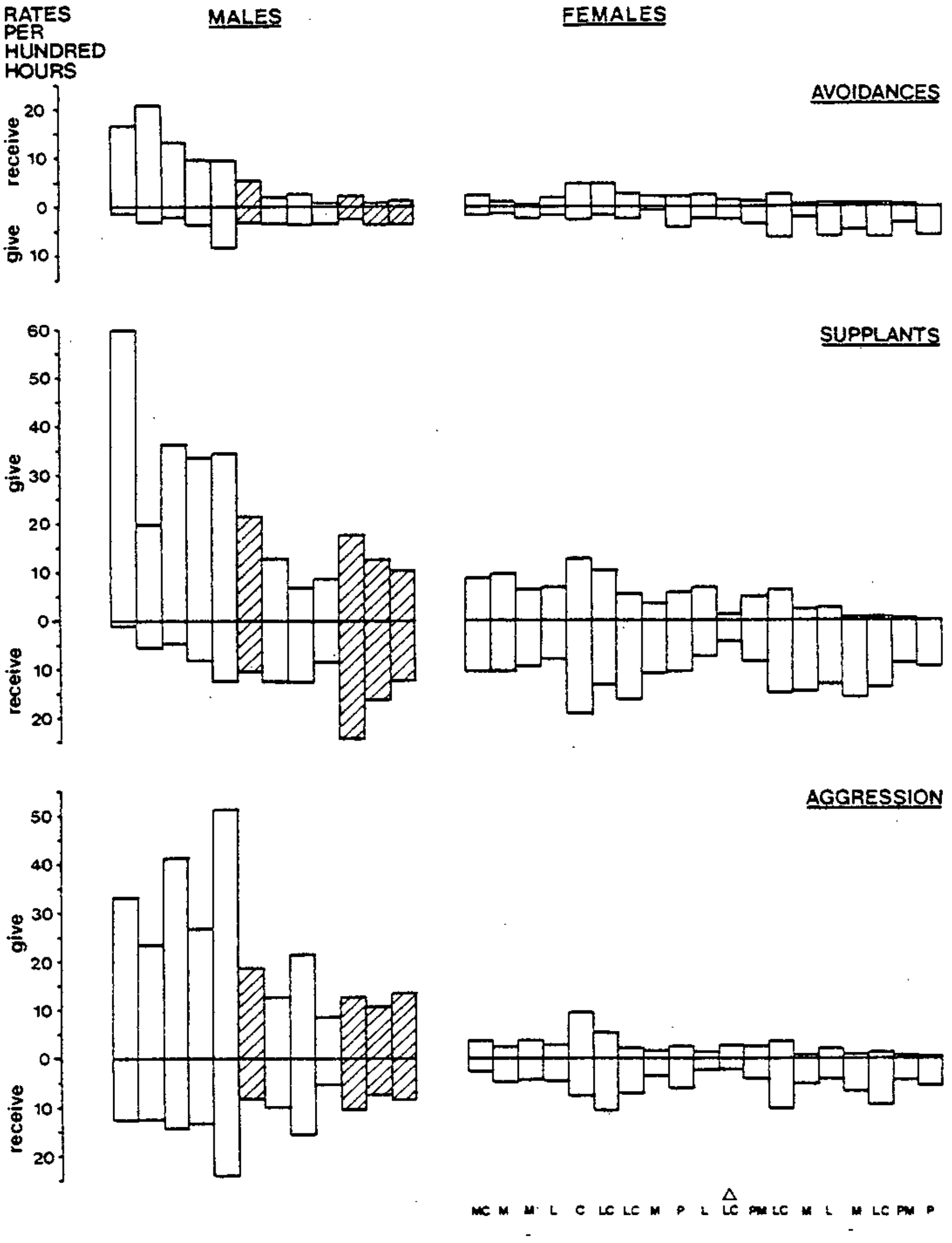


Fig. 6.1. The rate at which each subject gave and received agonistic interactions. Rates are expressed per hundred hours per subject, and so do not account for differences in availability of partners. Subjects in order of dominance rank, the highest rankers on the left: subadult males cross-hatched, females are C - cycling, P - pregnant, M - mothers, L - lactating, the sick female △ . Above the x-axes are shown the rates of interaction given, below are the rates received, except that for avoidance (top) the rate of being avoided is above, the rate of avoiding below. Solo and allied aggression are pooled.

Table 6.V Rates at which males and females gave and received agonistic interaction, with all partners including immatures, per 100 hours per subject (means and standard deviations). The lower bloc compares the subjects of each sex for the number of interactions given as a proportion of the number received (but the inverse of this for avoidances).

	Males (12)	Females (18)	Mann-Whitney (corr. obs.)	p
Behaviours				
Avoids received	7.09 (6.82)	1.81 (1.37)	47 (38)	<.02
Supplants given	22.76 (15.58)	5.20 (3.71)	12 (10)	<.01
Aggression given	22.77 (13.26)	2.48 (2.10)	1 (0)	<.01
Avoids given	3.63 (1.72)	3.42 (1.81)	93 (94)	n.s.
Supplants received	16.75 (13.08)	12.09 (3.25)	84 (96)	n.s.
Aggression received	11.91 (4.90)	5.91 (2.47)	21 (20)	<.01
Avoidance ratio	2.74 (3.67)	.71 (.79)		
Supplant ratio	6.47 (14.56)	.46 (.33)		
Aggression ratio	1.86 (.55)	.45 (.33)		

Table 6.VI Sex-differences in agonistic rates I. Mean dyadic rates of behaviours per 100 hours; with standard deviations in brackets: the behaviours listed on the left. The top row identifies the donors and recipients, note that the roles for avoidance are reversed^{x} - thus at top right is the rate at which females avoided males. Probabilities: *< .05, **< .01, ***< .001, estimated by Wilcoxon (T) and Mann-Whitney (U) tests: if the results of tests repeated on scores corrected for observability differed from the uncorrected scores, these are given in brackets.

Donor e recipient		Female-male	T	Female-female	U (N12.18)	Male-male	T (n,12)	Male-female
Behaviours								
Avoidance	$\bar{x}$	0		.06		.29		.22
	sd.			(.05)		(.32)		(.25)
	test		0.n,17**		65.5(59.5)		26(24)	
Supplant	$\bar{x}$	.00		.26		1.00		.57
	sd.	(.01)		(.18)		(.90)		(.34)
	test		0.n,17**		45(44)**		13(12)	
Solo aggression	$\bar{x}$	.03		.08		.84		.30
	sd.	(.03)		(.07)		(.66)		(.18)
	test		23.n,17**		14(13)**		6(6)**	
Allied aggression	$\bar{x}$	.03		.02		.44		.06
	sd.	(.03)		(.02)		(.49)		(.03)
	test		35(36) n,15		17(18)**		6(6)**	

Table 6.VII Sex differences in agonistic rates II. Comparison of rates in the same rank-direction. Layout as in Table 6.VI.

		Uprank			Downrank				
		Female-male	T	Female-female	Female-female	U (n11,17)	Male-male	T (n=11)	Male-female
Behaviours									
Avoidance	$\bar{x}$	0		.00	.13		.43		.22
	sd.			(.00)	(.08)		(.32)		(.25)
	test					35.5*		6*	
Supplant	$\bar{x}$	.00		.02	.49		1.94		.57
	sd.	(.01)		(.05)			(.99)		(.34)
	test		8 n,8			10(4)**		0**	
Solo aggression	$\bar{x}$	.03		.01	.15		.98		.30
	sd.	(.03)		(.01)	(.10)		(.63)		(.18)
	test		12(14)* n,14			14(11)**		0**	
Allied aggression	$\bar{x}$	.03		.00	.04		.25		.06
	sd.	(.03)		(.01)	(.05)		(.23)		(.03)
	test		1** n,12			23**		4**	

(ii) males tended to direct more agonistic behaviour at their own sex than at females, significantly so for overall rates of solo and allied aggression and for all four behaviours downrank.

(iii) females were never avoided by males in dyadic interaction, and rarely supplanted them. This agrees with the rarity of agonism uprank within their own sex. However, they did show aggression to males: albeit significantly less in solo aggression than they gave to females, but in allied aggression they gave equally to both. Furthermore, their rates of aggression to males (inevitably uprank) were significantly greater than their rates uprank to other females (Table 6.VII).

In summary, these results are as expected from the dominance difference of the sexes, to the extent that males gave all types of agonism to females, but females gave very little to males. However, agonistic interactions were more frequent between males than between females or between the sexes: and females gave more uprank aggression to males than to their own sex.

6.4.4 Class-differences in dyadic rates

Most class-rates were compared only downrank, except in the cases where uprank rates were also sufficient. When the data had been partitioned in this way, sample-sizes became too small to analyse in terms of the class both of subjects and interaction-partners, so that in all cases the partner-classes have been combined.

6.4.4a) Agonism between males The rates of behaviour of adult and subadult males are compared in Table 6.VIII. Adults tended to give more agonistic behaviour than did subadults, in that the subadults' rates were generally below those of the median adult, but this was significant only in solo aggression uprank. However, subadults showed higher rates of supplanting, apparently because they supplanted one another very often (2.77 per 100 hrs. ± 0.13). Similarly, adults tended to receive more agonism than did subadults, but the latter were only below median adult rate for avoidance and solo aggression downrank, and no differences were significant. Examination of class mean rates showed that for all behaviours interactions were more frequent within-class than between.

Table 6.VIII Agonistic interactions of adult and subadult males compared. Dyadic mean rates per 100 hours. Standard deviations in brackets, calculated downrank only unless indicated otherwise. Legend as in Table 6.VI. Note that the roles of giver/receiver are the inverse of those indicated for avoidance.

Male subjects		Given			Received		
		Adult	(n.3,8)	Subadult	Adult	(n.4,7)	Subadult
Behaviours							
Avoidance	$\bar{x}$	.49		.30	.90		.41
	sd.	(.37)		(.06)	(.43)		(.16)
	test		10(9)			3(4)	
Supplant	$\bar{x}$	1.76		2.41	2.42		1.98
	sd.	(1.06)		(.70)	(1.14)		(.79)
	test		6(7)			10(11)	
Solo aggression (downrank)	$\bar{x}$	1.06		.79	1.93		.74
	sd.	(.72)		(.30)	(1.40)		(.30)
	test		9(10)			6(4)	
(uprank)	$\bar{x}$	.89		.18	.49		.31
	sd.	(.70)		(.21)	(.28)		(.32)
	test		3* n.4,7			8(6)	
Allied aggression (downrank)	$\bar{x}$	.28		.16	.32		.18
	sd.	(.27)		(.06)	(.30)		(.14)
	test		10(11)			12	
(uprank)	$\bar{x}$	1.45		.17	.50		.40
	sd.	(1.61)		(.12)	(.58)		(.24)
	test		5(5) n.4,7			11(9)	

6.4.4b) Agonism between females The rates at which female class-members exchanged agonistic interaction with other females, downrank, are compared in Table 6.IX. Data on allied aggression were insufficient for statistical test. Reproductive state did not significantly affect rates of behaviour *given*, but it did affect the rate at which females were supplanted. The chief contrast was that pregnant females were supplanted least, while mothers were supplanted very often. In detail, all female classes supplanted mothers most and pregnant females least. Also six of the seven *uprank* supplants among females were to mothers. Despite the paucity of significant class-differences, the mean rates in Table 6.IX are patterned (in agonism given, χ^2_r 7.8, p .04; received, χ^2_r 6.3, p .09), in that cycling females tended to give and receive at high rates (except supplants received), while mothers gave and pregnant females received at relatively low rates.

6.4.4c) Male agonism to female Adult males tended to give more of all four agonistic behaviours to females than did subadults, but not significantly in any case (Table 6.X). Again this was because subadults' rates were near or below median adult rate, while *some* adults showed markedly high rates. The table also shows that adults interacted at random across the female classes, except in their supplanting which was directed especially to cycling females. However, the mean rates of the four behaviours showed the same pattern across the classes (from Table 6.X, χ^2_r 8.4, d.f. 3, $p < .05$) in that cycling females received the most of all four.

The subadults gave interaction at random to the female classes, and their mean rates to each class were not patterned consistently across the four behaviours (Friedman $\chi^2_r = 0.9$, d.f. 3, n.s.).

6.4.4d) Female agonism to males Female class-members showed no consistent pattern in their rates of aggression to males (Table 6.XIa). Although the mean rates suggest that cycling females were more aggressive, this was not true of all of them. Furthermore, females gave equal amounts of aggression to adult and to subadult males (Table 6.XIb, pooling solo and allied aggression); the few females who gave enough aggression to compare showed no consistent tendency toward adult or to subadult.

Table 6.IX Agonistic interactions of female classes, as dyadic mean rates per 100 hours downrank. Legend otherwise as Table 6.VIII, except that rates compared by Kruskal-Wallis H test; the H-values in brackets are derived from scores corrected for observability.

Class rates of agonism given

Behaviours		Cycling	Pregnant	Mothers	Lactating	Kruskal-Wallis H	p
Avoidance (rec.)	$\bar{x}$	.16	.10	.07	.19	6.41	n.s.
	sd.	(.13)	(.09)	(.08)	(.07)	(5.97)	
Supplants	$\bar{x}$	.73	.40	.30	.56	6.64	n.s.
	sd.	(.36)	(.35)	(.16)	(.24)	(7.45)	
Solo aggression	$\bar{x}$	.24	.13	.13	.15	2.42	n.s.
	sd.	(.20)	(.11)	(.19)	(.10)	(2.36)	
Allied aggression	$\bar{x}$	.14	.02	.02	.01	no test	
	sd.	(.23)	(.03)	(.03)	(.03)		

Class rates of agonism received

		Cycling	Pregnant	Mothers	Lactating	Kruskal-Wallis H	p
Avoidance (given	$\bar{x}$	.19	.12	.09	.14	2.54	n.s.
	sd.	(.12)	(.08)	(.09)	(.07)	(2.39)	
Supplant	$\bar{x}$	.47	.33	.85	.49	11.19	<.02
	sd.	(.24)	(.10)	(.33)	(.16)	(10.95)	
Solo aggression	$\bar{x}$	.37	.11	.13	.11	5.98	n.s.
	sd.	(.30)	(.05)	(.10)	(.07)	(5.35)	
Allied aggression	$\bar{x}$	.13	0	.07	.02	no test	
	sd.	(.19)	(-)	(.08)	(.03)		

<u>Table 6.X</u> Males' agonism to females. Dyadic mean rates per 100 hours, with standard deviations. Comparisons of adult with subadult by Mann-Whitney U; and of males' rates to female classes by Freidman 2-way Anova. Probability * $<.05$.

		to all females			by adult males to					by subadult males to				
		Adults	U n4,8	Subadults	Cycl.	Preg.	Moth.	Lact.	χ^2_r	Cycl.	Preg.	Moth.	Lact.	χ^2_r
Avoidance	$\bar{x}$	.23		.07	.36	.30	.19	.20	4.01	.04	.13	.02	.07	5.18
	sd.	(.25)		(.03)	(.44)	(.40)	(.23)	(.23)		(.06)	(.05)	(.03)	(.06)	
	test		10(9)											
Supplant	$\bar{x}$	.63		.45	1.35	.38	.39	.47	9.83*	.40	.30	.50	.47	3.00
	sd.	(.41)		(.07)	(1.60)	(.37)	(.23)	(.21)		(.17)	(.19)	(.20)	(.12)	
	test		12											
Solo aggression	$\bar{x}$	.33		.25	.75	.28	.24	.27	6.75	.38	.20	.24	.20	2.10
	sd.	(.22)		(.06)	(.65)	(.23)	(.11)	(.30)		(.26)	(.16)	(.13)	(.10)	
	test		13(16)											
Allied aggression	$\bar{x}$	.06		.05	.12	.02	.04	.08	1.95	0	.07	.07	.04	5.25
	sd.	(.04)		(.01)	(.12)	(.03)	(.04)	(.10)		(-)	(.04)	(.06)	(.03)	
	test		16(14)											

Table 6.XI Females' agonism to males. Dyadic mean rates of aggression per 100 hours, with standard deviations.

(a) given by female classes

Behaviours		Cycling	Pregnant	Mothers	Lactating	Kruskal-Wallis H	
Solo aggression	$\bar{x}$	.06	.00	.02	.02	2.65	n.s.
	sd.	(.06)	(.01)	(.03)	(.02)	(3.02)	
Allied aggression	$\bar{x}$	.06	.00	.02	.02	5.96	n.s.
	sd.	(.04)	(.01)	(.02)	(.03)	(6.53)	

(b) given by all females to each male class

		rates to Adults (8)	Subadults (4)	Wilcoxon T (n=8 females)
all female aggression	$\bar{x}$	.06	.06	16 n.s.
	sd.	(.05)	(.09)	

6.4.5 Interactions between adults and immatures

Adult-class rates of interaction with immatures are compared in Table 6.XII. The subject-rates can be approximated to dyadic rates by dividing by the number of immatures in the troop, 40. Avoidances were too infrequent for statistical test.

Adult classes differed in their rates of supplanting and aggression to immatures. In supplanting and solo aggression, this was apparently because subadults gave the most, followed by adult males and cycling females. Subadult males and lactating females were more prominent in allied aggression.

Adult classes did not differ in the rates at which they received aggression from immatures. However, they did differ in supplants received, mainly in that adult and subadult males received none, since there were no significant differences between the four female classes ($H = 7.57$, corr. obs. 7.51, d.f. 3, n.s.).

In only a small proportion of these interactions was the sex of the immature partner identified, but in over 80% of such cases these were young males ($n = 201$). Since only 57% of the troop's immatures were males, this may indicate a sex-difference in behaviour, or it may be a bias in observer recognition, but this sex ratio was not the same in all adult-immature interaction. It was approximately the same in interactions which male subjects gave and received, but female subjects received proportionately less interaction from immature females than they gave (Table 6.XIII).

6.4.6 Conclusion

Males were more 'successful' than females in that they gave relatively more agonistic behaviour in proportion to the amount received. This was solely because of the large amount they gave, since male and female received equal amounts (cf. Dittus, 1979). Males gave more than females for two reasons. First, males showed interaction to all classes of partner, and at higher rates than females did, while females gave very little to males: this much of the pattern may be attributed to the higher rank of the males. Secondly, the rates of supplanting and aggression between males were so high that they elevated the males' agonistic rates even further above those of females.

Table 6.XII Agonism given by adults to immatures (top four rows) and received by adults from immatures (lower four rows). Mean subject-rates per 100 hours, with standard deviations. Classes compared by Kruskal-Wallis H-test.

		Male subjects:		Female subjects:				Kruskal-Wallis H	
Given		Adult	Subadult	Cycling	Pregnant	Mothers	Lactating		
Avoidance	$\bar{x}$	.14	.27	.11	0	0	.03	no test	
(rec)	sd.	(.24)	(.20)	(.25)	-	-	(.09)		
Supplant	$\bar{x}$	1.21	2.56	.75	.07	.37	.35	19.71	$p<.01$
	sd.	(.66)	(1.16)	(.34)	(.15)	(.58)	(.43)	(19.95)	
Solo	$\bar{x}$	1.78	2.86	1.68	.42	.59	.67	15.21	$p<.01$
aggression	sd.	(.92)	(1.12)	(1.39)	(.32)	(.45)	(.31)	(17.83)	
Allied	$\bar{x}$	.28	1.06	.90	.68	.22	1.15	14.74	$p<.02$
aggression	sd.	(.26)	(.58)	(.54)	(.61)	(.32)	(.95)	(15.58)	
Received									
Avoidance	$\bar{x}$	0	0	.36	0	0	.25	no test	
(given)	sd.			(.54)			(.28)		
Supplant	$\bar{x}$	0	0	1.57	.49	.76	1.36	21.52	$p<.001$
	sd.			(1.11)	(.37)	(.70)	(.55)	(21.44)	
Solo	$\bar{x}$	.08	.79	1.11	.51	.82	.47	10.66	n.s.
aggression	sd.	(.12)	(.65)	(.62)	(.50)	(1.04)	(.45)	(10.83)	
Allied	$\bar{x}$	.06	.17	.51	.42	.59	.18	7.71	n.s.
aggression	sd.	(.11)	(.11)	(.42)	(.33)	(1.32)	(.19)	(7.07)	

Table 6.XIII The sex of immature partners. Agonistic interactions given and received by male and female subjects with immatures of each sex.

	Immature partners		
	Males	Females	
Male subjects give:	47	10	no test
receive:	10	1	
Female subjects give:	32	20	χ^2 13.89
receive:	73	8	$p < \cdot 001$

Males did not receive less agonism than females despite their higher rank, and this again was because of the high rates between males. Females received more agonism from other females and immatures than did males, but males received so much more from one another that the <u>total</u> they received was as high as that of females, and for aggression even higher.

Why therefore was agonistic interaction so much more frequent between males than between females? Other authors have also found this, either absolutely (Seyfarth, 1976; Stoeker, 1974) or in proportion to affiliative interaction (Rowell, 1967b) and it did not appear to be caused by instability in the male hierarchy (6.3.6: c.f. Washburn & DeVore, 1961). Conspicuous contexts of male interaction were over feeding sites (by supplanting), access to some social partners, and particularly in aggression over oestrus females (6.2.3: Chapters 7 & 8), but in a number of their interactions there was not obviously any resource under dispute (6.11.3). Because male-male agonism is reportedly frequent in a number of species (e.g. Chalmers, 1968; Struhsaker & Leland, 1979; Drickamer, 1975: but c.f. Deag, 1977) it may be referred to its ultimate cause as follows.

Because the sexes differ in the way in which they may increase the numbers of their offspring, the benefits they derive from behaving agonistically may also differ (Symons, 1978). A male's agonistic interaction with other males may more directly lead to an increase in reproductive success, by allowing monopoly of oestrus females, than may a female's agonism to other females, which may at most achieve access to food or social partners, or protection of offspring. While these last may <u>contribute</u> to reproductive success, yet competition may be more expensive to a female in terms of energy and reproductive failure. Altmann (1980) has argued that females' reproductive cycle puts them under considerable nutritional stress, particularly during lactation, so that high levels of <u>active</u> competition may not be worthwhile. Secondly, frequent involvement in agonistic interaction may produce levels of stress that inhibit ovulation (refs. in Dunbar, 1980, p.261, especially Bowman <u>et al</u>., 1978) or increase risk of foetal loss during pregnancy (Myers, 1972; Holm, 1979).

In interactions between females, mothers were little involved but they received numerous supplants, which may be attributed to their evading the approaches of others interested in their infants (Rowell, 1969b; Seyfarth, 1976; Altmann, 1980). However there was no evidence that they received substantially less aggression than did other females (cf. DeVore, 1963; Rowell et al., 1968; Saayman, 1972; Seyfarth, 1976). The fact that pregnant females received least aggression and fewest supplants suggests that their peripherality may have reduced interference from other females (Saayman, 1972). Other studies report that oestrus females show high rates of agonism, either given (Bolwig, 1959; Maxim et al., 1963) or received (Hall, 1962 ; Dunbar, 1980 , but cf. Saayman ibid.). Here the cycling females only tended to have higher rates than other females, and while a number of supplants between such females were clearly over proximity to adult males, more detailed data would be required to establish whether they competed over males more than other classes did (as in Hall ibid; Mori, 1979, but cf. Seyfarth, 1978b). Females sometimes chased other females away from particular males.

Cycling females also exchanged more agonistic interaction with males, especially adults. Thus interactions were comparatively frequent in pairs that mated often (8.4.5c). Males commonly supplanted their female consorts from food sources, and cycling females were sometimes supplanted when males approached for rear-greetings or inspection. Swollen females also received threat during consort challenges by rival males (7.5.3a). Given that mothers associated with some adult males frequently, it was surprising that they also did not exchange frequent agonism with males. Males sometimes chased females possessively from the vicinity of other males, especially cycling females: and when other troops were close by, adult males commonly chased or herded females away from the strangers (as in Buskirk et al., 1974; Cheney & Seyfarth, 1977; Packer, 1979a).

Males gave more agonism to immatures than did females, and received less, which is as predicted from their higher rank. Subadults directed supplants and solo aggression to immatures particularly frequently (also Saayman, 1972 , for aggression). At least half these supplants were to large juvenile males (aged about 3-4 years), and this in conjunction with the high supplant rate among subadult males suggests that such agonism may be especially common between natal males approaching adulthood. Agonistic interactions between adults and juveniles are further discussed by Oliver and Lee (1978) and Lee and Oliver (1979).

5. DOMINANCE RANK AND RATES OF BEHAVIOUR

6.5.1 Introduction

This section examines whether individuals' agonistic rates were determined by their position in the hierarchy. Many studies show that high-ranking animals tend to give more agonistic interaction, and receive less, than do lower rankers, at least for some behaviours (Rowell, 1966b; Seyfarth, 1976; Bramblett, 1978; Lee & Oliver, 1979, for baboons: Bernstein, 1969; Lindburg, 1971; Deag, 1977, for macaques). Such observations might be predicted in that animals who are dominant to more others may have more opportunity to exchange those behaviours which are the prerogative of the dominant in any pair. Because a linear hierarchy was found in this study, the prediction is tested by comparing subjects' dominance-rank orders with their rank-orders for rates of behaviour given and received. The analysis first examines the overall rates at which subjects exchanged agonism with all partners, per hour. Such rates are important in terms of feeding-efficiency and other long-term variables (6.1.1). Thereafter the analyses examine the effects of dominance rank on interactions within and between the sexes.

It should be noted that not all studies have found that dominance rank is related to rates of behaviour. Bygott (1979) found no such relation, and some descriptions of male-male aggression state that the most aggressive males are not of highest rank (e.g. Rose et al., 1971; Southwick, 1967).

Even if high rankers show more agonistic behaviour because of their position in the hierarchy, the question remains as to whether they are inherently more assertive or aggressive: for example, the highest-ranker often shows considerably more aggression than its closest subordinates (e.g. Hall, 1962 ; Dunbar, 1980). Therefore an analysis is made of the rate at which subjects directed agonism to subordinates of their sex (i.e. dyadic mean rate downrank), thus comparing individuals' rates when differences in their availability of subordinate partners is taken into account. This analysis is presented in parallel to that just described. For behaviours which occurred sufficiently frequently uprank, the rates of behaviour are compared with rank in the same way, to estimate whether tendency to challenge dominants was related to rank.

6.5.2 Dominance rank and subjects' rates of behaviour

For each subject was calculated the rate of each behaviour given and received with all partners, per hundred hours, as in 6.4.2. These rates are illustrated in Fig. 6.1. Secondly, for each was calculated the ratio of agonism given as a proportion of agonism received (but, for avoidance, the inverse of this). Table 6.XIV compares these rates and ratios with two variables: the first is dominance rank; the second is time spent near other baboons (clustering, 2.VIIIb) to test the hypothesis that those who spent more time with other baboons would interact more. The conclusions are as follows:

(i) Higher ranking subjects in each sex were avoided more, and gave more supplants and aggression.

(ii) The tendency for lower rankers to receive more agonistic behaviour was generally weak, but significantly the lower ranking females avoided more, and the lower ranking males were supplanted more. The higher ranking males tended to receive more aggression, but not significantly.

(iii) The higher rankers in each sex tended to give more agonism in relation to the amount they received than did the lower rankers. Overall the rate of receipt of agonism was the least accurate predictor of an animal's rank.

(iv) Subjects who spent more time near other baboons did not generally interact more; however, the more peripheral females avoided more often.

(v) Examination of the data in Fig. 6.1 show that certain animals interacted conspicuously more or less than those of similar rank. Among males, the newcomer A2 was avoided most but he supplanted comparatively little. Newcomer A1 supplanted at an exceptionally high rate, but received least of all. The most aggressive male was A5, who also received most aggression. Among the females, those who were conspicuous were F5, F6, F7 and F13, all of whom were cycling females for at least part of the study. The sick F11, who was very peripheral, exchanged fewer supplants than other females.

Table 6.XIV Subjects' rates of giving and receiving agonistic behaviours (with all classes of partners, including immatures) per hundred hours, compared with (a) dominance rank, and (b) time spent near other baboons (i.e. in clusters, 2.VIIIb). Dominance rank is also compared with the ratio between agonistic rate given/received, per subject. Comparisons by Spearman r_s, repeated with observability corrections (in brackets). Probabilities only assigned to uncorrected data if confirmed with correction, * <.05, **< .01, ***< .001

	Avoids rec.	Supplants given	Aggression given	Avoids given	Supplants rec.	Aggression rec.
Males (12)						
Dominance	.902**	.790**	.755**	-.493	-.776**	.553
+ obs.corr.	(.944)	(.797)	(.797)	-.199	-.741	.573
Clustering	-.119	-.028	.084	.155	.350	.301
+ obs.corr.	(-.273)	(-.119)	(-.126)	(-.276)	(.140)	(-.119)
Females (18)						
Dominance	.537*	.864***	.775***	-.731***	-.030	-.157
+ obs.corr.	(.479)	(.820)	(.728)	(-.765)	-.346	-.278
Clustering	.105	.310	.155	-.497*	.069	-.359
+ obs.corr.	(.025)	(.276)	(.131)	(-.534)	(-.210)	(-.453)

Dominance rank vs. ratio for

	Avoidance	Supplanting	Aggression
Males (12)	.916***	.881***	.699*
Females (18)	.679**	.848***	.787***

6.5.3 Dominance rank and interactions within and between the sexes

The following sections compare subjects' dominance ranks with (a) their dyadic mean rates of interaction with all partners of the sex concerned, and where appropriate (b) their dyadic mean rates given downrank (and, for some aggression, uprank). These rates are also compared with the amount of time spent near members of the partner-sex, estimated as the percent of all their nearest-neighbour records for which one member of that sex was present in 15 metres (2.V-VIII), again to test the hypothesis that interaction rate would reflect association frequency. In some cases tests have not been made because there were insufficient interactions to rank the subjects, and solo and allied aggression have sometimes been combined to overcome this.

6.5.3a) Interactions between males Comparisons are made over all males in Table 6.XV, and repeated separately for adults and subadults in Table 6.XVI. Analyses of rates uprank and downrank are made only for the twelve, but not for each class. The following conclusions emerge:

(i) High ranking males were avoided more, overall and in both classes. The overall result persisted when availability of subordinates was accounted for (Table 6.XVc), indicating that higher rankers were avoided more than expected from their position in the hierarchy.

(ii) Higher ranking males supplanted more, and lower rankers received more supplants. The former tendency was shown by both classes, the latter only by adults. The overall correlation disappeared when downrank rates only were considered, and so must be attributed merely to the greater availability of recipients to the high rankers. There was also a tendency, not confirmed with the observability correction, that males who spent more time near other males were also supplanted more.

(iii) High ranking males gave more solo aggression, and were more aggressive than expected merely from their position in the hierarchy (Table 6.XV column c). However the correlation was not significant among adults, so that the overall result may be in part because adults gave more aggression than subadults, who were of lower rank (6.4.4a). Low rankers did not receive more solo aggression.

(iv) The males who gave most allied aggression were not the higher rankers, but the higher rankers received more.

Table 6.XV Male-male agonism. Comparisons of males' dominance rank, and their association frequency with other males, with (a) rates of agonism with all partners (b) rates of aggression given uprank, and (c) rates of agonism given downrank, using dyadic mean rates. Spearman r_s coefficients, repeated with observability correction in brackets. Probability assigned only if confirmed with this correction, *< .05, **< .01.

	a) 12 males, all partners		b) 11 males, dominant partners		c) 11 males, subordinate partners	
	Dom.rank	Male assoc.	Dom.rank	Male assoc.	Dom.rank	Male assoc.
Avoidance rec.	.937** (.944)	-.472 (-.629)	-	-	.755** (.782)	-.173 (-.346)
Supplants given	.839** (.860)	-.413 (-.455)	-	-	-.100 (.082)	.509 (.364)
Solo aggr. given	.818** (.839)	-.399 (-.455)	.546 (.609)	-.273 (-.300)	.673* (.664)	-.155 (-.209)
Ally. aggr. given	.140 (.119)	.133 (.147)	.427 (.391)	-.055 (-.027)	-.073 (=)	.346 (=)
Avoidance given	-.657 (-.448)	.448 (.217)				
Supplants rec.	-.874** (-.741)	.762 (.533)				
Solo aggr. rec.	.140 (.294)	.245 (.042)				
Ally. aggr. rec.	.811** (.790)	-.434 (-.420)				

Table 6.XVI Male-male agonism: dominance within class. Comparisons between subjects' dominance ranks and dyadic mean rates of agonism given and received with other males. Spearman r_s values as in Table 6.XV.

	Adult males (8)		Subadult males (4)	
	r_s	corr.obs.	r_s	corr.obs.
Avoidance rec.	.898**	(.929)	1.000	(=)
Supplants given	.762*	(=)	1.000	(=)
Solo aggr. given	.476	(.595)	1.000	(.800)
Ally. aggr. given	-.238	(-.333)	.800	(=)
Avoidance given	-.833*	(-.762)	-.800	(.200)
Supplants rec.	-.810*	(-.762)	-.200	(.400)
Solo aggr. rec.	-.143	(-.262)	.800	(.600)
Ally. aggr. rec.	.833*	(.786)	.800	(=)

6.5.3b) Interactions between females Data in Table 6.XVII compare females' interaction rates with dominance rank and with their tendency to associate with other females. Similar correlation coefficients were calculated for each reproductive class: they have not been presented here, to save space, but will be summarised below. The conclusions from Table 6.XVII are these:

(i) Higher ranking females were avoided more, and gave more supplants and solo aggression. Every female class also showed strong positive coefficients for these measures. However, none of these correlations was significant downrank (column b in the table), which suggests that high ranking females were not generally more assertive or aggressive than expected from their position in the hierarchy.

(ii) Lower ranking females avoided more, and received more supplants and solo aggression: all four classes shared the same tendency for these behaviours, some significantly so.

(iii) There was no evidence that females who spent more time with other females also interacted more: rather the reverse seemed to be the case, since most correlation coefficients were negative. This was probably because mothers spent most time with females but interacted little, while cycling females were associated less but interacted more.

6.5.3c) Interactions between the sexes Correlation coefficients are presented in Table 6.XVIII. Aggression from female to male was so infrequent that solo and allied have been combined.

(i) High ranking males were avoided more by females, and gave them more supplants and solo aggression. The same tendencies were significant for adult males and evident for subadults. High ranking adult males also received more aggression from females. Males' aggressive exchanges with females are illustrated in Fig. 6.2. The younger subadults were involved more than expected from their dominance rank, since the trend among adult males is quite clear. High ranking adults received more aggression mainly because females were more aggressive to the newcomers A1 and A2 and to resident male A3. The males' agonistic rates with females were not closely related to the time they spent near them.

(ii) Higher ranking females gave more aggression to males, a tendency apparent in all three classes for whom data were sufficient to compare.

Table 6.XVII Agonism between females, and dominance rank. Females' dominance rank and their time in association with other females (dyadic association frequency) compared with (a) dyadic mean rates of agonism exchanged with all other females, and (b) dyadic mean rates of agonism to subordinates. Spearman r_s values as in Table 6.XV.

	a) 18 females, all partners		b) 17 females, to subordinates	
	Dom. rank	Female assoc.	Dom. rank	Female assoc.
Avoidance rec.	.519*	-.253	-.164	-.095
	(.603)	(-.159)	(-.321)	(-.163)
Supplants given	.876**	-.159	.277	-.417
	(.827)	(-.193)	(.253)	(-.473)
Solo aggr. given	.668**	-.275	-.036	-.618**
	(.654)	(-.298)	(-.094)	(-.627)
Ally. aggr. given	.439	-.210	.114	-.062
	(.399)	(-.269)	(-.105)	(-.191)
Avoidance given	-.785**	-.175		
	(-.808)	(-.151)		
Supplants rec.	-.911**	.206		
	(-.893)	(.018)		
Solo aggr. rec.	-.640**	-.321		
	(-.699)	(-.337)		
Ally. aggr. rec.	.062	-.068		
	(-.012)	(-.294)		

Table 6.XVIII Dominance rank and agonism between the sexes. Subjects' dominance rank, and association frequency with the opposite sex, compared with dyadic mean rates of agonism exchanged. Solo and allied aggression have been pooled when calculated from female to male. Spearman r_s values presented as in Table 6.XV.

Male subjects

	Twelve males		Adults (8)	Subadults (4)
	Dom.rank	Female assoc.	Dom.rank	Dom.rank
Avoidance rec.	.806** (.839)	.249 (.259)	.881** (=)	.800 (=)
Supplants given	.767** (.832)	.354 (.140)	.850** (.952)	1.000 (=)
Solo aggr. given	.699* (.636)	.273 (.098)	.881** (.905)	.800 (=)
Ally. aggr. given	.470 (.608)	.416 (.336)	.443 (.571)	.633 (.400)
Total aggression rec.	.300 (.270)	-.145 (-.242)	.823* (.707)	-.400 (-.200)

Female subjects

	All females (18)	
	Dom.rank	Male assoc.
Total aggr. given	.584* (.547)	.363 (.287)
Avoidance given	-.406 (-.499)	-.307 (-.414)
Supplants rec.	.653** (.591)	.604* (.507)
Solo aggr. rec.	.441 (.284)	.340 (.247)
Ally. aggr. rec.	.437 (.382)	.342 (.292)

FIG. 6.2

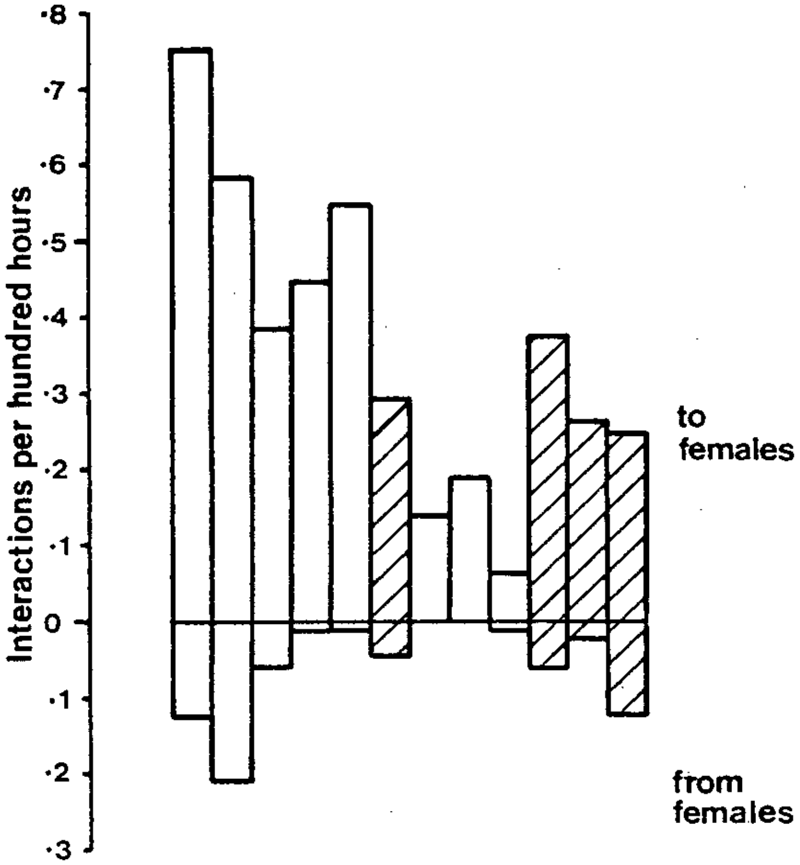


Fig. 6.2. Males' rates of aggressive interaction with female opponents. Dyadic mean rates per hundred hours with which males gave aggression (above x-axis) and received it (below) with female partners, pooling both solo and allied aggression. Males arranged in descending order of dominance rank from the left, subadult males cross-hatched.

The correlation coefficients for agonism received suggest that lower ranking females tended to avoid males more (n.s.) but that otherwise the higher rankers received more, significantly in the case of supplants (this was also apparent within three of the four female classes). However the females who were supplanted more were also those who spent more time near males, so that these results were probably not independent.

6.5.4 Interactions with immatures

Results of comparisons between subjects' interaction rates with immatures (as subject rates per 100 hours) and dominance rank are in Table 6.XIX. Clustering (2.VIIIb) was used as an estimate of proximity to immatures, and also compared with interaction rates. Data on immatures' avoidances, and aggression to adult males, were insufficient for analysis.

(i) None of the males' interaction rates were significantly related to dominance rank or clustering. Coefficients over all males suggested that lower rankers interacted more, almost certainly due to the high rates of the subadults (6.4.5) and not because of dominance rank *per se*.

(ii) Higher ranking females gave more supplants and solo aggression to immatures. The lower rankers also *tended* to receive more supplants and aggression, since all coefficients were negative (as were eight of the nine calculated for particular classes), but not significantly so. Females' interaction rates were not significantly related to the time they spent among other baboons.

6.5.5 Summary: dominance rank and agonistic rates

The pattern of subjects' overall rates per hour may be explained in terms of the detailed relations between classes.

6.5.5a) Male subjects

(i) The fact that higher ranking males were avoided more reflects especially avoidance received from other males (more than expected merely from their high rank position) and from females. The fact that lower ranking males did not avoid more may reflect the low rates of subadult males, because the low ranking *adults did* avoid more.

(ii) The high supplant-rates of the higher ranking males were reflected in their supplants both to males and to females. Lower ranking males received more supplants, but these were entirely from other males.

Table 6.XIX Adults' dominance rank, and interaction with immatures. Adult class-members' dominance rank, and percent time near other baboons (clustering: 2.VIIIb) compared with subjects' rates of interaction with immatures per hundred hours. Spearman r_s values, repeated with observability corrections as in Table 6.XV.

	a) Twelve males		b) Adults (8)	Subadults (4)		c) All females (18)	
	Dom.rank	Clustering	Dom.rank	Dom.rank		Dom.rank	Clustering
Supplants given	-.123 (-.035)	-.021 (-.196)	.611 (.476)	-.400 (.400)		.592* (.551)	.209 (.170)
Solo aggr. given	-.105 (-.070)	.294 (-.063)	.599 (.762)	-.800 (=)		.669* (.587)	.278 (.202)
Ally. aggr. given	-.531 (-.610)	.415 (.392)	.133 (-.108)	-1.000 (=)		.121 (.091)	-.256 (-.329)
					Supplants rec.	-.437 (-.475)	-.003 (-.036)
Total aggr. rec.	-.402 (-.392)	.248 (.167)	-	-1.000 (=)	Solo aggr. rec.	-.349 (-.406)	-.407 (-.453)
					Ally. aggr. rec.	-.498 (-.447)	-.391 (-.449)

(iii) The fact that higher ranking males gave more aggression reflects their high rates of solo aggression to males (giving more than expected merely from their rank position) and to females. The lower rankers did not receive more aggression, apparently because male allied aggression was given more to high rankers, and high-ranking adults also received more aggression from females.

6.5.5b) Female subjects

(i) The fact that low-ranking females avoided more and high-rankers received more avoidance, overall, was largely because this pattern obtained among females alone: but emphasised because lower rankers also tended (n.s.) to avoid males more.

(ii) The higher rates of supplants given by high-ranking females were directed both to females and to immatures. However, lower rankers did not receive more supplants, because of opposing tendencies that low rankers were supplanted more by females while high rankers were supplanted more by males (arguably because they spent more time near them).

(iii) Higher ranking females gave more aggression overall, apparently because they gave more aggression to males, and more solo aggression to both females and immatures. However, the lower rankers did not receive more overall, despite receiving more solo aggression from other females, and this was again because the higher rankers tended to receive more from males, albeit not significantly.

6.5.6 Conclusions

Dominance rank emerges as a useful intervening variable in that it predicted the patterning of individual differences, of the sort 'higher rankers give more and receive less', for several behaviours. Although such correlations for avoidance and supplanting within each sex were an inevitable result of the way dominance was assigned, yet they were also found for agonistic behaviour between the sexes, and between adults and young; for aggression among females; and for a variety of non-agonistic behaviours (e.g. 4.2.7; 4.3.9b) which were not so implicated by definition.

The majority of supplants took place over feeding sites; and aggression over prized foods such as fungi and meat was sometimes conspicuous. The data presented here and in section 6.4 above therefore have some relevance to feeding competition. Other authors have found that adult and subadult males are less often interrupted during feeding than are other animals, and so may have longer feeding bouts (Post et al., 1980; Rhine & Westlund, 1978). It was surprising therefore that females did not avoid, nor receive supplants, more than males (6.4.2). As noted earlier, this was because males showed these behaviours to one another so frequently: however, a large number of their interactions did not involve food at all; and so this result may not reflect feeding competition, especially since a male can more easily obtain a feeding site from a female or immature without having to challenge another male. However, the number of measures in which high rankers gave more agonism, and received less, strongly suggest that high rankers would be at an advantage in feeding competition. This is especially likely for supplanting, as demonstrated for the juveniles of this troop by Lee and Oliver (1979), and in terms of feeding interruptions at Amboseli by Post et al (1980).

Because the direction constancy of interactions between females was so high, position in the female hierarchy was strongly predictive of rates of agonistic interaction. Analysis of rates downrank gave no suggestion that higher rankers were any more assertive or aggressive than expected from their position in the hierarchy. Most individual differences were therefore attributable to dominance rank modified slightly by the effect of reproductive state, in that cycling females tended to interact more.

Avoidance and supplant rates among males were closely related to dominance rank in the expected way. But in aggression, this was not the case. Higher rankers tended to receive more allied aggression, reflecting the direction of this behaviour uprank and the frequency with which middle-ranking males allied against high-ranking newcomers. In solo aggression, high rankers gave more, but the amount received was independent of rank and suggested rather that a number of males who gave more aggression also tended to receive more. Thus the focal males A3, A4, A5 and A7 were prominent in aggression given and received, with A5 showing most of both.

A more striking pattern between males was that when availability of subordinates was accounted for, the higher rankers still received more avoidance, and gave more solo aggression, than the low rankers.

Examination of individual scores revealed that three adults were particularly responsible, namely A1, A3 and A5, and that they also tended to supplant downrank at very high rates. The eight adults' rank-order for solo aggression downrank was highly correlated with the rate at which they were avoided by subordinates (r_s .881, corr. obs. .714, $p < .05$) suggesting that these males may have been avoided because they were so aggressive.

In interactions between the sexes, there was a tendency for high ranking females to be more often involved. In part this must reflect their tendency to spend more time near males (4.2.7). Among males, the higher ranking adults exchanged more agonism with females. The fact that the females' aggression to males was directed especially to A1, A2 and A3 parallels the direction of allied aggression which males gave to these three in particular (6.11.1).

Subadult males interacted with females more than expected from their rank, in that their rates were comparable to those of middle-ranking adults although their own ranks were generally lower. Young males approaching adult size are reported to rise in the female hierarchy in a number of species (langurs, Jay, 1965; chimpanzees, Bygott, 1979; and baboons, Hausfater, 1975; Lee & Oliver, 1979), so that the high rates here may represent residual antagonism related to dominance changes. Subadult males also showed a tendency to redirect threat at nearby females when being supplanted by adult males.

6. AGONISM AND DOMINANCE RANK-DIFFERENCE

6.6.1 Introduction

Agonistic interaction is sometimes reported to be more frequent between animals of similar dominance rank, and while in some cases this may be merely because there are more partners available at closer ranks (e.g. Christopher, 1972), there are sufficient reports of particularly high rates at close ranks, both of agonistic behaviour (Bernstein & Sharpe, 1966; Alexander & Bowers, 1969; Moore, 1978) and of social attention (Emory, 1976). This may be explained in terms of competition for resources, which is likely to be keenest between animals of similar competitive ability: for example Post *et al* (1980) found greater overlap in diet between closely-ranked classes. Alternatively, it may represent competition for increased rank itself: most dominance-changes between baboon males involve adjacent rankers (Hausfater, 1975). This is supported in that macaques, who are forcibly removed from their group, will, on return, seek out aggressively the animal next below in rank, as though reaffirming status (Conaway & Koford, 1964; Vessey, 1971). However, some studies do not find agonism more frequent at close rank (Seyfarth, 1976; Bygott, 1979); and DeWaal (1977) suggests that it may be restricted to pairs of unstable dominance, or to newly-formed groups.

The following section examines the rank-difference of agonistic interaction by methods described in 2.XIIIc).

6.6.2 Comparison of rates

Figs. 6.3 and 6.4 show the dyadic mean rates of agonism between all pairs at each rank-difference, with 1 as adjacent rankers: the most extreme rank-differences have been pooled due to diminishing sample size. Rates are shown downrank only, for females, but downrank and uprank separately for males. The correlation coefficients (listed on the figures) are all positive, suggesting that agonism tended to be more frequent between closer-ranking pairs, but this tendency was only significant for avoidance and allied aggression among females, and for both types of aggression uprank and downrank among males. The result for avoidance uprank among males is based on too few interactions to be reliable.

Data in Table 6.XX test the hypothesis that each subject's most frequent recipient of agonism would be within two places of rank. The hypothesis is rejected except in the case of allied aggression between females.

6.6.3 Conclusion

Overall there were slight tendencies for agonistic interaction to be more frequent at closer ranks within each sex, but only one clear case for it to cluster at particularly close rank. Examination of the dyadic rates in Figs. 6.5, 6.6 and 6.17-20, show a number of high frequency dyads, and while some look like cases of intenser competition between close rankers, yet there was only one pair with possibly unstable

FIG. 6.3

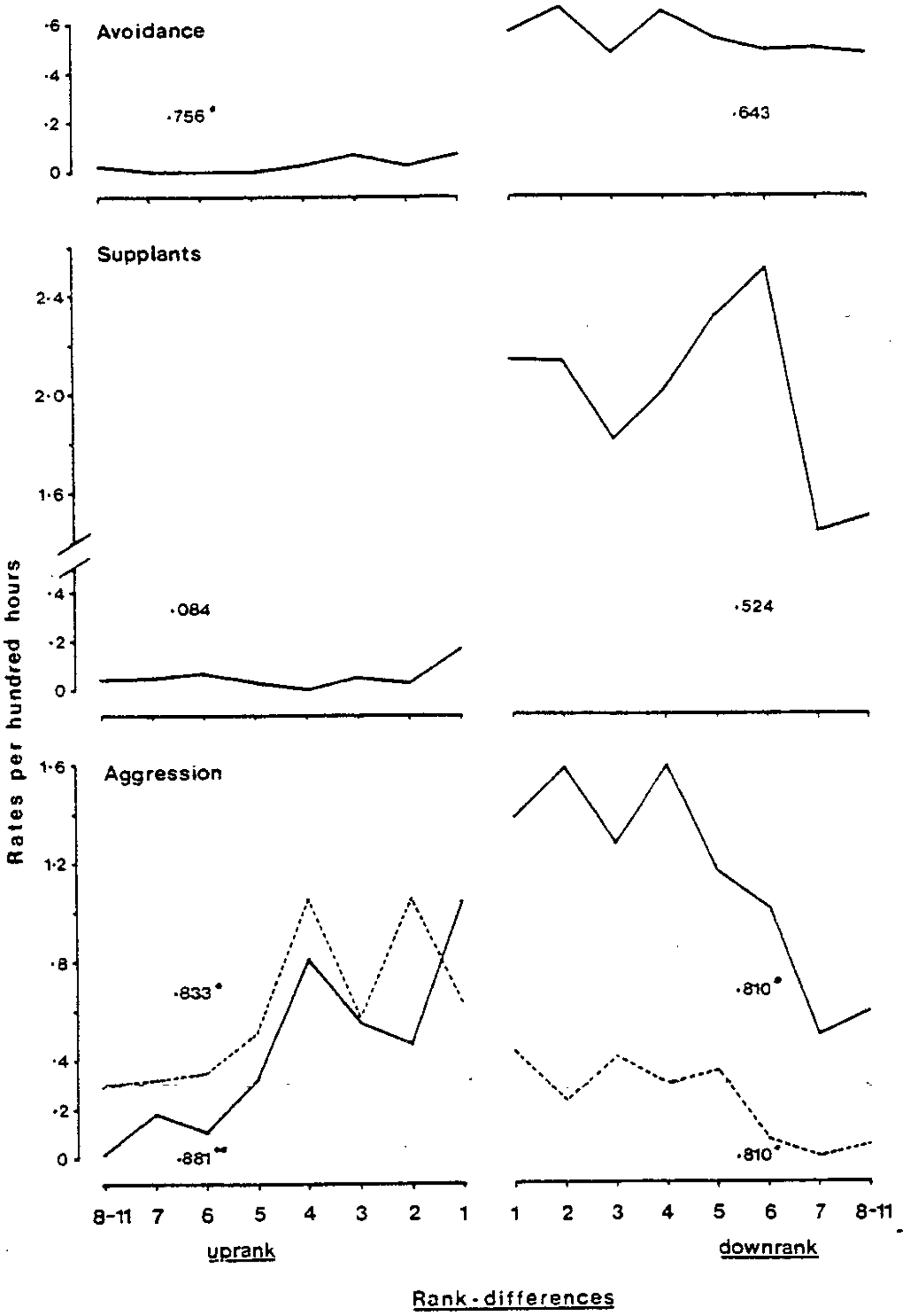


Fig. 6.3. Dominance-rank difference and rates of agonistic interaction between males. Mean dyadic rates of interaction between pairs at each rank-difference, with rates to dominants (on left) and to subordinates (on right) separately. Allied aggression shown by dotted lines. Extreme rank-differences (8 to 11) have been pooled. Spearman r_s values compare rate and rank-difference; * $p < .05$, ** $p < .01$.

FIG. 6.4

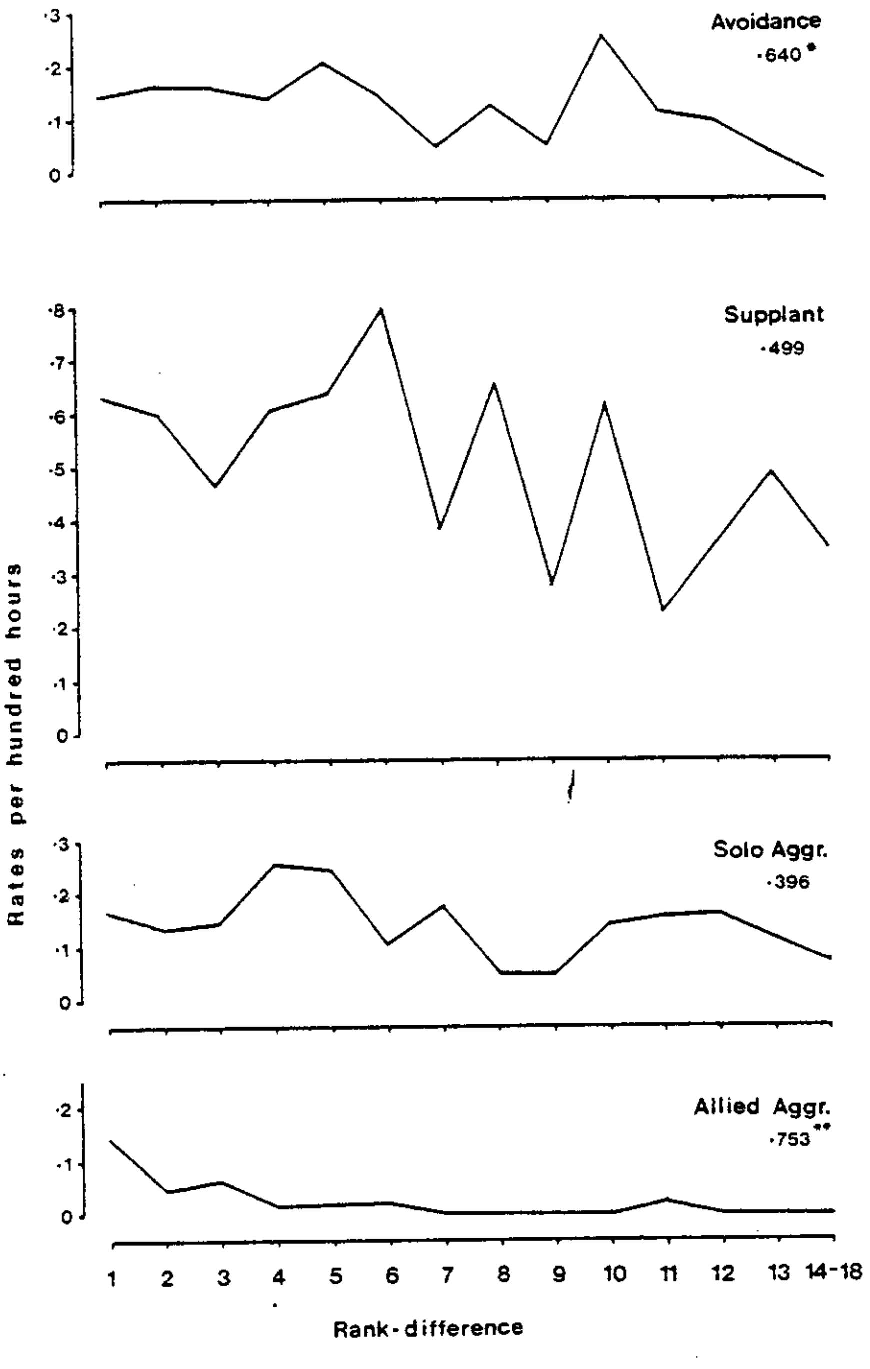


Fig. 6.4. Dominance-rank difference and rates of agonistic interaction between females. Diagrams as in Fig. 6.3, except that only rates downrank are shown, and solo and allied aggression are plotted separately. The vertical scale is twice that of 6.3. * p < .05, ** < .01.

<u>Table 6.XX</u> Comparison between the number of first-recipients of agonistic behaviour within and beyond two places of dominance rank from the donors. Binomial probabilities two-tailed (p).

		a) between females			b) between males					
rank-places		downrank only			uprank			downrank		
		1-2 :	3+		1-2 :	3+		1-2 :	3+	
Avoidance rec.	obs.	5.2	10.8	$p_c 1.00$	4	3	$p_c 1.00$	6	4	p .52
	exp.	4.6	11.4		4.1	2.9		4.5	5.5	
Supplants given	obs.	7	9	p .56	4	5	$p_c 1.00$	6	5	p .76
	exp.	4.6	11.4		4.4	4.6		5	6	
Solo aggr. given	obs.	4	10	$p_c 1.00$	6	5	p .76	6.5	4.5	p .76
	exp.	4.1	9.9		5	6		5	6	
Ally. aggr. given	obs.	7	3	$p < .05$	4	6	p 1.00	6	4	p .66
	exp.	3	7		4	6		4.8	5.2	

FIG. 6.5

AVOIDANCES & SUPPLANTS

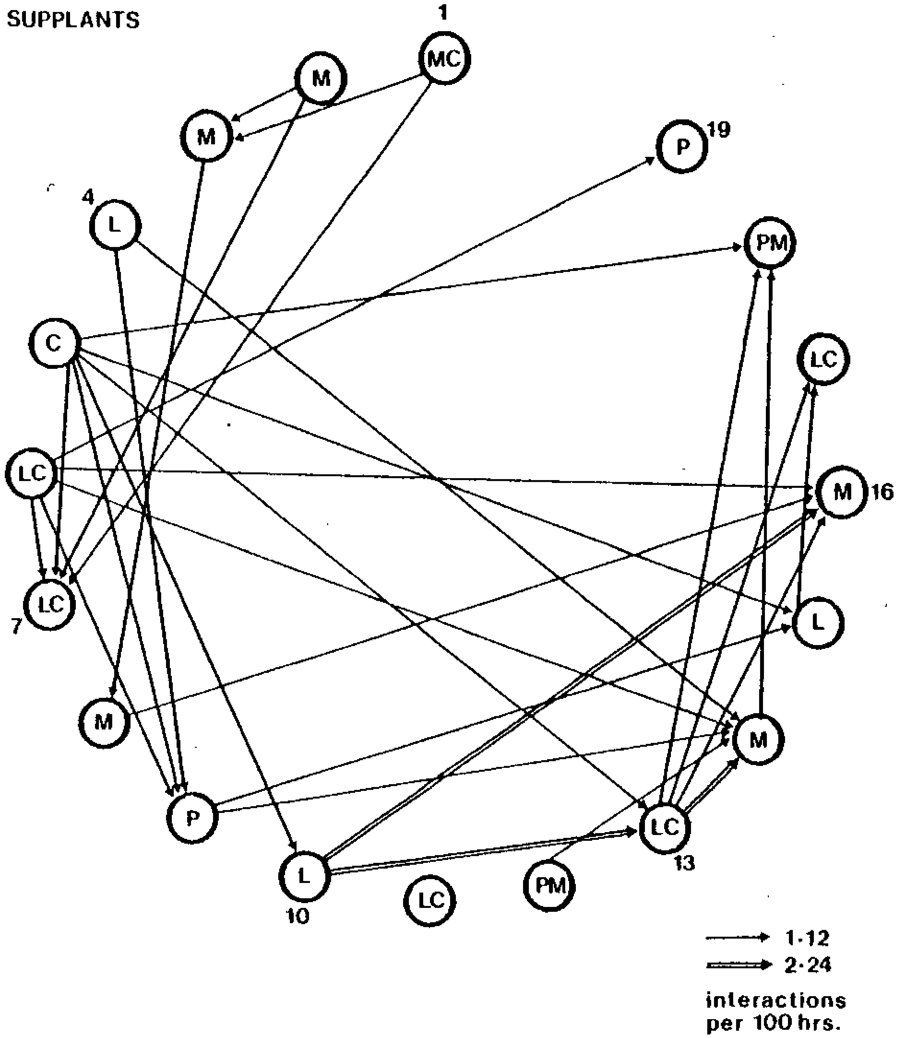
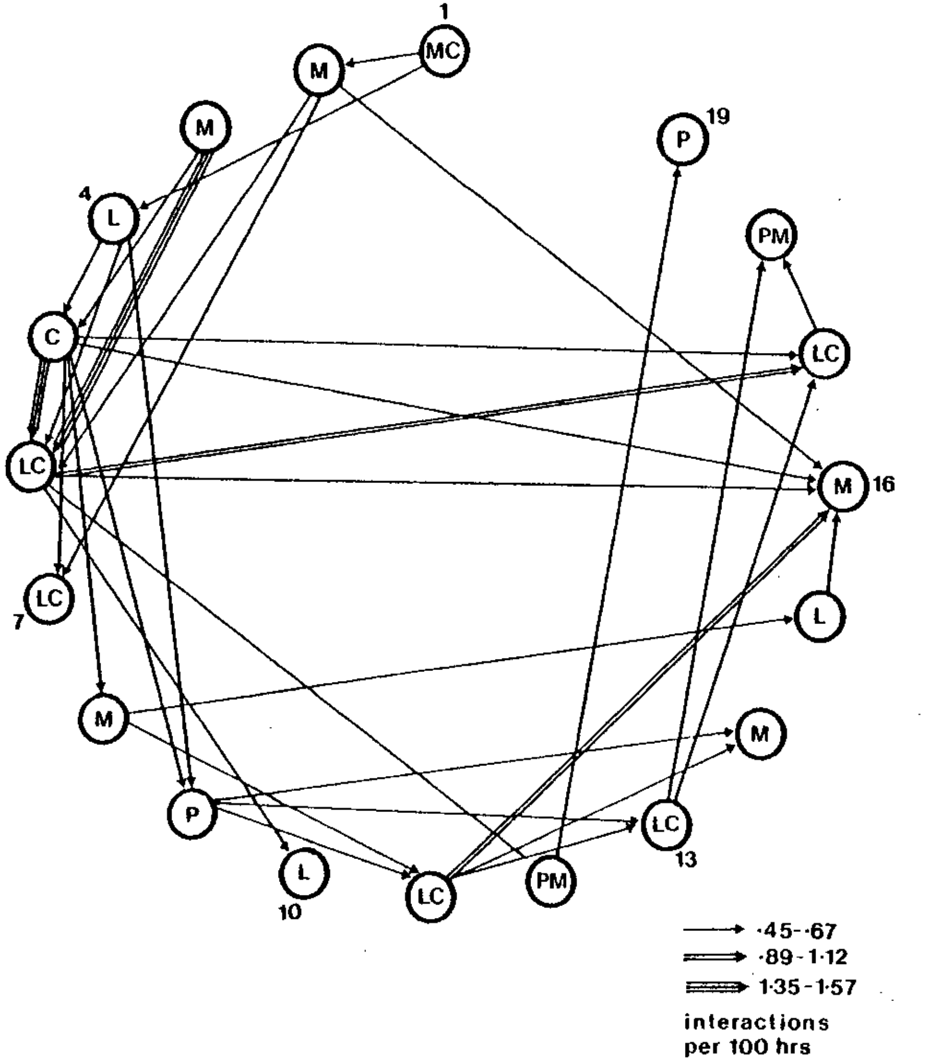


FIG. 6.6

AGGRESSION



Figs. 6.5 & 6.6. Agonistic interactions between pairs of females. Subjects arranged in descending order of dominance rank anticlockwise from the top, ranks of every fourth female shown for reference. Females are C - cycling, P - pregnant M - mothers, L - lactating. Fig 6.5 combines avoidance received with supplants given; arrows account for 41% of 472 interactions recorded. Fig 6.6 combines solo and allied aggression, arrows accounting for 56% of 155 interactions, and critical values are lower than in 6.5. Arrows run from donors to recipients.

dominance (A6 and A7), and there were equally conspicuous pairs at more distant ranks. Therefore, while competition between close-rankers may partly explain the distribution of such pairs, other factors may also be involved in each sex.

Avoidances between females were not concentrated between particular pairs, and <u>did</u> decrease at disparate ranks, but any such pattern for supplants was obscured by the high rates given to mothers: of the 17 most frequent pairs, 12 had mothers as recipients. The distribution of aggression among females was characterised only by the concentration of allied aggression to subordinates within four places of rank. One interpretation is that females only <u>need</u> allies against close-rankers, but this is further discussed in relation to kinship in 6.7.11 below.

Apart from a few pairs of adjacent-ranked males showing particularly frequent agonism, the close-rank pattern among males was apparently determined by four factors (Figs. 6.17-20). First, there were often high rates among the focal males, perhaps reflecting their association together or with females in common. Secondly, there were high rates of supplanting between subadults, which were necessarily close in rank. Thirdly, the distribution of adult male aggression reflected more the males' involvement in aggressive competition for oestrus females, much of which centred around adults 1 to 7, and so tended to be within six rank-places. Whether these patterns produce the closer-rank effects, or <u>result</u> from the similar competitive abilities and therefore close ranks of the males involved, is not clear. There were also some dyads which appeared to show particular antipathy; adult males tended to supplant the higher-ranking subadults, who were not especially close in rank. These relations are further discussed in section 6.10 below.

7. <u>POLYADIC INTERACTIONS AND ALLIANCES</u>

<u>6.7.1</u> <u>Introduction</u>

Agonistic interactions within pairs of animals are often affected by the proximity or intervention of a third party (Kummer, 1967; Struhsaker, 1967). Such interventions may affect long-term dominance relationships, so that it is possible to distinguish an animal's rank due to its competitive ability (basic rank) from its rank depending on its alliances with others (dependent rank) (Kawai, 1958). In matrifocal troops, the ranks of adult females often depend on their mothers' ranks, as in macaques (Kawamura, 1958; Koford, 1963; Missakian, 1972; Dittus, 1979) and baboons (Hausfater, 1975; Moore, 1978) but not in Hanuman langurs (Hrdy & Hrdy, 1976), and this is commonly attributed to maternal intervention in daughters' disputes (Marsden, 1968; Eaton, 1976; Cheney, 1977). Female baboons may assume ranks which their mothers had at their birth even when the mothers no longer maintain those ranks (Hausfater et al., in prep. cited Altmann, 1980; also in macaques, Sade, 1972b) and this may depend less on maternal intervention than on early identification processes (Altmann ibid.), possibly enhanced by exploitative alliances later on (Walters, 1980). Either way, alliances may perpetuate the matrilineal ranking system, and tend to be more frequent between kin both in macaques (e.g. Kaplan, 1977; Massey, 1977) and in baboons (Nash, 1978b; Walters, 1981). In macaques, alliances between females may control the entry of immigrant males into troops (Vessey, 1971; Bernstein et al., 1974; Packer & Pusey, 1979). In species breeding in one-male units females tend also to ally against the unit-male (Hall, 1967; Dunbar & Dunbar, 1975; Hrdy, 1977; Mori, 1979).

Alliances also occur between non-relatives, whereby animals may improve or defend their rank positions (Koyama, 1967; DeWaal, 1978), or become more fully integrated into their troop (Kaplan, 1978); and alliance is often a feature of the 'control role' of high rankers (Bernstein & Sharpe, 1966). In baboons, the occurrence of male-male alliance was early recognised (e.g. Stoltz & Saayman, 1970), forming the basis for the 'central hierarchy' concept of Hall & DeVore (1965) and providing evidence of reciprocal altruism (Packer, 1977b). However, Hausfater (1975) found that polyadic aggression comprised as few as 2% of agonistic bouts at Amboseli.

The following section analyses the distribution and importance of two types of polyadic interaction: first, triadic avoidances and supplants, and secondly, polyadic aggression, which is qualitatively rather different from the first.

6.7.2 Triadic avoidance and supplant

Occasions when one animal moved out of the way of the advance of two others simultaneously are here considered. These comprise 39 avoidances (from beyond arm's reach), and 17 supplants (from within it). The oncoming pair were not considered to be in 'alliance', in contrast to aggressive interactions (6.7.4). When these triads were broken down into their constituent dyads, they were distributed between the sexes as shown in Table 6.XXI. These rates differ most strikingly from the corresponding solo rates (Table 6.VI) in that females were avoided by males and appeared to supplant them. All such cases from female to male involved cycling females travelling with an adult male; in 26 of these 28 interactions the female was fully swollen, and in 24 the oncoming pair were in consort. Table 6.XXII shows that these amounted to the majority of triadic interactions. In 36% of them the male who moved away was of <u>higher</u> rank than the oncoming male, which is a far higher proportion than the 3.6% uprank found for <u>dyadic</u> supplant and avoidance between males (Table 6.IV). However, in all 19 cases where a female deferred to the pair she was of lower rank than the oncoming female.

The remaining nine interactions provided five cases of a female deferring to female(s) dominant to herself, three cases of a male deferring to higher ranking males, and <u>one</u> of a male being supplanted by two subordinate males. Finally, there were six cases (not included in Tables 6.XXI & XXII) where one male was avoided by two or more other males simultaneously, but the avoiders were always subordinates.

6.7.3 Discussion

These data show that triadic supplants and avoidances followed the rank-direction of dyadic interactions, except in two respects. First, a male travelling with a swollen female was more likely than usual to be deferred to by a male dominant to himself (also Packer, 1979b). This provides strong evidence for a process analogous to rival inhibition in hamadryas baboons (Kummer <u>et al</u>., 1974): and is further discussed in 8.5.2.

Secondly, females in such pairs were deferred to by males normally dominant to themselves. Such interactions may underly the early reports that females assume the dominance rank of their male consorts (e.g.

Table 6.XXI Triadic avoidances and supplants. I: Dyadic mean rates per 100 hours, within and between the sexes, estimated by breaking down triads into component dyads. Note that the behaviours differ so that column two shows female avoidance of males but male supplanting of females.

		Male-male	Male-female	Female-male	Female-female
Avoidance	$\bar{x}$	.052	.014	.025	.008
	sd.	(.066)	(.023	(.039)	(.018)
	n.	30	13	24	11
Supplant	$\bar{x}$	.011	.011	.004	.007
	sd.	(.026)	(.024)	(.019)	(.019)
	n.	6	10	4	9

Table 6.XXII Triadic avoidances and supplants. II: Interactions listed by donor-pair, and recipient.

	Avoidances		Supplants	
	by male	by female	of male	of female
Donors				
Consort pair	20	8	4	6
Cycling female with male	4	1	-	4
Two males	3	2	1	-
Two females	-	1	-	-
Other	-	-	-	2

Hall & DeVore, 1965), but the fact that they were only deferred to by females subordinate to themselves shows that this interpretation was not supported here.

6.7.4 Polyadic aggression described

Aggressive interactions which included alliances between two or more animals simultaneously directing aggression to a common opponent are included here as polyadic aggression. Many of these were attempts to aid the victim of an attack, apparently in response to gestures of fear by the recipient. Other alliances were clearly solicited by gestures such as screaming with tail up (see Fig. 3, in Saayman, 1971b) or by the rapid head-turning gestures described variously as 'enlistment' (Hall & DeVore, 1965), 'soliciting' (Ransom, 1971; Packer, 1977b) and 'head-flagging' (Walters, 1980). Some alliances may have merely been coincident parallel aggression, and some occurred when two male antagonists redirected aggression at nearby females. No attempt is made here to distinguish which partners initiated these alliances, nor to separate 'coalitions' from 'aids' (cf. Cheney, 1977).

Cases where two or more animals concurrently received aggression from a common opponent are here classified as defensive alliances. In 231 instances of males allying together, only 17.7% were in defence: these included some cases of a consort male allying with another against an aggressive rival. 25.9% of 58 male-female alliances were in defence, mostly being consort-pairs under attack; and 8.7% of 46 female-female alliances were in defence. Because many defensive alliances differed qualitatively from alliances in aggression given, all of them have been omitted from the analyses that follow. The remaining 222 polyadic interactions have already been analysed in terms of 'who was aggressive to whom' under the heading of allied aggression. The following sections describe who allied with whom.

6.7.5 Individual differences in alliance

Fig. 6.7 shows the amount of each subject's aggression which was given in alliance, or received from alliances, as a proportion of its total incidents of aggression given or received respectively. There is no clear evidence that high rankers were preferred as allies, nor allied against more (note that some of the proportions were calculated

FIG. 6.7

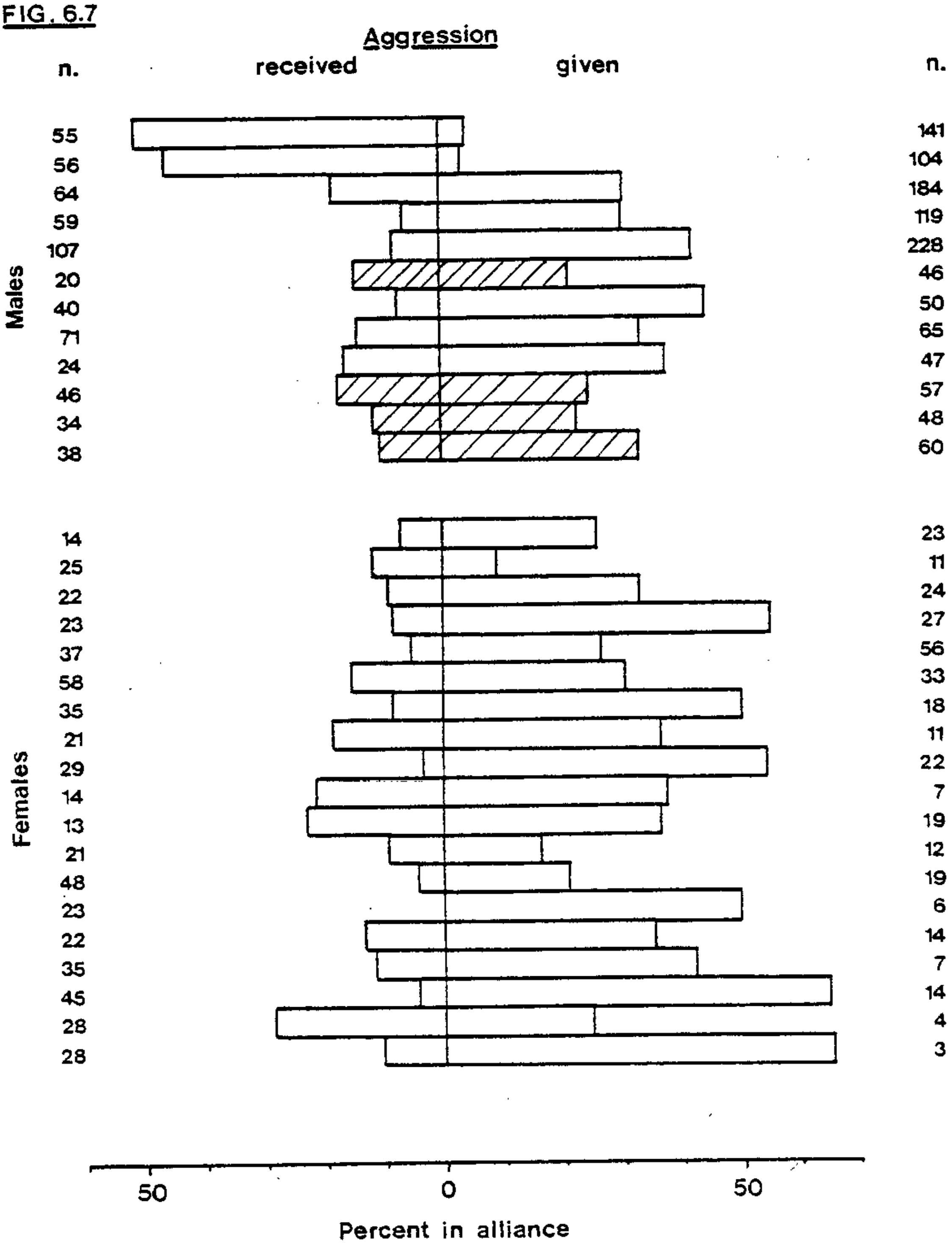


Fig. 6.7. The percent of each subject's total incidents of aggression in which he or she received aggression from allied opponents (on left) or gave aggression when allied (on right).

from small sample sizes, especially in aggression given by low-ranking females). However, the two newcomer males A1 and A2 were conspicuous for the frequency with which they were allied against, and for the rarity with which they allied with others. Comparison of proportional alliance in aggression given and received over twelve males yields r_s -0.608, $p < .05$.

6.7.6 The proportion of alliance in each dyad

The likelihood that any two animals would be seen acting in alliance depended partly on opportunity; i.e. the rate of aggression of each. Therefore pairs' tendencies to ally were calculated as follows. The number of times the subject gave aggression allied with a particular partner was expressed as a proportion of the total number of times the subject gave aggression at all, excluding aggression directed at that partner or given when that partner was absent from the troop. This was the dyadic alliance proportion between the subject and the partner; in any pair it differed slightly depending whether the more or less aggressive partner was considered as subject. This measure assumes that the likelihood that either partner showed aggression was unaffected by the presence of the other, a naive and probably false assumption but necessary for this analysis.

6.7.7 Alliances within and between each sex

The mean percent of their aggression given in which subjects of each sex were allied with at least one male, female, or immature are shown in Table 6.XXIII. Females allied with one another most, next with immatures, and least with males. Conversely, males allied with males most, much more than with females or immatures. The latter result is surprising, since there were fewer males available as potential allies than there were females. Therefore when the same data are presented as mean dyadic alliance proportion across all partners of each sex (Table 6.XXIV), which allows for the availability of partners, it emerges that females allied with both sexes about equally, whereas adult and subadult males both showed a strong tendency to ally more with males. Furthermore, comparing tendencies to ally with immatures, females did not in general do so more than males (despite their contrast in Table 6.XXIII, U = 100, n 12, 18, n.s.); however, subadult males

Table 6.XXIII Mean percent of each subject's aggression given in which it was allied with *at least one* male, female, or immature. The percentages are not mutually exclusive, since a subject could be allied simultaneously with male, female, and immature.

		Allies		
		Males	Females	Immatures
Subjects				
Males	$\bar{x}$	22.0	3.2	2.8
	sd.	(13.1)	(2.9)	(3.7)
Females	$\bar{x}$	8.1	19.3	11.4
	sd.	(6.9)	(10.1)	(17.6)
Male classes				
Adults	$\bar{x}$	25.2	1.8	.8
	sd.	(15.0)	(1.5)	(.9)
Subadults	$\bar{x}$	15.7	6.0	6.9
	sd.	(4.9)	(3.2)	(4.1)

Table 6.XXIV The percent of each subject's aggression given in which it was allied with *each* male and female (i.e. mean dyadic percent). Means and standard deviations (brackets).

	Male allies	Female allies	Wilcoxon
Male subjects (12)	3.4 (2.2)	0.2 (0.2)	T 0,n 12 $p<.01$
Female subjects (18)	1.1 (0.8)	1.2 (0.7)	T 64,n 17 n.s.
Adult males (8)	3.9 (2.4)	0.1 (0.1)	T 0,n 8
Subadult males (4)	2.3 (1.2)	0.4 (0.3)	no test

allied with immatures significantly more than adults did ($U = 1$, n 4.8, $p < .01$). These tables therefore suggest that subadult males showed alliance patterns intermediate between those of adult males and females, allying with females and young more than adult males did, but allying with males more than females did.

6.7.8 Alliance and dominance rank

(a) Table 6.XXV compares subjects' dominance ranks with their tendency to ally with each class (measured as mean dyadic alliance proportion). Lower ranking males allied more with females, in part no doubt due to the greater tendency of subadults, but the trend is apparent in each class. Secondly, low ranking adult males allied more with other males; these low-ranking adults tended also to be older (6.7.10 below). Thirdly, the higher ranking females were allied more with males.

(b) The dyadic alliance proportions were used to calculate mean proportions at each rank-difference as in 2.XIII c(i). Separate estimates were made for the dominant partners, and the subordinate partners, in each pair, but they provided similar patterns (Fig. 6.8). Considering only the dominant partners, the mean alliance proportions were greater at closer ranks, both in females ($p < .01$) and in males ($p < .05$). The result among females was because all such alliances occurred within eight places of rank. Data presented below suggest that this result among males was because resident adults tended to ally frequently and to be closer in rank.

6.7.9 Alliance, association, and grooming

Preceding analyses suggested that subjects tended to groom their more frequent associates (4.4.2). Other studies suggest that alliance may be more frequent between grooming partners (Dunbar, 1980 ; Seyfarth, 1980). Accordingly the distribution of alliances was compared with those of association and grooming. Alliances among females and between the sexes are examined first: then the more frequent alliances between males are analysed in greater detail.

6.7.10 Alliances among females and between the sexes

For each subject, every partner of a given sex was differentiated according to whether it was:

Table 6.XXV Dominance rank and alliance proportion. Comparisons between subjects' dominance ranks and their mean dyadic alliance proportions with males and with females. Spearman r_s values, probabilities * $<$.05, ** $<$.01.

	Dominance cf. ally males	Dominance cf. ally females	Ally males cf. ally females
Males			
all (12)	-.154	-.739**	-.074
adults (8)	-.857*	-.431	.204
subadults (4)	.800	-1.000	-.800
Females (18)	.477*	.041	.152

FIG. 6.8

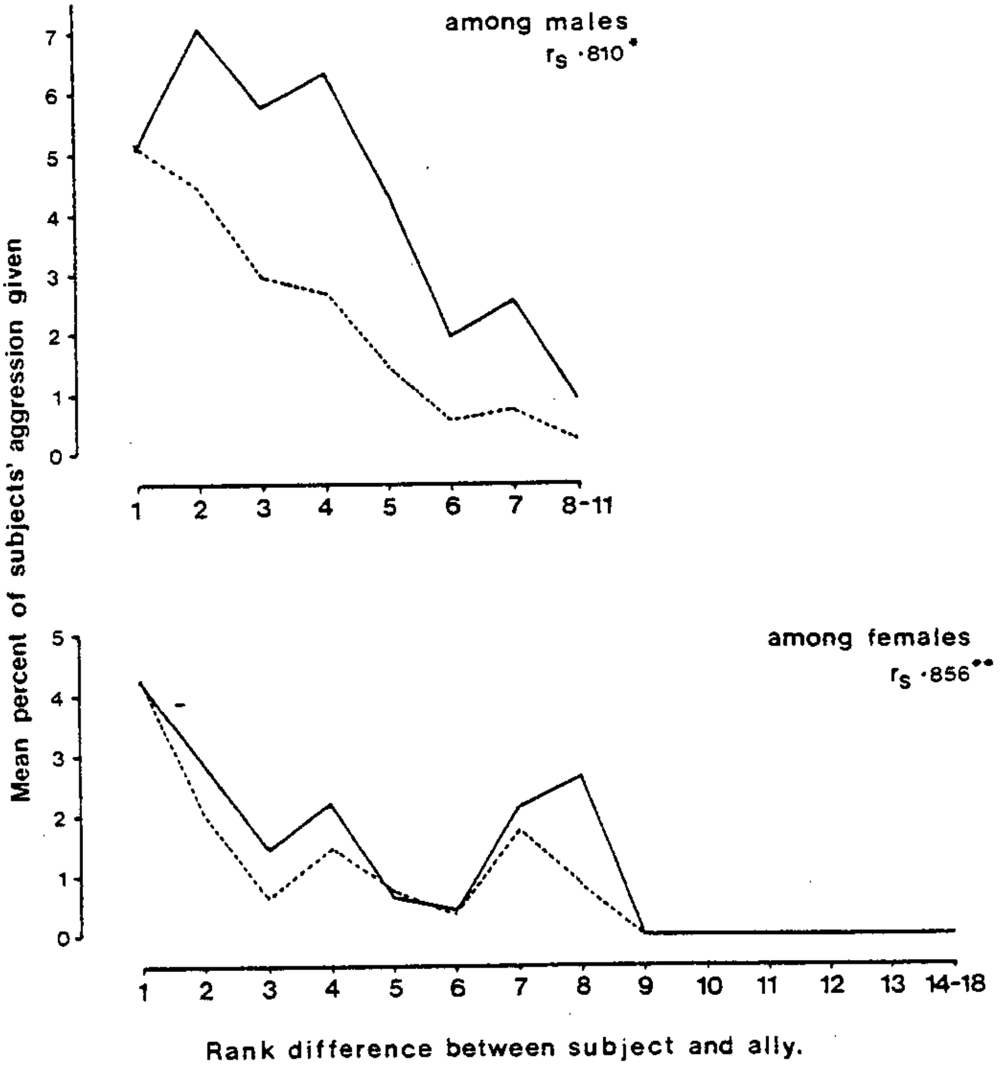


Fig. 6.8. Dominance-rank difference compared with tendency to ally with partners of the same sex. The dyadic alliance proportions (6.7.6) allowed calculation of the mean contribution by allies at each rank-difference to the aggression of each subject. The results are presented twice, as the mean percent contribution to the dominant partner (solid line) and to the subordinate partner (dotted line) of the pairs concerned. Spearman r_s values apply only to the former: * $p < .05$, ** $p < .01$.

(1) an associate: if the partner was nearest neighbour more often than the subject's mean neighbour frequency with that sex (2.XIIb).

(2) a groomee: if the subject groomed the partner more often than its dyadic mean rate with that sex.

(3) an ally: if subject and partner ever gave aggression in alliance, but excluding defensive alliances.

The interactions between these measures were compared two at a time. For example, each subject's partners were classified within a 2 x 2 matrix discriminating non-associates and associates, non-groomees and groomees, to assess whether more partners than expected were both associates and groomees. The general trend was found by pooling the matrices of all subjects and testing for the independence of the two measures by chi-square. Then the number of subjects who supported the overall trend was compared with the number who did not by binomial test. The results are in Table 6.XXVI. Thus the data at the bottom left show that among all male to female dyads, the female was both non-associate and non-groomee in 112; she was an associate only in 53, a groomee only in 18, and both associate and groomee in 33. The latter figure is underlined to show it is greater than expected, and significantly so with χ^2 15.93, $p < .001$. It is also shown that 11 males showed this trend, one did not, which has a binomial probability of $p < .01$.

The table therefore shows in column (a) that association and grooming coincided between the sexes, but not significantly among females. Column (b) shows that alliance was not generally related to association, while column (c) shows that females tended to groom their allies in both sexes, but that the males' tendency to groom their female allies was not general to all males.

6.7.11 Alliance and association among males

Male-male alliances were so frequent that it was possible to compare proximity with how often they allied, rather than whether they did or did not as above. For every subject, the dyadic alliance proportion with each partner was compared with that expected if the partner had allied in a proportion equivalent to the percent of time he spent within 15m of the subject. The association frequency was estimated from the proportion of focal samples through the minute for which each

Table 6.XXVI Estimates of the concordance between association, grooming, and alliance. 2 x 2 tables show interaction between the measures in terms of dyads less (-) or greater than (+) average. In each part the measure listed first (e.g. Association in part a) contributes the rows of the matrix, the second measure the columns. The figures to right of matrix show how many subjects did (>) or did not (<) support the overall trend. Probabilities * < .05, ** < .01, *** < .001

		a) Association/Grooming					b) Association/Alliance					c) Grooming/Alliance				
		-	+		>	<	-	+		>	<	-	+		>	<
Female to female	-	117	86		10	8	138	24		8	8	183	23		13	3*
	+	48	55				120	24				75	25			
	2			2.92					.08					8.72**		
Female to male	-	108	21		15	1**	111	18		8	4	133	19		12	2*
	+	46	41				68	19				46	18			
	2			22.68***					1.75					6.68**		
Male to female	-	112	18		11	1**	111	19		5	5	146	19		7	2 n.s.
	+	53	33				68	18				33	18			
	2			15.93***					1.04					13.89***		

male was seen within 15m of the subject, (2.V - 2.VIII), and reciprocal frequencies in each pair were averaged to reduce the variance.

In every pair the observed numbers of interactions with and without alliance are compared with the number expected to be in alliance, according to this hypothesis, in Table 6.XXVII (Appendix II). For each pair the expected number without alliance may be found by subtracting the expected <u>in</u> alliance from the total observed. For those cells with an expected alliance greater than 5, the proportions observed and expected were compared by chi-square. The deviations from expected are patterned in a certain way which is summarised in Fig. 6.9. The pattern which emerges is as follows:

(i) Many of the pairs show very close correspondence between observed and expected (Table 6.XXVII). This means that a number of alliances, although very frequent, cannot be considered exceptional given the association frequency between the partners.

(ii) All of the pairs involving newcomer adults (the two left-hand columns and the two upper rows) showed less alliance than expected: and all testable showed significantly less, involving 13 pairs.

(iii) Pairs which include subadult males (the four right-hand columns, the four lower rows) nearly all show less alliance than expected, significantly in 17 pairs.

(iv) Only in pairs of resident adult males (the remaining cells) was alliance more frequent than expected. Those significantly greater all involved male A5, who contributed to a high proportion of the aggression of A3, A4 and A7.

6.7.12 Dyadic relationships

Figs. 6.10, 6.11 and 6.12 all illustrate the rates per hour at which pairs gave aggression when in alliance together. The dyadic mean rates between the sexes, in Fig. 6.10 show that the males who allied most with females were the four focal adults, and the three younger subadults. When expressed as a proportion of the aggression given by each male (as dyadic alliance proportions) the higher proportions were found for these three subadults and A7, while the lowest are found for the two newcomers and A6. The figure also shows the tendency of higher-ranking females to ally more with males.

FIG. 6.9

Allies

Subjects	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8	S_1	S_2	S_3	S_4
A_1		--	--	-	-	-	-	--	-	---	--	---
A_2	-		-	-	-	-	-	-	-	--	-	--
A_3	---	--		-	+	-	--	---	-	---	---	---
A_4	-	-	+		+++	+	+	+	-	---	--	--
A_5	--	--	=	+		+	+	-	-	---	---	---
A_6	▪	-	▪	+	+		+	▪	+	-	-	-
A_7	-	-	-	+	+++	▪		-	-	-	-	-
A_8	▪	-	-	-	-	▪	-		▪	▪	-	-
S_1	▪	-	▪	-	▪	▪	-	▪		▪	-	-
S_2	-	-	-	-	-	-	-	-	▪		--	-
S_3	-	-	-	-	--	-	-	-	-	--		-
S_4	-	-	-	-	-	-	-	-	-	-	-	

more	less	p.
+	▪ -	n.s. or no test
+	-	·05
++	--	·01
+++	---	·001

Fig. 6.9. Alliance and proximity among males. The matrix illustrates for aggression given by subjects on the left the tendency for each partner (top) to act in alliance proportionally more or less than expected from the proportion of time he was within 15m of the subject. Data abstracted from Table 6.XXVII in Appendix II. Plus-signs indicate those who allied more than expected.

FIG. 6.10

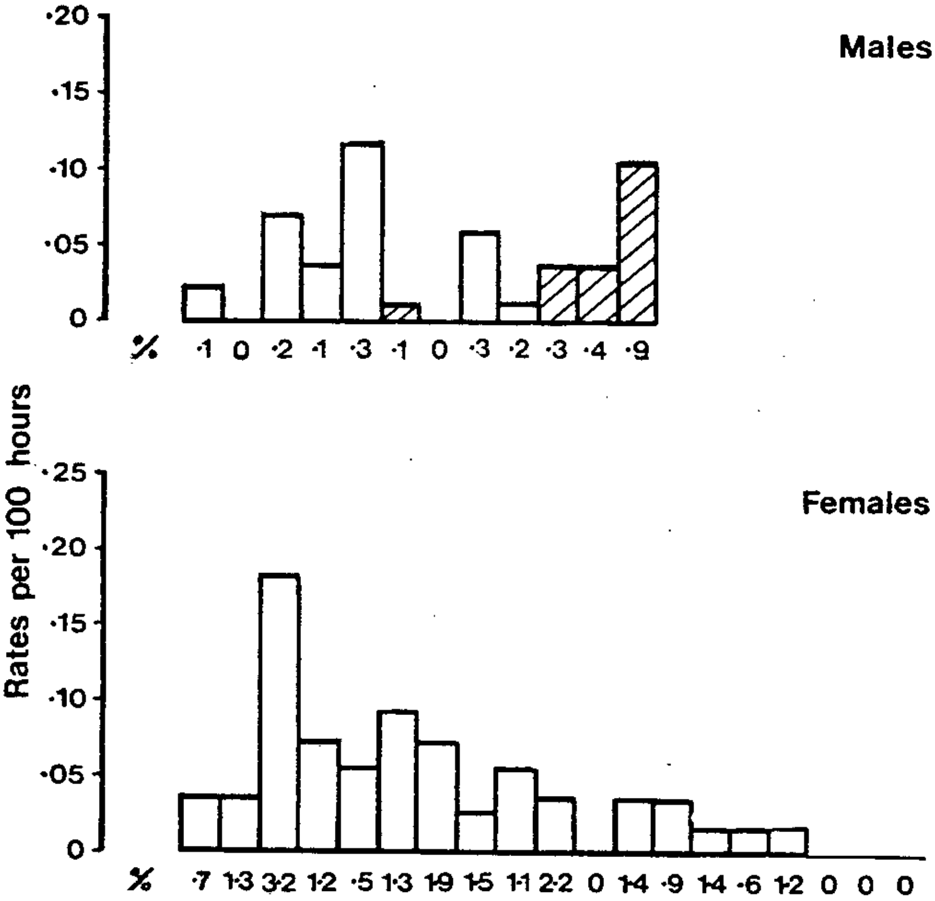


Fig. 6.10. Subjects' tendencies to act in alliance with members of the opposite sex. Histograms show mean dyadic rate per hundred hours at which each subject gave aggression when in alliance with one or more of the opposite sex; defensive alliances are excluded. The same data are expressed below each histogram as the subject's mean dyadic alliance proportion with that sex, i.e. as the percent of the subject's aggression given in which allied with that sex averaged across partners.

The allied pairs which were also more frequent associates and groomers, for comparison with data in Chapter 4, were F1 with A3, F2 with A5, F3 with A4 and A7, F5 with A1 and A3, F7 with A5, and F13 with A7. Thus all involved females who were mothers or cycling females, and the males were all focal males except A1.

The pattern of alliances between females is in Fig. 6.11. The tendency to ally at fairly close ranks is obvious: in this it resembles more the pattern of grooming (Fig. 4.14), which highlights grooming to close-rankers and to mothers, than the pattern of association (Fig. 4.6), which illustrates mainly the association between mothers. Pairs which allied and groomed each other above average involved F5 with F3, F6, and F7; F6 with F7 and F14; F8 with F11; F10 with F17; and F12 with F13 and F16 (from the analysis in 6.7.8).

The dyadic mean rates of alliances between males in Fig. 6.12 show clearly the partnership between A3 and A5, and the latter's links with the other resident adults. If the males are compared for the proportion of their aggression given in which they were allied with other males (as dyadic alliance proportions) the highest scores among adults are found for the older males A6 and A8, thereafter the four focal adults, and least the two newcomers, suggesting that older males were less likely to show aggression on their own (ref. 6.7.8a). Of the six most frequently allied pairs, three were frequent associates, and in three the dominant partner directed most of his agonistic behaviour (among all males) to the subordinate ally. Although A5 did not associate frequently with A6 or A8, he allied with both, and they both received more agonistic interaction from him than from other males. Thus allied pairs included frequent associates and antagonists (6.10.3c).

6.7.13 Conclusion

These patterns of alliance must be understood not only in terms of who allied with whom, but also against whom (6.4 & 6.5). Considering female subjects first, their alliances tended to be with one another or with immatures rather than with males, but this was much as expected from partner availability. When in alliance they gave aggression at highest rates to lower-ranking females, then uprank to males, and least to immatures. This distribution uprank to males but downrank to females is confirmed by Walters (1980) at Amboseli. When females allied against

FIG. 6.11

ALLIANCES

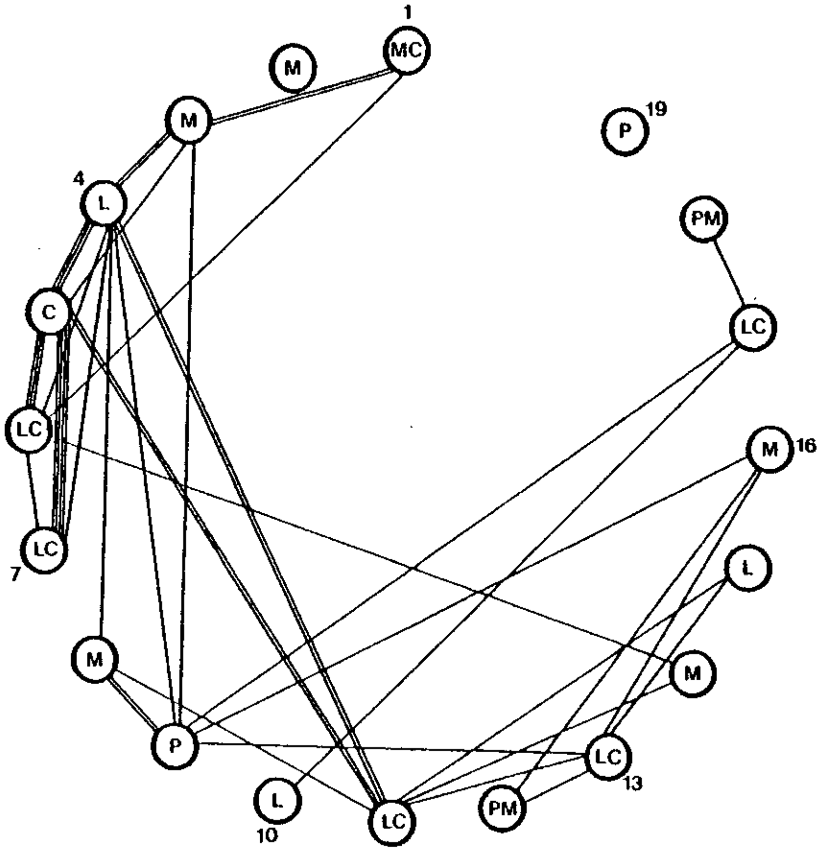
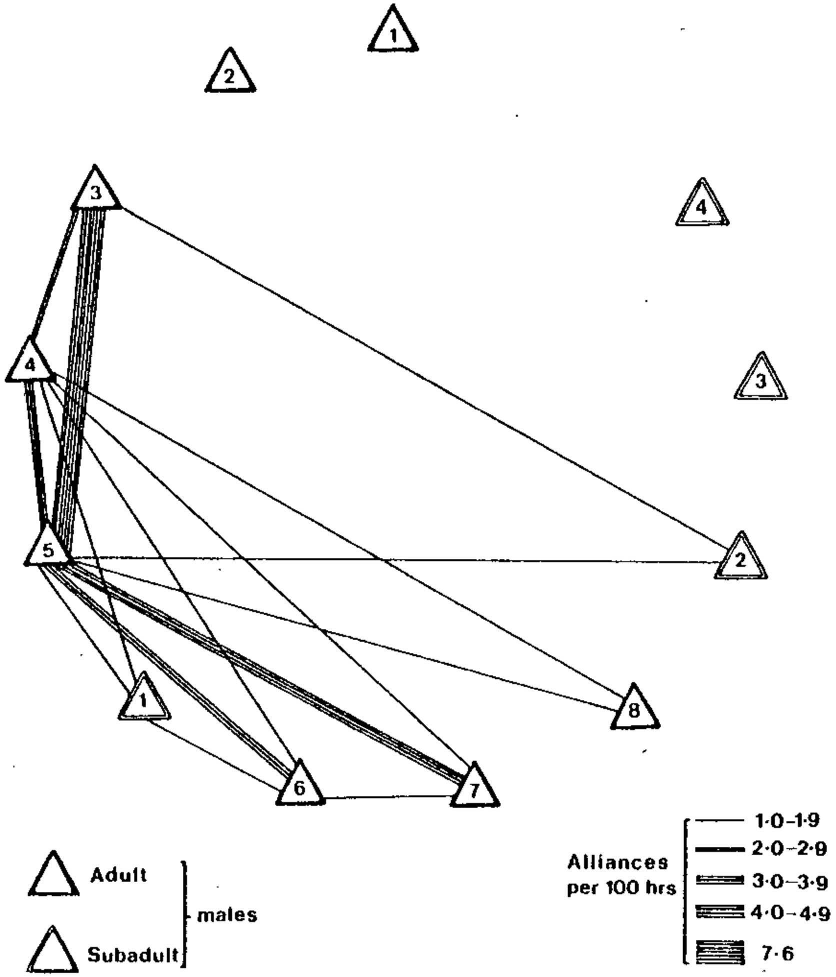


FIG. 6.12

ALLIANCES



Figs. 6.11 & 6.12. Alliances between females (6.11) and between males (6.12), in aggression given (i.e. excluding defensive alliance). Subjects arranged anticlockwise in descending order of dominance rank; females are C - cycling P - pregnant, M - mothers, L - lactating, the rank of evey third female given for reference. Males identified by dominance rank within class. Among females, one line corresponds to one alliance (0.22 per 100 hrs), the multiple lines multiples of this. All their 42 alliances are shown. Among males the critical values are higher, and the links shown account for 73% of their 195 alliances recorded.

males their allies tended to be males (in 65% of 23 instances); but against females their main allies were immatures (54% of 26), while against immatures their main allies were females (47% of 45 instances).

In females' relations with one another, three patterns were obvious. First, they allied more with those close in rank (also Seyfarth, 1976; Kaplan, 1977), who tended also to be grooming partners (also Seyfarth ibid.). This was evident in aggression to male, female, and immature. Secondly, their aggression to females was almost all downrank, which supports Cheney's (1977) conclusion that higher-ranking allies are probably more effective. Thirdly, much of this aggression was to females close in rank, again irrespective of the identity of the allies. It has already been suggested that they might only need allies against close-ranked competitors. However, in about half these interactions the allies were immatures, and in 9 of these 14 instances the recipient was the female adjacent in rank below the aggressor. This suggests that the females may have been supporting offspring against females of similar rank. If the immatures had solicited these as coalitions the aggressors would be likely to rank above the recipients (Cheney, 1977; Walters, 1980) but they would be unlikely to be so often next in rank above unless the immatures were soliciting their mothers against targets selected according to maternal rank (as described in Walters, ibid. pp. 72-73). Alternatively, the pattern corresponds to that expected of females close to the mothers' rank aiding the offspring (Cheney ibid.). The fact that the recipients were so close in rank suggests that these interactions were concerned with acquisition of dependent rank within, or between close-ranked, matrilines. Similar processes may underly the tendency for females to ally with close rankers. However Cheney (1977) has proposed that this pattern might be produced without kinship if (a) high rankers are more attractive as allies, because more effective, (b) these high rankers gain least from helping lower rankers, and (c) females learn to ally most with those who reciprocate: then reciprocation and alliance would be more frequent at close ranks.

Packer and Pusey (1979) proposed that in contrast to macaques, alliances between female baboons are ineffective in limiting the entry of males into troops, and the data here support this in that only 8% of aggression given by females to males was by female-female alliances (n = 50 incidents). Alliances between males (see below) are probably far more important.

Alliances between females and males coincided with the females' grooming partnerships (also Seyfarth, 1978b). Incidents in which females allied with subadult males tended to be against females or young (10 of 13 instances), while those in which they allied with adult males were more often against adult males (10 of 15 instances), most against newcomer adults. The latter, with the fact that their allies were more often the focal adults, suggest that males' involvement in females' allied aggression depends upon their seniority. The occasions on which males aided females against other males most often involved mothers.

Subadults showed proportionately more alliance with females than did adult males, perhaps in accordance with their kinship as natal males; and among them the younger ones were most involved. Walters (1980) also noted that subadults intervened in disputes of females and young more than did adult males. In their alliances against females and young, subadults allied with all classes; but when allied against adult males, their allies were much more likely to be other adult males.

It was conspicuous that adult males allied very frequently with one another, and against one another. This accords with the intensity of male-male antagonism revealed by dyadic interactions. The fact that females and immatures allied with them less was in part because they were not involved in such antagonism, since 43% of polyadic aggression between males was in competition over oestrus females. But as Packer (1977b) explains, intervention by a non-male into a dispute between males would do little to affect the outcome, and provide little benefit for the intervenor. Most alliances of this sort were directed against A1 and A2, and often involved many animals in concerted chasing of these males.

The alliance partnerships between males strongly reflected their association together (as in Hall & DeVore, 1965; Saayman, 1971b). The low involvement of the subadult males may reflect the infrequency of their involvement in competition for oestrus females, but more likely illustrates Packer's argument (above). The low alliance scores of the newcomers may be because they were unfamiliar with the residents, or because as young adults they lacked the necessary social skills; Packer (1979a) found that older males solicited alliance more successfully. In contrast, frequent alliances between resident adults suggested that their familiarity had allowed development of co-operative aggression. Their antagonism against the newcomers in part reflected the high consorting activity of these two, but it also paralleled a number of reports that older males tend to ally against younger adults (Saayman, 1971a, 1972 ; and Ransom, quoted in Nash, 1976, p.66, provides a clear example), and that there is antagonism between resident and unfamiliar males (Hamilton <u>et al</u>., 1975; Packer, 1979a).

The relationships of alliance here were very close to Hall and DeVore's concept of a 'central hierarchy' which was originally described in terms of alliance. The significance of this pattern is stressed by Bernstein (1976) in that it extends males' competitive ability past their physical prime, as also in gelada females (Dunbar, 1980). This is entirely plausible, and illustrated here in that the older males showed alliance with males in a higher proportion of their aggression. However, the frequent agonism <u>between</u> members of some of the more commonly allied pairs (Fig. 6.12, cf. Figs. 6.18-20) shows that 'central hierarchy' relationships are far from being affiliative. It is more likely that they arise because immigration of newcomer males presents a threat to the reproductive potential of the residents, who therefore benefit by allying against them. Although many such alliances were in competition for females against the newcomers, yet short-term interest in a female cannot explain the readiness with which A5 repeatedly aided A3 for very little return (8.3.14). Thus while baboons <u>may</u> learn to ally only with partners who reciprocate (Cheney, 1977), the presence of assertive newcomers may provide a more immediate pressure for the formation of alliances which may be reciprocal, such as those documented by Packer (1977b).

8. APPROACH INTERACTIONS BETWEEN MALES

6.8.1 Introduction

Most field studies of baboons characterise the relations between males as antagonistic (e.g. Hall & DeVore, 1965; Stoltz & Saayman, 1970; but cf. Rowell, 1966a) and compare their dominance rank and rates of approach-retreat and aggression. However there are a number of interactions between males which, while not obviously affiliative, do not fall into these categories of agonism. Nearly all accounts of baboon behaviour make brief reference to interactions which include presenting, mounting, touching genitals, and other forms of contact. Only two studies have analysed them in detail. Kummer's (1968) description of hamadryas baboons recognised such behaviours during the co-ordination of travel (the I-D system) and in the relationship between follower and leader males of a unit, leading to a series of experiments on dominance, possessiveness, and inhibition which involve such behaviours (e.g. Kummer et al., 1974, 1978). More relevant here, Sugawara (1979) has analysed the relation between dominance and contact interactions in hamadryas/olive-baboon hybrids.

This section analyses the distribution of three types of interaction among adult and subadult males. They are referred to as approach interactions, since all occurred within arms' reach but were not included as supplants or aggression. They are passes, when one male approached and left another without stopping or making contact: contact, when two males exchanged a variety of gestures including presenting, standing in contact, arm-round, chewing of cheek-fur, handling genitals etc.: and mounts, a particular category of contact. For definitions see Appendix I.B iv & v, C xvi. Although a few of these interactions occasionally appeared playful (e.g. cheek chew) they were more often tense (6.8.6). The procedures of analysis are exactly those used above for supplants.

6.8.2 Rank-direction of approaches

Table 6.XXVIII shows that the three types of approach showed similar proportions of about 26% uprank (χ^2 heterogeneity 0.01, d.f. 2, n.s.). This was the same direction constancy as solo aggression between males (comparing approaches and solo aggression: χ^2 1.26, d.f. 1, p .30, n.s.).

Table 6.XXVIII Rank-direction of approaches between males. The percent downrank is indicated. Calculated from all dyadic interactions, including animals in consort and carrying infants. Chi-squared compares distribution with 50:50 expected. Wilcoxon compares subjects' dyadic mean rates in each direction.

Behaviour	n	% downrank	χ^2	p	Wilcoxon	p
Pass	107	73.8	24.3	$<.001$	T=11,n 10	n.s.
Contact	154	74.0	35.6	$<.001$	T=10,n 10	n.s.
Mount	78	74.4	18.6	$<.001$	T=16,n 9	n.s.

However comparisons of individuals' scores revealed that these tendencies were not common to all males. For example, interactions were given at higher rates to dominants than to subordinates in *passes* by A2, *contact* by A7, and *mounting* by S2.

6.8.3 Class-distribution of male approaches

Subjects' rates of approach interaction uprank and downrank were used to compare adult and subadult males. No significant differences were found in the rates at which adult and subadult exchanged these behaviours (Table 6.XXIX): mean rates *received* by adults tended to be higher than those received by subadults. Further analyses of these data to see whether the classes gave approaches equally to adult and subadult revealed no differences uprank, but that *downrank* adults gave most to *adults* in terms of contact (T = 0 ± obs. corr., n = 6, p .05) and mounting (T = 1 ± obs. corr., n = 7, p .05).

6.8.4 Dominance rank and rates of approach

Males' dominance ranks are compared with their dyadic mean rates of approaches (a) given and received with all males; and rates given (b) uprank and (c) downrank separately, in Table 6.XXX. Their overall rates are also compared with time spent in proximity to other males. The conclusions are:

(1) Higher-ranking males tended to give more approaches, significantly so in passing and mounting. The same tendencies existed among adults, significantly for passing, and among subadults.

(2) Considering rates only downrank, and thus accounting for the availability of subordinates, these tendencies disappeared; but higher-ranking males still mounted more than expected from their position in the hierarchy.

(3) There were no indications that low-ranking males received more approaches *overall*. However, this may have been because subadults tended to receive less (see above): among adults alone, lower rankers *did* tend to receive more, significantly in the case of mounting.

(4) The males who were most often near other males gave more contact to subordinates.

Table 6.XXIX Approaches between male classes. Mean dyadic rates of approach interactions of each class, comparing rates uprank and downrank separately by Mann-Whitney U-test. Results of comparisons on scores corrected for observability given in brackets only if different from uncorrected. Probabilities all > .05.

		Uprank			Downrank		
		Adult		Subadult	Adult		Subadult
Rates given			U(n4,7)			U(n3,8)	
Pass	$\bar{x}$	.24		.09	.26		.41
	sd.	(.32)		(.11)	(.11)		(.23)
	test		10			7(8)	
Contact	$\bar{x}$	.18		.16	.42		.34
	sd.	(.12)		(.10)	(.38)		(.24)
	test		12(12)			11(11)	
Mount	$\bar{x}$	.05		.08	.19		.04
	sd.	(.07)		(.11)	(.20)		(.08)
	test		12(13)			4(5)	
Rates received			U(n3,8)			U(n4,7)	
Pass	$\bar{x}$	.11		.04	.54		.24
	sd.	(.04)		(.08)	(.29)		(.16)
	test		5(7)			6(7)	
Contact	$\bar{x}$	.14		.08	.52		.40
	sd.	(.06)		(.08)	(.29)		(.31)
	test		5(7)			11(11)	
Mount	$\bar{x}$	.08		.04	.34		.08
	sd.	(.03)		(.08)	(.26)		(.07)
	test		8(8)			6(7)	

Table 6.XXX   Male approach interactions and rank.
Males' dominance ranks, and association frequency with other males, compared with interaction rates (a) exchanged with all partners, (b) given to dominant partners, and (c) given to subordinate partners, using dyadic mean rates. Spearman r_s values, repeated with observability corrections (in brackets): probabilities assigned only if confirmed with this correction, $* < .05$, $** < .01$

(a) with all partners

	12 males		8 Adults	4 Subadults
	Dom.rank	Male assoc.	Dom.rank	Dom.rank
Pass given	.762** (.727)	-.322 (=)	.952** (.881)	.800 (=)
Contact given	.504 (.483)	.133 (.175)	.595 (.667)	.400 (=)
Mounts given	.636* (.664)	-.070 (-.168)	.714 (.691)	.800 (=)
Pass rec.	.035 (-.035)	-.021 (-.056)	-.429 (-.595)	.400 (=)
Contact rec.	-.091 (.000)	.035 (-.189)	-.571 (-.595)	.800 (1.000)
Mount rec.	.091 (.084)	-.224 (-.259)	-.714* (-.738)	.400 (=)

	(b) Given uprank (11 males)		(c) Given downrank (11 males)	
	Dom.rank	Male assoc.	Dom.rank	Male assoc.
Pass given	.541 (.523)	.028 (.009)	.191 (.082)	.227 (-.082)
Contact given	.327 (.346)	.246 (.082)	-.055 (-.182)	.636* (.700)
Mounts given	-.307 (-.289)	.470 (.405)	.835** (.872)	-.330 (-.468)

6.8.5 Dominance rank-difference and rates of approach

The mean rates of approach between males at each rank-difference are compared in Fig. 6.13; and the numbers of subjects with first partners within and beyond two rank-places are compared with the numbers expected from availability in Table 6.XXXI. Two significant results emerge:

(i) Males contacted more distant-ranked subordinates progressively less.

(ii) Males tended to pass subordinates within two places of rank more than other subordinates.

6.8.6 Conclusions

These approach interactions should be considered alongside the more intense agonistic interactions already described (6.10 below). However there are some details which may be considered separately. In their direction constancy downrank, they were strikingly similar not only to one another but also to solo aggression. This substantiates Sugawara's (1979) conclusion that mounting is a behaviour of dominant partners, and this appears to be true also of passing and contact. However, while all behaviours tended as a result to be given <u>more</u> by higher ranking males, yet the lower rankers did <u>not</u> tend to receive more: this was mainly because low-ranking subadult males received less than did the lowest ranking adults. This is explained in that most interactions occurred downrank among adults, and the highest dyadic rates of contact and mounting were between <u>resident</u> adults. This alone may be the reason that contact was more frequent at closer ranks.

Dyadic rates of approach interactions are illustrated in Fig. 6.17. Some males were conspicuous for their high interaction rates: A3 gave all behaviours unusually frequently, mostly to A4, A5, and other resident adults. S2 gave more of all three than expected from his low rank, and A5 gave much contact especially to A3, A6, and A7. A5 also received many contacts and passes, as did S3 many passes, S2 many contacts, and A7 was mounted often especially by A3.

It has already been mentioned that these interactions often appeared tense. The few that were recorded as <u>play</u> were between subadult males, and it was conspicuous that S4, as lowest ranking male, was involved in fewest approach interactions. The remainder, however, appeared purposeful and assertive, and several contact interactions caused the recipient

FIG. 6.13

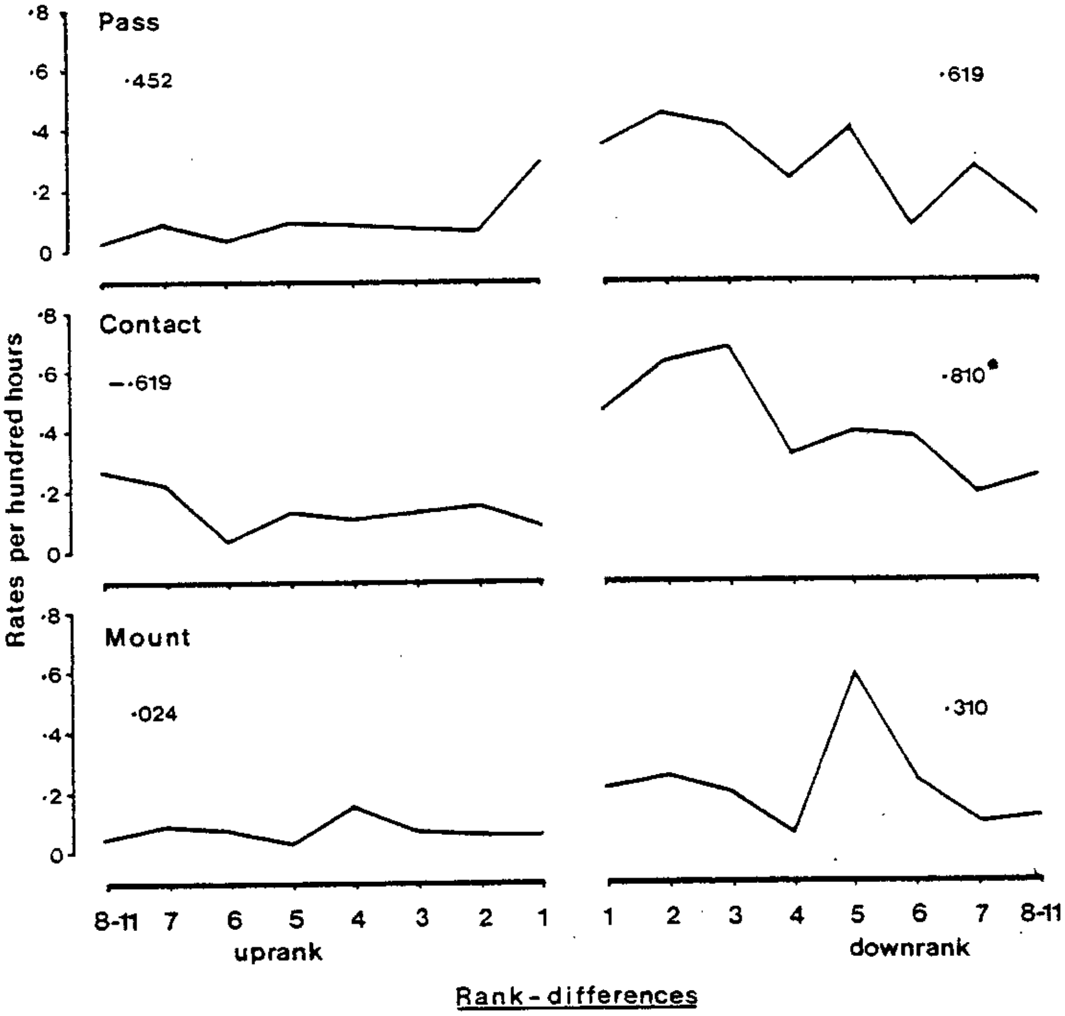


Fig. 6.13. Dominance-rank difference compared with rates of approach interactions between males, as dyadic mean rates per hundred hours. Caption as Fig. 6.3. Spearman r_s values compare rate and rank-difference. * $p < .05$.

<u>Table 6.XXXI</u> Rank-difference and male approach. The number of first-recipients of male approaches within and beyond two dominance rank places from the donors. Binomial probabilities two-tailed.

		Uprank			Downrank		
rank-places		1-2 :	3+		1-2 :	3+	
Pass	obs.	4.3	2.7	p .10	8	3	p <.01
	exp.	2.4	4.6		3.5	7.5	
Contact	obs.	4	6	p < 1.00	5.5	4.5	p .30
	exp.	3.2	6.8		3.1	6.9	
Mount	obs.	3	4	p .68	2	6	p 1.00
	exp.	2.0	5.0		2.1	5.9	

to be supplanted, or even to turn and attack. When A3 was in consort with a female whom he appeared to prefer (8.5.2) he initiated contact interaction with other males at an increased rate, although no male in consort ever actually mounted another male (cf. Hall & DeVore, 1965).

In the field, many of these interactions appeared to be attempts to supplant other males. This may explain the frequency of contact and mounting among resident adults, because they often associated, and were probably familiar enough to approach one another more often than the newcomers. A more general explanation, which would also account for the 26% of interactions directed uprank, would be that they represent a way by which a male may test his competitors, at low risk, and so continually re-assess the current dominance relationships. For example, S2, not yet of full size, directed most aggression downrank, but he approached at very high frequency uprank. In contrast ageing A7, presumably attempting to defer a decline in rank with age, directed the majority of both approaches and aggression at his dominants.

9. MALE-INFANT INTERACTION

6.9.1 Introduction

Many field studies of baboons report distinctive interaction between adult males and infants. As in other primates, these vary between the extremes of care by males, and exploitation (Deag & Crook, 1971; Hrdy, 1976; Packer, 1980). Males show great interest in black infants, and are very protective to them (e.g. DeVore, 1963). They also carry infants while interacting with each other, and while this may represent protectiveness to the infant yet it also alters relations between the males such that the one carrying the infant may become temporarily dominant to the other, and less likely to be threatened (Packer, 1980; also Kummer, 1967). This is most obvious when a male under threat inhibits his antagonist by gathering up an infant, as reported by Rowell (1967b), Stoltz & Saayman (1970), Ransom and Ransom (1971) and Altmann (1980). Such interactions fall within the definition of agonistic buffering (Deag & Crook, 1971) and are considered exploitative because they risk stress or injury to the infant (Seyfarth, 1975; Hrdy ibid.; Packer ibid.). Similar interactions are reported in hamadryas (Kummer ibid.), geladas (Dunbar Dunbar, 1975; Mori, 1979) and mangabeys (Homewood, 1975; Struhsaker & Leland, 1979).

The following pages describe 381 interactions between males and infants, including 57 instances where one male carried an infant while interacting with another male. The former are referred to as male-infant interaction, the latter as male use of infants. They are analysed to compare the males in this respect; and to look for male selectivity among infants, because the explanations of such interactions hinge upon the possibility of kinship between male and infant.

6.9.2 Behaviours and contexts

(a) Behaviours: The males' behaviour to the infants was categorised as interest (peering or vocalising at the infant, often within arm's reach); manipulation (handling or grooming the infant, both on or off the mother); and carrying (standing, with the infant clinging dorsal or ventral on the male) as defined in Appendix I.B xii-xv. These behaviours occurred at a mean rate per hundred hours of 9.8 times for each adult and 2.0 times for each subadult male. The former rate was about twice that at which female subjects groomed other females (4.57 times) so that male-infant interactions were comparatively frequent.
(b) Contexts: Table 6.XXXII presents two classifications of the context of male-infant interactions. Some contexts were assigned in the field, the remainder were derived from the sequence of interactions on the checksheets, and so provide only a rough guide. The first classification is in terms of general social context (a): the second depends upon the interactions exchanged between the male who interacted with the infant and other males, within one minute on either side of the male-infant interaction (b).

Most male-infant interactions occurred without any particular cause or context being recognisable to the observer. Very few were obvious responses to the distress of an infant, but closer observation of the infants might have revealed more. A few interactions appeared possessive, when two males competed for access to a mother-infant pair, and included grooming of the mother. It is not clear whether males were more likely than usual to interact with infants when consort pairs were near, but some interactions were clearly in response to their presence. However the most frequent context was when the male was

Table 6.XXXII The 381 male-infant interactions classified (a) according to general context, and (b) according to the male's interaction with other males during, or within one minute of, interaction with the infant.

(a) General context	%
Near a consort pair: including 0.5% when the male was near consort aggression and 2.6% in which actually involved.	9.1
Close to males interacting agonistically (mostly chases)	2.9
The subject is involved in male-male agonism or obviously tense situation.	26.5
The subject interacts with the infant in apparent possessiveness with respect to another male.	1.6
The subject interacts with the infant in apparent response to infant's distress.	0.5
Nothing unusual	59.6

(b) Male-male interaction context	%
The male gives interaction to another male (0.9% with aggression, 2.1% without) then within 1 min. interacts with infant.	3.0
The male receives interaction from another male (3.4% with aggression, 7.5% without) then within 1 min. interacts with infant.	10.9
The male interacts with infant, then while carrying it gives interaction to another male (1.4% with aggression, 2.0% without).	3.4
The male interacts with the infant, then while still manipulating or carrying it receives interaction from another male (4.2% with aggression, 3.2% without)	7.4
No male-male interaction during or within one minute of interaction with infant.	75.3

Table 6.XXXIII The types of male-male interaction in which one of the participants carried an infant.

		% carries infant	ppn. by donor
Pass	107	10.3	.55
Contact/Mount	246	.4	(0)
Avoidance	146	.7	(1.0)
Supplant	539	2.0	.18
Solo aggression	378	8.5	.34
Allied aggression	245	.4	(1.0)

χ^2 64.07
df. 5. $p < .001$

involved in agonistic interaction or obvious tenseness with nearby males. Thus males would interact with infants immediately at the outbreak of agonism nearby, and about 14% of interaction occurred immediately after exchange of agonism with another male. A further 10% involved males who carried infants while interacting with other males: more of these were in receipt of agonism, and in 4.2% of all cases this was aggression received, mainly chasing. Males also interacted with infants when among males gathered at a meat-eating: and on four occasions a male withdrew from competitive aggression over an oestrus female by interacting with an infant.

Table 6.XXXIII shows that infants were not carried equally often in all kinds of male-male interaction. Infants were used more frequently by the recipients of supplants and solo aggression, and by donors and recipients of passes.

6.9.3 The males compared

Adult males did not interact with infants at significantly higher rates than did subadults (U = 12, corr. obs. 11, n 4.8, n.s.), but as in several measures of male-infant interaction the subadults tended to score below the median adult.

For all males were calculated five different estimates of involvement with mothers and their infants, including infant-use. These are illustrated in Fig. 6.14. It is clear that males who spent most time with mothers also interacted more with infants (r_s 0.860, corr. obs. 0.895, $p < .01$). Secondly those who interacted more with infants also carried them in a higher proportion of their interaction with other males (r_s 0.897, corr. obs. 0.886, $p < .01$), despite the fact that only 10.8% of infant interactions comprised infant use. Other data confirmed that those males who carried infants in a higher proportion of interactions given also carried them in a higher proportion of interactions received (r_s 0.630, $p < .05$).

The males who interacted with infants most were resident adults A3, A4, A5, and A7: these and S1 and A8 (who interacted less frequently with males) also used infants in a conspicuously high proportion of their male-male interaction. Interaction-rate with infants was not related to the males' dominance ranks (r_s -.119, corr. obs. -.053, n.s.) nor to the time they spent in 15m of other males (r_s .354, corr. obs.

FIG. 6.14

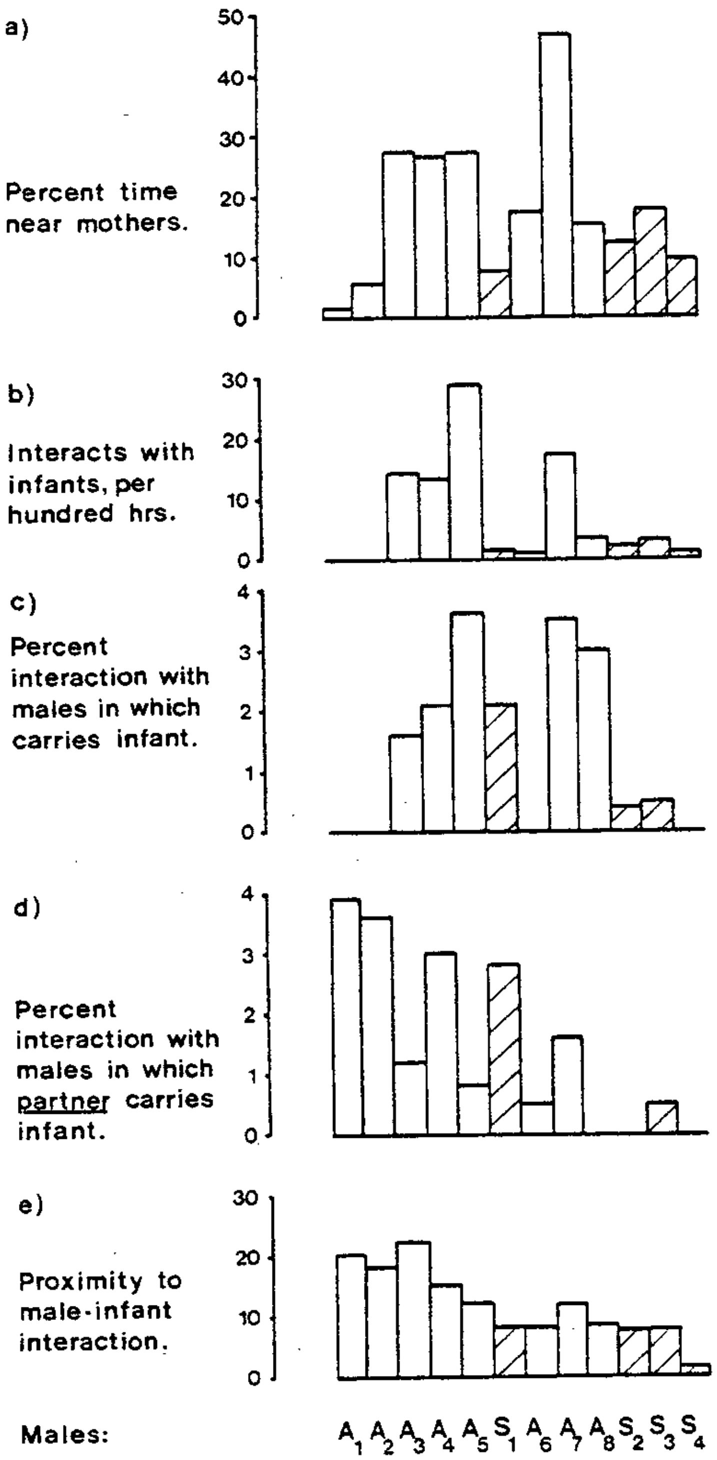


Fig. 6.14. The twelve males compared for five measures related to infants. Males arrayed in descending order of dominance rank from the left, with subadults cross-hatched. The measures are: a) percent samples with mothers as nearest female neighbours; b) rate of interaction with infants, per hundred hours per male; c)percent of interactions with other males in which carried infant; d) percent of all interactions with other males in which the other carried an infant; e) the percent of all 381 male-infant interactions (excluding the male's own) for which he was within 25m at the time.

.319, n.s.).

When males were carrying infants their interactions tended to be with high rankers (Fig. 6.14d). The proportions of each male's interaction in which the opponent carried an infant was greater for higher-ranking males (r_s .836, $p < .01$: test repeated without newcomers A1 and A2, r_s .745, n 10, $p < .05$), but not obviously higher for those who spent more time near mothers (r_s -.180, n.s.). In the 23 pairs of males between whom infant use was seen, the user was the subordinate in 16, and the dominant in 3, while both used infants in 4: corresponding proportions cited by Packer (1980) were 14, 7, and 4 respectively. It was shown above that males used infants more in interactions received than given (Table 6.XXXIII) and this was true of seven of the eight males who used infants at all. In the 36 interactions received by males carrying infants, 89% were downrank, in accordance with the majority of male-male interaction. But in the 21 interactions where the donor carried an infant, 62% were uprank, attributable especially to A3, A5, A7, and A8.

Other features of Fig. 6.14, a to d, are: (i) the relatively low involvement of subadult males in infant-interaction and use; and (ii) the marked contrast between the newcomers (A1 and A2) and the resident adults. The newcomers spent least time near mothers, and neither interacted with nor used infants, but they had infants carried against them proportionately more than other males.

The sociogram in Fig. 6.15, shows the number of times each male interacted with each other while carrying an infant, including interactions given and received. The majority of infant-users carried them against newcomers A1 and A2, accounting for 44% of the 57 interactions. But resident adults also used infants against one another (also in 44%). The subadults were little involved.

6.9.4 Proximity to male-infant interaction

Males often interacted with infants in apparent response to the presence or behaviour of a nearby male. Therefore at each male-infant interaction was recorded the identity of all other males within 25m radius. Fig. 6.14e shows the percentage of all male-infant interaction (except his own) for which each male was near. Those nearby most often tended to be the higher rankers (r_s .937, $p < .01$)

FIG. 6.15

USE OF INFANTS

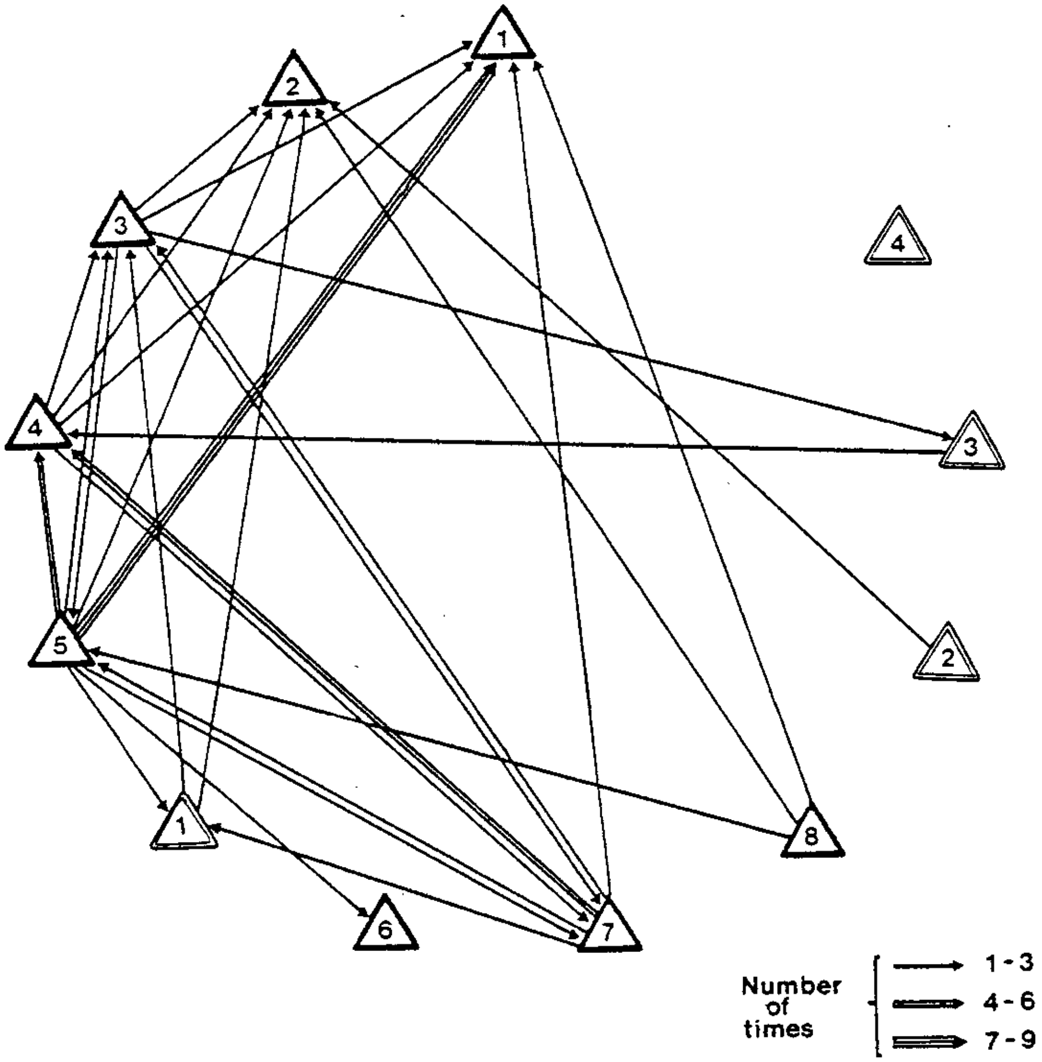


Fig. 6.15. The number of times each male carried an infant when interacting with another, irrespective of which male was the active partner in the interaction. The arrows run from the male carrying the infant to the interaction partner; all 57 such interactions are shown. Males arranged in order of dominance rank descending anticlockwise from the top. Adult males are the solid triangles, subadults the double triangles, numbered by dominance rank within class. Adults 1 and 2 were the newcomers.

even discounting the newcomers (r_s .963, n 10, $p < .01$). This was unexpected because high-rankers were not near other males more often (4.2.7), but was consistent with the fact that most interaction-partners of infant-users were higher rankers (Fig. 6.14d).

Furthermore, in 74 male-infant interactions it was possible to identify one of the nearby males as 'responsible' for the male's interaction with the infant, either because it had just shown agonism to the male who then interacted with the infant, or because it was chasing other animals nearby. These males most often 'responsible' tended again to be high rankers, who were responsible for a higher proportion of those interactions which they were near than were lower rankers (r_s .911, $p < .01$: discounting the newcomers, r_s .923, n 10, $p < .01$). On this measure the most prominent males were the newcomers, A1 (31%) and A2 (32%): followed by the focal males and the large subadult, A5 (19%), A4 (17%) S1 (16%) A3 (15%) and A7 (13%). All others were below 10%.

6.9.5 Males' selectivity between infants

The following analysis is largely devoted to the interactions of four males, A3, A4, A5 and A7, who between them were responsible for 86.1% of male-infant interaction and 82.5% of male-infant use. In 60% of all interactions the infant could be identified, and the males' 'choice' of these infants was analysed in terms of the infant's identity, age, sex, and maternal rank. 'Access' was also estimated as the proportion of the male's interactions with each in which he carried the infant.

6.9.5a) Characteristics of the infants Male-infant interactions involved black rather than brown infants in 86.1% of cases, which is significantly more than expected from their availability among all infants of 40% (χ^2 329.71, d.f. 1, $p < .001$). However, when males did interact with brown infants, they tended to carry them in a higher proportion of interactions than they did with black infants ($T = 1$, $n = 7$ males, $p < .05$).

FIG. 6.16

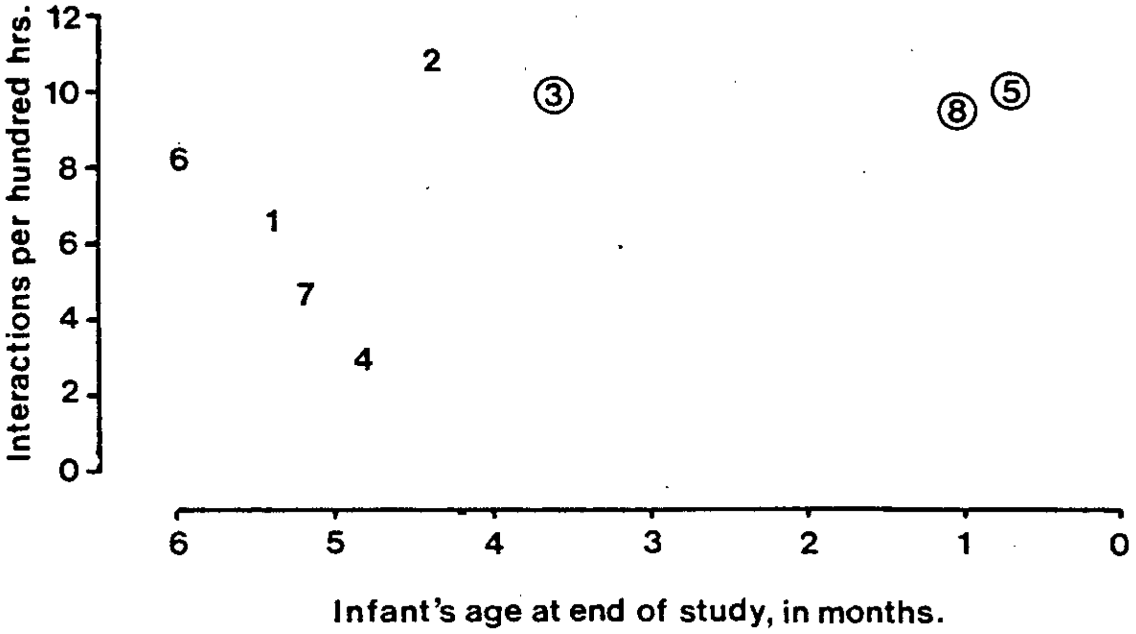


Fig. 6.16. The eight black infants compared for their interaction rates with males. They are numbered in order of the relative dominance ranks of their mothers; female infants are circled, and they are arranged in order of decreasing age from the left.

The eight black infants are compared for their observed interaction rates with males during the study in Fig. 6.16. The infants are differentiated in terms of age, sex, and maternal rank, but the data only suggest that age was important in that the four youngest received more interaction ($U = 0$, n 4.4, $p < .05$). The earliest interactions of the three newborn infants were confined to interest by the males: they were not seen to be carried until respectively the 5th, 5th, and the 3rd week of life (in order of age on the graph).

Considering the decline in interaction rate with infant age, two male-infant pairs showed declines in interaction in the 12th week, two in the 14th, and one on the 18th, although one pair still interacted frequently in the 24th week.

6.9.5b) Identity of the infant Table XXXIV shows that the four males who interacted with infants most often differed in their choice of infants, and that for three males their most frequent partners among infants tended to be offspring of their more frequent associates among the mothers. The exception was that A3 interacted at a high rate with the newborn infant of F18 who was not a frequent associate of his.

The data in Table 6.XXXIV, when compared with the male-female partnerships of association (Fig. 4.7) and grooming (Fig. 4.15) confirm these patterns. Male A3 carried the infant of his main associate and grooming partner F1 throughout the study. He interacted also with the infant of F2, and the newborn infants of F3 and F18 neither of whom were associates or grooming partners. In contrast, A4 interacted almost entirely with the infants of frequent associates F1 and F3, with whom he also groomed. He carried F1's infant rather less than did A3. Male A5 interacted especially with the infants of F2 (till age 10 weeks) and F14 (throughout); both of these mothers, especially F2, were his associates and grooming partners. The infant of F14 was also a frequent partner of A7, who associated with the mother; this male was also the first one seen to carry all three of the newest infants, whose mothers F3, F12, and F18 were all his grooming partners.

Although there were insufficient interactions with recognised infants to determine conclusively which males interacted with or used which infants against which other males, the distribution of interactions allows the following statements.

Table 6.XXXIV Selectivity in males' interactions with infants. For the four males who interacted most often with infants are shown (a) the number of their interactions with each one, and (b) the Spearman r_s values obtained when their interaction rates with each infant were compared with their dyadic neighbour frequencies with the respective mothers. Finally, column (c) shows how the mothers of the two main infant partners ranked among the eight mothers in order of neighbour frequency to the male. The infants are named by the dominance ranks of their mothers.

	(a) Interactions with each infant								(b) Interaction rate and association with mothers		(c) Association rank of 2 main mothers	
	Infants											
	1	2	3	8	12	14	16	18	r_s	p(n=8)	1st	2nd
Males												
A3	7	8	5	2	2	2	3	10	.139	n.s.	2	8
A4	13	0	15	1	0	2	0	0	.944	$<.01$	1	2
A5	2	40	1	6	1	20	7	0	.826	$<.05$	1	3
A7	3	0	20	3	7	10	4	5	.922	$<.01$	2	4

χ^2 (pooling infants 8,12,16 and 18), 133.95
$p<.001$

No infant interacted exclusively with any one male, nor any male with any one infant. Most infants had two more frequent male partners. When pairs of males interacted particularly often with the _same_ infant (as did A5 and A7 with F14's infant), one male interacted appreciably more than the other. Males did not select a particular infant to interact with when near a particular other male. In 15 pairs in which _both_ males interacted with infants when near each other, 10 shared interaction with the _same_ infant, at different times when the other was near. Finally, in the 13 cases where the four males in Table 6.XXXIV used _recognised_ infants, eight used infants who were their first or second interaction partners in that table.

_6.9.6_ _Discussion of male-infant interaction_

It is not known which males had fathered the infants observed in this study. The newcomers could have fathered at most the two born at the end, but these infants accounted for only 7% of interactions of recognised infants. In contrast, the six resident adults (plus three who emigrated before the study began) could have fathered any of them, and data presented in Chapter 8 suggest that among them the prime-age adults would have done most of the mating before A1 and A2 joined the troop. The preceding data show that it was just these males - the higher ranking resident males, the possible fathers - who interacted with infants most. The fact that they tended to interact especially with the infants of those mothers with whom they shared affiliative bonds (at least in the short-term) suggests that _some_ of them were even more likely to be the fathers of the infants concerned (from descriptions of longer-term bonds in Ransom & Ransom, 1971; Seyfarth, 1978b; Altmann, 1980). Their interaction with their infant partners occurred not only in relaxed social contexts, but also when there was more risk of aggression both to the male and the infant, which is consistent with previous evidence that males care for _and_ exploit the same infants (Altmann _ibid_.; Packer, 1980).

The males who interacted most with infants did so especially with respect to high-ranking males, by interacting with infants when they were near and in apparent response to their behaviour, and by carrying infants _against_ them. They did this especially with respect to the newcomers, the males least likely to be the fathers; frequent use of infants against newcomers was also reported by Ransom and Ransom (1971), Buskirk et al (1974) and Nash (1976). However, they also did this against other resident adults and subadults, more so against the high rankers who were more likely to include the fathers. The observation that newcomers did not interact with infants at all agrees with a tendency reported by Packer (1980), although the opposite pattern may occur in geladas (Dunbar & Dunbar, 1975).

In all, the identities of the males who interacted with infants suggests that males who might be the father do so most, and they do so with respect to males who are probably not the father as well as to other males who might be, and that their access to particular infants is mediated through their relationships with the mothers. The fact that pairs of males shared frequent interaction with the same infant suggests either that males do not limit interaction to their own offspring, or more likely that they cannot recognise them. Thus if they selectively interact with infants that are more likely to be their offspring, as reported by Altmann (1980; but cf. Packer, 1980), this selectivity must be determined by familiarity with the mother, as is apparently the case for some selectivity in infanticide (Angst & Thommen, 1977; Hrdy, 1979b).

To interpret males' relationships with infants it is necessary to account both for care and exploitation. The probable adaptive significance of the first is that males may protect infants which are likely to be their offspring. While few interactions were obviously protective, many could be adequately explained in this way, as when males gathered-up infants at the proximity of a newcomer or high ranker, or at the outbreak of aggression nearby. This is supported also in that it was the possible fathers who interacted most. This distinction between males as possible or not possible fathers is made because of the question of infanticide. Infant-killing has been attributed to immigrant males in a variety of cercopithecines (reviewed in Angst & Thommen, 1977; Hrdy, 1979b), and in theory immigrant male baboons might increase their reproductive success in this way (Altmann et al., 1978). There are indeed scattered reports of baboon males killing infants (Saayman, 1971b; Nicolson in Hrdy, 1979b; Altmann, 1980; Busse, 1980; Packer, 1980), but insufficient to conclude that it is a purposive behaviour of immigrant males. The reason it is so infrequent may be that male reproductive tenure in multi-male troops is probably longer than in the one-male groups where infanticide is more commonly reported, so that other reproductive tactics might be more expedient. This is particularly likely in the face of resident males' protectiveness of immatures (Packer, 1979a), and the co-operation in defence shown between these and other troop-members (Smuts in Hrdy, 1979b). At Ruaha, for example, a large part of females' aggression to males, and most 'gang attacks', focussed on the two newcomers (6.11.1). However, there may still be a risk of infanticide (Hamilton & Busse, 1980), although it may not explain all male-infant interaction since 60% of the cases of males carrying infants (N = 209) occurred when neither of the newcomers was within 25m. Also the resident adults interacted very much with infants when near one another, yet infanticide risk among residents is theoretically less because of uncertainty about paternity.

The second facet of male-infant interaction that requires explanation is why males exploit infants. The data here were insufficient to confirm Packer's (1980) observations that males carrying infants receive less threat but gain increased dominance. However, the contexts of many interactions were completely consistent with this, especially in the timing at which males interacted with infants (when near high rankers; or after interaction with another male, etc.) and in the males' ability to withdraw from agonistic exchanges by so doing (also Gilmore, 1977; Seyfarth, 1975). More obviously, males used infants offensively by gathering them up before approaching and passing another male (also Gilmore ibid., but not in Seyfarth ibid.), behaviour which appeared to increase rather than reduce the risk to the infant.

Why a male should be able to gain such advantage is not clear. Popp and DeVore (1974) suggest that a male carrying another male's offspring may deter a male who might be the father from attacking, effectively as a hostage. While this theory might explain agonistic buffering between female japanese macaques (Kurland, 1977, p.115), it is inconsistent with the absence of infant-use by newcomers in this study, although it cannot be discounted in interactions between resident adults. Packer (1980) refutes this on similar grounds. Although Hrdy (1976) predicted in similar vein that males should care for their own offspring but exploit offspring of others, the evidence is rather that they care for and exploit infants that may be their own (see above). The logic of this might be that the infant-user, by risking his infant, advertises to his opponent the increased costs of any aggression he may receive, and therefore his greater likelihood of escalation (by analogy with Popp & DeVore, 1979, p.326), but a realistic explanation of its development might be as follows. Male baboons are well known to be intensely protective to some or all black infants (DeVore, 1963; Hall, 1963 ; Rowell et al., 1968; Seyfarth, 1978b; Packer, 1980); this behaviour is so widespread that it may have a strongly genetic basis. Because this protectiveness is so intense, it is inevitable that baboons would learn to avoid any male who was protecting an infant or perhaps merely close to one. Conversely, the protecting males would learn the increased effectiveness of their agonistic behaviour when paired with a black infant. They could therefore rely on it (a) defensively, to avoid or withdraw from conflicts; and in some cases (b) to use it offensively, by carrying an infant when interacting with another male. The possibility that this is a learned response is supported by the marked individual differences in rates of interaction with infants seen even between the focal males, as also in Barbary macaques (Deag, 1980; Taub, 1980b). Deag and Crook (1971) also suggest that troops differed in this respect, which again might implicate learning.

Packer (1980) explains the apparent paradox that males care for and exploit infants which might be their relatives on the basis that the risk to the infant is so small that it is offset by the gain to the infant in protection, and the gain to the male in protectiveness and use, an example of mutualism. Male use of infants, as interpreted here, differs from other forms of social buffering in baboons in that it is derived from a particular response (defense of infants), and in that the male can move about while carrying the infant (provided the infant co-operates: Altmann, 1980), and so use it offensively as well as defensively. Although the interactions at Ruaha resemble some of the cases included as agonistic buffering in Barbary macaques (Deag & Crook, 1971), it remains to be seen whether the explanation given above might apply to the more elaborate exchanges of infants described for that species (Deag, 1980; Taub, 1980b).

10. RELATIONSHIPS AMONG MALES

6.10.1 Introduction

The preceding sections have included descriptions of a number of aspects of behaviour between males, and the present section attempts to summarise these and to portray their dyadic relationships. Although a number of studies have biased their descriptions towards the behaviour of males (e.g. Hall & DeVore, 1965; Stoltz & Saayman, 1970), probably mis-representatively (Hausfater, 1975), yet at Ruaha the frequency of agonistic behaviour between males exceeded that between females far more than can be explained by observer's bias. Relevant descriptions of male-male interaction may be found in Hall & DeVore (*ibid*.), Rowell (1967b), Saayman (1971b), Seyfarth (1975): while interesting case-histories are given in Altmann and Altmann (1970), Ransom (1971), Hausfater (1975), Nash (1976) and Altmann (1980).

The interactions between all males are summarised in six sociograms, Figs. 6.12, 6.15 and 6.17-20 (compare also Fig. 4.5, association). Some behaviours have been combined, thus all approaches (Fig. 6.17) and avoidance and supplant (Fig. 6.18). The relative thickness of the lines is important within each sociogram, but cannot be compared between them since behaviours varied so much in frequency that the critical values differ in each case.

6.10.2 The general pattern of interactions

Different age-classes of males are compared below, but the general patterns common to them all may be summarised first.

6.10.2a) Rank-direction of behaviours Much of the direction and rate of interaction was determined by dominance and rank. In each pair, nearly all avoidance and supplant were downrank; an average of about 70% of approaches and solo aggression were downrank, but about 70% of allied aggression was *up*rank. The exceptions to this were that three adult males gave more solo aggression uprank than down, and these three A5, A6 and A7, were all *below* median adult rank (Fig. 6.19). Secondly, three males showed marked tendencies to approach uprank, namely S2, S3 and especially A7 who did so more than downrank.

6.10.2b) Rank-difference A number of behaviours were more frequent between closer rankers, but in most cases this could not be separated from the fact that focal adults both associated and interacted more (e.g. 6.6.3 & 6.7.9). However, the dyadic rates revealed a number of adjacent-ranked pairs between whom agonism was particularly frequent. Those in which the dominant gave interaction (all behaviours combined) more to the immediate subordinate than to any other were as follows: A4 to A5, A6 to A7, A8 to S2, S2 to S3, and S3 to S4. Both S1 and A7 also gave comparatively frequent solo aggression to the male next above in rank. However, although dominance relations between adjacent pairs might be expected to be more ambiguous than in other pairs, the dyadic scores gave no evidence that in close-ranked pairs the subordinate was proportionately less likely to avoid than to be approached, nor less likely to be supplanted once approached, than in more distant-ranked pairs.

6.10.2c) Consortship Although males consorting swollen females may gain temporary increase in dominance (6.2.2, 6.7.3), there was no evidence that males in consort directed more aggression uprank or downrank than usual. Rather, the direction of interaction of consort males reflected the rank-position of the main consorters and their rivals, notably in that rival males tended to challenge uprank when in alliance (8.3.10).

6.10.3 Age-differences, and male-male relationships

Adult males' differences in apparent age closely paralleled their differences in dominance rank and seniority, so that the effects of age cannot be separated quantitatively. However it is possible to infer the influence of age by comparing the behaviour of the four distinct age-sets of males, as follows.

6.10.3a) Subadult males The four subadults could be tentatively aged in order of increasing size, with S4 youngest, then S3 and S2 similar, then S1. They associated often with other males, and because of this and their low rank received large numbers of supplants. The youngest, S4, had the fewest interactions with other males: both S2 and S3 tended to approach higher rankers, especially S2 who was also the most frequent supplantee of nine other males (Fig. 6.18). The younger three differed

FIG. 6.17

APPROACHES

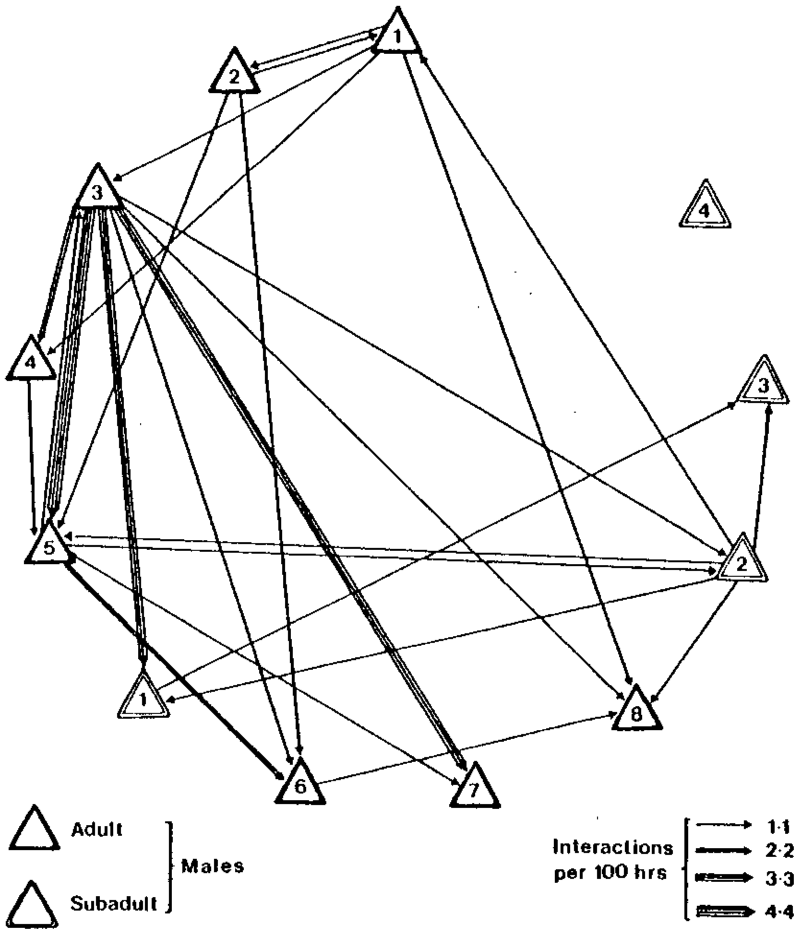
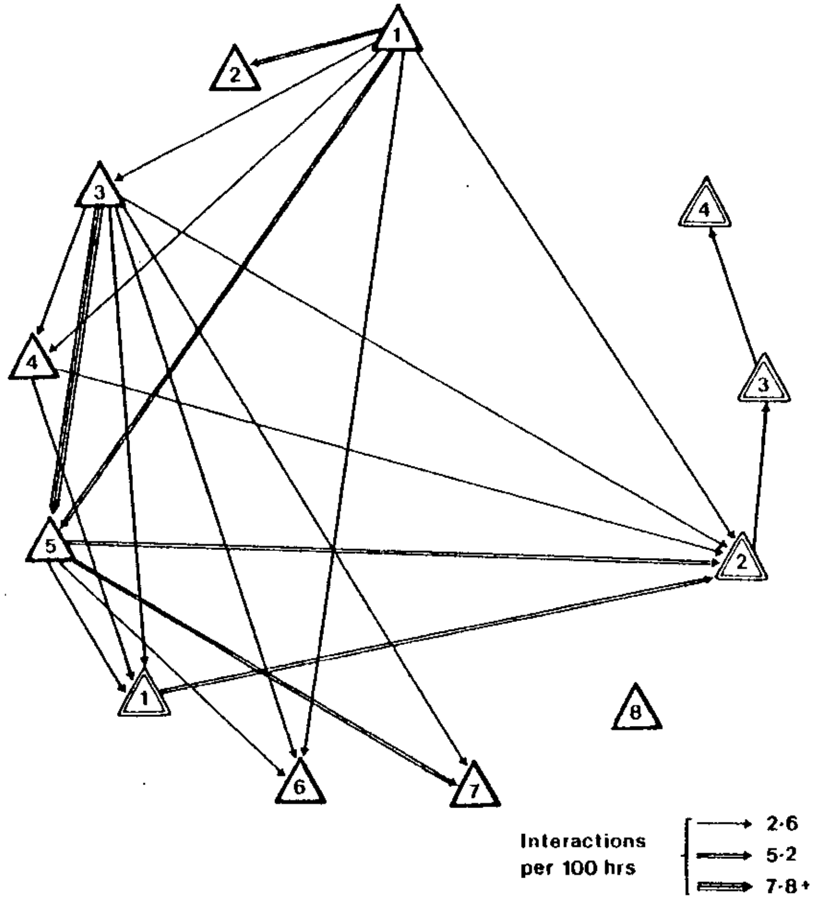


FIG. 6.18

AVOIDANCES & SUPPLANTS



Figs. 6.17 & 6. 18. Non-aggressive interactions between males. Dyadic rates of interaction between pairs, in which the arrows run from donors to recipients. Males arranged anticlockwise in descending order of dominance rank, named by dominance rank within class. In Fig. 6.17, approaches combine passing, contacting, and mounting, and the links shown account for 53% of the 350 interactions seen. In Fig. 6.18, supplants given were combined with avoidances received in each pair, arrows running from the supplanter/avoidee; 699 of such interactions were seen, so that critical values are higher than in Fig. 6.17, and the arrows account for 51% of them.

FIG. 6.19

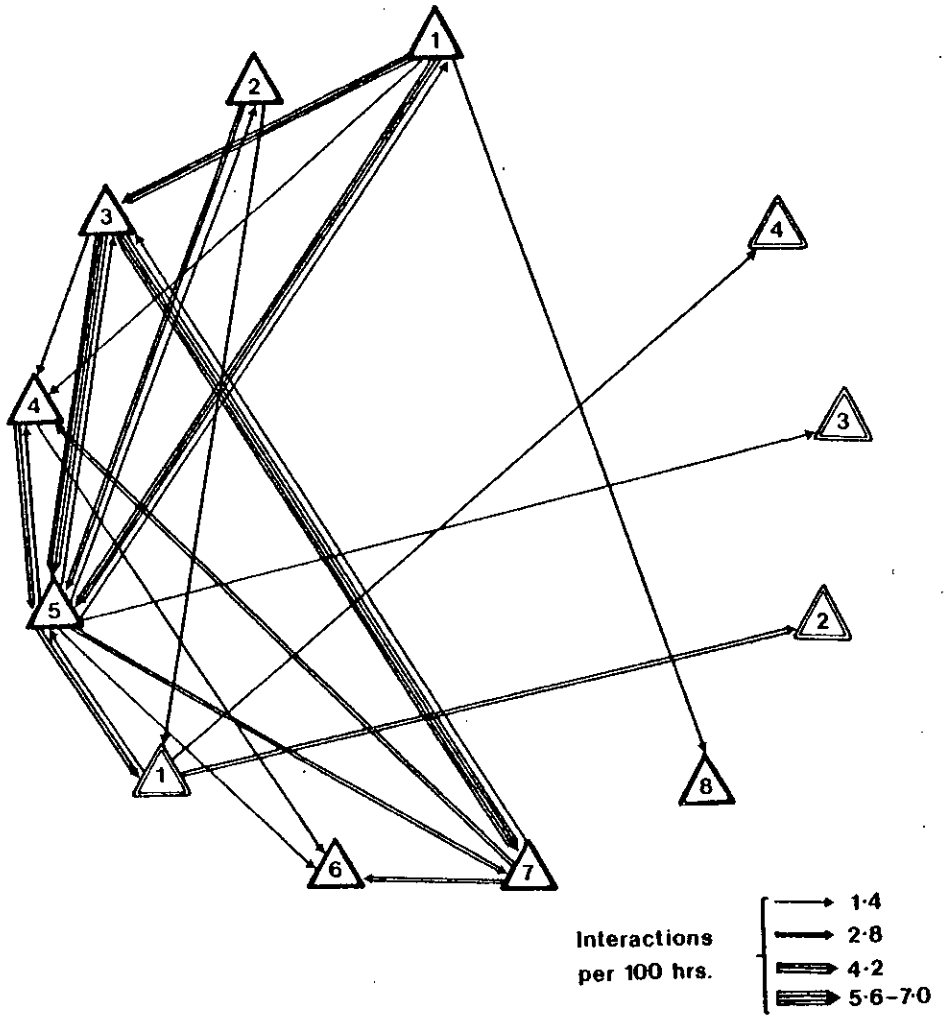
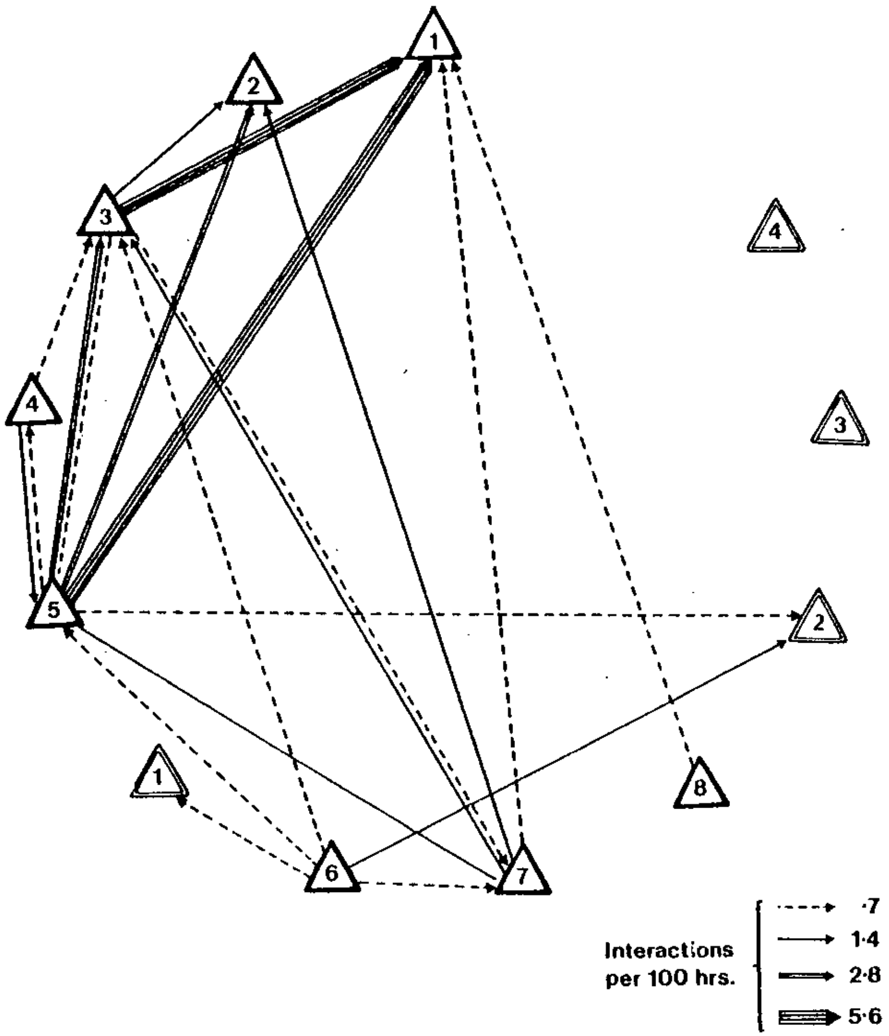

SOLO AGGRESSION

FIG. 6.20


ALLIED AGGRESSION

Figs. 6.19 & 6.20. Aggressive interactions between males. Dyadic rates of interaction per hundred hours, in which arrows run from aggressors to recipients. Males arrayed and identifiable as in Fig. 6.17. In Fig. 6.19, the links portray 66% of the 453 cases of solo aggression between these animals. Fig. 6.20 shows the rate at which each male gave aggression to each other male when allied with other animals (including non-male allies); such interactions were less frequent (244 observed, of which 73% included on the figure) but the critical values have been kept the same as in Fig. 6.19 to allow comparison. However an extra ten partnerships at lower rates have been included as dotted lines.

from the lower-ranking adults in that they gave very little aggression uprank, whereas S1, who ranked among the adults, did (6.10.2b). However S1 was not involved in aggression over oestrus females. The subadults allied with males, females, and immatures, and sometimes used infants.

In their relations with one another, subadults most conspicuously tended to supplant the subadult next below in rank (Fig. 6.18), including S1 to S2 who was four ranks below in the whole male hierarchy. In their relations with newcomer adults, S2 approached A1 quite frequently, and in turn was supplanted by him; and the subadults' allied aggression to males was most often to A2. However the subadults' main feature was that the younger three associated unusually with focal males A3, A4 and A5, and interacted often with them, mainly in receipt. The departure of S1 from the troop did not follow any increase in aggression or supplants received from other troop-members.

6.10.3b) Young adult males/newcomers Because of their high rank, A1 and A2 were able to give agonism to all other males, but A1 was particularly assertive and aggressive to his subordinates. A2 was more peripheral, interacted less, and was avoided proportionately more. They seldom allied with others, and did not use infants. A1 supplanted A2 very often, but they exchanged much less aggression than either did with resident males. Their most salient feature was that they directed frequent solo aggression to focal males, who in turn allied aggressively against them; both received much aggression from A3 and A5 in competition for oestrus females. The resident males also interacted with infants with respect to these newcomers.

6.10.3c) Prime-age resident males A3, A4 and A5 were all focal males (in their association with mothers) and all three showed high rates of agonistic interaction, mainly with one another and with newcomers, and they allied and used infants frequently. Their relations with one another and with A7, the older focal male, were very conspicuous in that they spent much time in proximity, and this was reflected in their interaction. Thus they exchanged more agonism together than they did with other resident males, including frequent solo aggression and supplanting most of which fell upon A5 and A7. Despite this frequent antagonism, they tended to act in alliance together, not only against newcomers but also against one another and other resident males

(Figs. 6.12, 6.20). Thirdly, they most often interacted with and used infants, including with respect to each other. A3 and A5 were particularly assertive and aggressive, A4 rather less so, and the conspicuous pairing between A3 and A5 as associates, antagonists, and allies, is apparent in the sociograms. At least some of their antagonism was in competition for proximity to mother-infant pairs. Their interactions with older adults were less frequent, and accorded with their relative ranks. A6 and A8 both allied with A5.

6.10.3d) Older adults The common features of A6, A7 and A8 were their low ranks, and their tendency to give proportionately more of their aggression in alliance. They also showed relatively high proportions of contact aggression in their solo aggression to other males (Collins, in prep.). Otherwise they differed. A6 and A8 represent peripheral, older adults of low rank, who interacted at low rates with other males and relatively little with infants. The aggression they did show was more to the focal males than against the newcomers, although A8 exchanged aggression with A1 and appeared unusually resistant to A1's attempts to supplant him. In contrast to these two, A7 retained several features of prime adults in his behaviour as a focal male (discussed above), but his tendency to approach and aggress uprank may represent a pattern of challenge by an ageing male of declining rank (6.8.6).

6.10.4 Discussion

The pattern of relationships among the males suggest that dominance is related to age in the form of an inverted U-shape, the highest rankers being young adult and prime males (also Owens, 1975; Packer, 1979a). The low rank of the subadults appeared due to their size, since they were very assertive to one another in supplanting, but not assertive to adult males except possibly by approaching them; with the exception of S1 who showed them some aggression and was of full size. The data accord with other reports that subadults rise in rank as they approach adult size (Ransom, 1971; Altmann *et al*., 1977) and may attain high rank among adults, but that subadults' emigration is not immediately caused by aggression received within the troop (6.10.3a; Packer, 1979a; cf. Altmann & Altmann, 1970).

Although the newcomers here occupied the highest ranks this is not always the case at other study sites (Hausfater, 1975; Nash, 1976; Packer, 1979a; pers. obs.). Its occurrence here confirms a contrast with macaques in which newcomers take low ranks (Sugiyama, 1976; Bernstein & Gordon, 1980) and senior males become the high rankers (Drickamer & Vessey, 1973). The prime adults occupied <u>relatively</u> high ranks, and both A3 and A5 showed high rates of solo agonism to their subordinates, perhaps to endorse those ranks. They did not appear to rely on alliances and use of infants to <u>maintain</u> rank so much as to buffer them during interaction with higher rankers and newcomers (cf. alliances in macaques, Wilson & Vessey, 1968). The implication was that individual ability determined dominance rank, but that males could do better than from their rank alone by allying and using infants.

If A7 is correctly characterised an ageing focal male, and A6 and A8 as males that are no longer focal, then age appears to bring a decrease in competitive ability, and in assertiveness and aggressiveness. It also brings a waning of bonds with mothers (4.5.6) which may explain the low infant-interaction rate of males A6 and A8, (but cf. Saayman, 1971b). The older males' reliance upon alliances parallels the case of old male Kovu in Hall & DeVore (1965).

In sum, the individual differences between males follow three main axes of variance. These are:

1. <u>Age</u>: which affects assertiveness (i.e. tendency to approach and supplant) and aggressiveness. Both are relatively low in subadults and in older adults, but high in young adults and prime males.
2. <u>Dominance rank</u>: in that it expresses for each male the number to whom he may give agonistic behaviours, and the number from whom he is likely to receive them, and thus the ratio between given and received. A male's attained rank at any time probably reflects opportunity, in terms of the number and ability of competitors, and the male's age, as it affects assertiveness and aggressiveness.
3. <u>Seniority</u>: length of residence in the troop affects two important aspects of the males' relationships:

(a) <u>relations with females</u>: This is important in that the high-ranking resident males' relationships with mothers allow access to their infants, defining them here as focal males. Older males may lose these relationships.

(b) relations with males: Prime-age resident adults associate together more, although it is not clear whether they associate with one another or with females in common. Such association brings higher rates of exchange of agonism, and also frequent alliance. It is not clear whether the alliance is a consequence of the association, or vice versa, or whether both result from a third factor such as sharing relationships with mothers. Seniority appeared also to determine who allied against whom, as residents against newcomers, but this might have been partly because of the frequent consortship of the newcomers with swollen females. The older males appeared to retain these alliances, but were less frequently involved in aggression in general.

These three factors suggest interpretations of male-male relationships described at other sites. For example, Saayman (1971b) and Stoltz and Saayman (1970) observed an old focal male (Y), and a prime adult (ST), both of whom allied together and used infants against a more peripheral, aggressive α - male (B). And Seyfarth (1975, 1978b) described a β-male, Pierre, who was favoured by lactating females, and who allied with troop-members and used infants, against aggressive α-male Rocky. The information above suggests that both these α-males were probably more recent immigrants to their troops.

11. DISCUSSION OF AGONISTIC BEHAVIOUR

Four aspects of agonistic behaviour merit further discussion. The first is a point of detail, the remainder are more general issues.

6.11.1 Agonism against newcomers

It was described in 6.4.3 how females gave more aggression to males than to dominants of their own sex. Although some of this was directed at subadults, most of the remainder was to the three highest-ranking adults, and this was true of both solo and allied aggression. A similar tendency against A1, A2 and A3 was also found in allied aggression by males (including subadults), in aggression by immatures, and in males' interaction with infants. While some of the aggression from males was attributable to competition against the high-rankers' consorting activity, yet much occurred in other contexts. First, conflicts between resident males were sometimes redirected against newcomers (see example in 6.2.3). Secondly, both newcomers showed bouts of assertiveness when in the space of a few minutes they would supplant several animals, males and females, but without taking over any resource; A2 also tended to chase females on the periphery. If the recipients of such agonism showed distress, others were likely to respond with group aggression to the newcomer. In 21 cases where three or more animals allied against an adult male, only two were against A3, and all the rest were against the two newcomers. Only one of these was a consort dispute, and in the most intense incident twelve animals simultaneously attacked A1.

The concentration of aggression on these three might have been a response to their high rank; they were clearly avoided most by other males and thus presumably more feared. However, aggression against newcomers might be expected if such males are more likely to commit infanticide, (Busse, 1980), as discussed in 6.9.6. Without observational evidence that these newcomers were motivated to do so, however, it is better to ascribe the aggression to its more immediate causes, the unfamiliarity and assertiveness of these two males. Both were avoided more by females than were other males.

6.11.2 Dominance, and linearity of hierarchy

The pattern of agonistic interactions in this study agree with the theory that animals minimise the costs of competition by establishing dominance relationships in which one partner generally concedes to the other without aggression (Lack, 1966, p.766). It cannot be said that the function of hierarchies, such as the one found in this study, is to reduce aggression but rather that animals' attempts to avoid aggression result in relationships which may, as here, be arranged hierarchically. Why therefore should the relationships be hierarchical, why should relationships in different pairs be transitive? One reason is that in matrilineal groups, the ontogeny of dominance relations produces a hierarchy. Matrilines dominate one another in linear order, apparently because of patterns of alliance by one matriline against the next; dominance might therefore reflect the size of matrilines (Dunbar, 1980 ; Silk et al., 1980) or their history of growth and fission. Secondly, within each matriline, dominance rank reflects birth-order and reproductive value (Schulman & Chapais, 1980), and is established at least in part through alliances (6.7.1). Both these mechanisms are responsible for the linear rank-order of female baboons and macaques.

Linear hierarchies among transferred (unrelated) males, and among females who do not rank according to matriline and birth-order (e.g. langurs, Hrdy & Hrdy, 1976) are harder to explain. One possibility is that the hierarchy is an exact portrayal of the animals' rank-order of competitive ability. For example, Packer (1979a) found that male dominance rank was correlated with body weight, itself a likely determinant of physical ability, so that this explanation is feasible. However there is also evidence from other species, of feedback mechanisms in which dominance rank may affect (a) body weight, which may decrease after a decline in rank (Dittus, 1977), and (b) hormone levels, which may change as a result of rank-changes (Bernstein _et al_., 1974) and may themselves affect agonistic behaviour (Mazur, 1976). Thus dominance rank might affect competitive ability, and ability itself cannot be considered independent of the past history of the animal, and need not _a priori cause_ linearity. Other explanations may be found in the development of dominance relations. While two animals may learn their relative dominance through their history of competitive interaction, there are grounds for believing that monkeys can learn their dominance also by observing the interactions of others, and extrapolating to themselves (Rowell, 1966b, 1974), a process which would make relationships transitive and hierarchies linear. Monkeys are certainly capable of extrapolating serial order to some degree (McGonigle & Chalmers, 1977). That they can also assess the relative ranks of others is suggested by the behaviour of reintroduced group-members to those of adjacent rank (Conaway & Koford, 1964; Vessey, 1971; also 6.6.1), and by cases where animals solicit the aid of those who rank _above_ their opponents (DeWaal, 1977; Walters, 1980).

Finally, Wade (1978) has proposed that whenever animals attempt to dominate opponents by forming exploitative alliances with partners who are already dominant to the opponents (as in Wade, 1976; Cheney, 1977; DeWaal, 1978), then a linear ordering will result. This is essentially the logic of the matrilineal system described above, but does not accord with the alliances between males in this study.

6.11.3 Maintenance of dominance

Rowell (1966b) concluded that dominance relationships were maintained especially by subordinates, since subordinate behaviours were nearly all uprank whereas 'dominants'' behaviours were not so restrictedly downrank. She also observed that unsolicited submissive behaviour more frequently expressed dominance relations than did threats by the dominant (Rowell, 1974). While in this study the subordinate often 'decided' the outcome of an interaction in that an approach only became a supplant if the recipient left, and threats were often not pressed home if the recipient ignored them, yet dominant and subordinate behaviours should not be compared quantitatively (as in Rowell's comparison of direction constancy) when they differ qualitatively. 'Dominant' behaviours may also be used to challenge uprank, while some submissive behaviours are never used downrank (DeWaal, 1977; Noë et al., 1980). These submissive behaviours may provide the clearest index of an established relationship, in the way that 'first submission' represents a turning-point in a dominance-change (Noë et al., ibid; Walters, 1980), yet occasional aggression by the dominant may reinforce the status-quo as effectively as frequent submission by the subordinate. In Deag's (1977) study, threats were almost equally often downrank as the direction of avoidance, and they were more frequent, allowing the conclusion that dominant and subordinate contribute to the relationship. Although in this study it was not clear what proportion of the 'dominant's' and 'subordinate's' behaviours were actually initiated by the dominant and subordinate partners (because of ad libitum recording) yet data in Tables 6.XVa and 6.XVIIa, show that in eight comparisons of dominance rank and rates of agonism given and received within each sex, dominance rank was more closely correlated with the dominant's behaviour in four and the subordinate's in four. Thus both partners appear to contribute equally.

An appreciable number of agonistic interactions were not contests for any resource at all (as "displacements" in Altmann, 1980), especially supplants between males, and such interactions appeared to be reassertions of existing dominance relations. Similar "dominance-oriented" interactions have also been reported by Struhsaker (1967), Rowell (1974) and Moore (1978), and have clear analogies with dominance displays in chimpanzees (Goodall, 1968; Bygott, 1979). Also, animals have been observed to achieve dominance over chosen opponents by persistent assertiveness of this sort (Hall, 1967; Nash, 1976; Walters, 1980). The frequency of such interactions in baboons implies that maintenance of dominance relationships is at least as important as the value of any single resource, probably much more so. Therefore those predictions that the outcome of agonistic encounters, or even the order of dominance hierarchies, should be affected by the relative value of the resource to the contestants (e.g. Popp & DeVore, 1979, p.331; also Clutton-Brock & Harvey, 1976, p.218) may not be strictly applicable if they do not account also for the relative value of maintaining the dominance relationship for the benefit of access to other resources (e.g. Curtin, 1980).

6.11.4 Comparison of behaviour within each sex

Agonistic relations within each sex differed chiefly in that among males interactions were much more frequent, were more often uprank, and individuals' rates were less closely dependent upon their position in the hierarchy, than they were among females. These conclusions have been discussed separately in 6.3.6, 6.4.6 and 6.5.6, but since Walters (1980) also found that dominance particularly constrained behaviour between females, the question remains as to why they contrast with males in this respect.

One explanation is the one already given for the difference in rates within each sex (6.4.6), which is that the short-term benefits of behaving agonistically differ for male and female (Symons, 1978, p.179). Thus only males may directly increase their number of offspring by such behaviour, while females are less free to expend energy, and they risk reproductive failure by agonistic interaction. In the longer term also, although reproductive success may be related to lifetime dominance rank in both sexes (Drickamer, 1974b; Dittus, 1979; Saunders & Hausfater, 1978), yet variance in reproductive success is greater in males than in females, (Bateman, 1948), so that a male gains more by increasing his rank than does a female. In proximate terms, this means that a male on joining his breeding group must establish as high a rank as possible, must maintain it for as long as possible against subsequent immigrants, and must defer the costs of his decline in competitive ability as he ages by forming relationships with males and females in the troop (6.10.4). Such priorities necessitate more frequent agonistic behaviour uprank and down, and may result in high rates of rank-changes compounded by immigration of males from elsewhere.

In contrast, females may gain relatively less by increasing their rank, and because their priority is to minimise energetic and social costs for the sake of reproduction they are also more constrained to accept dominance relationships. Furthermore, dominance ranks are not upset by immigrants but only less frequently by adolescents maturing into the adult hierarchy (Altmann & Altmann, 1979; Walters, 1980) and possibly by females declining in rank with age (Moore, 1978). Walters (ibid.) attributes the stability of their relations, and the direction constancy of their behaviour, to the higher rankers defending their rank (and greater probability of reproductive success) so effectively by alliances that lower rankers are unable to solicit alliances to challenge them. Chapais and Schulman (1980) argue persuasively in the same vein that females will tend to ally with the dominant rather than the subordinate in any conflict, and this explanation is likely to be correct. However it is not necessarily the case that direction constancy is imposed by alliances. Agonistic interactions between female Hanuman langurs are almost all downrank (Hrdy & Hrdy, 1976), yet they very seldom act in alliance (Hrdy, 1977, p.181). However, since langur hierarchies are not stable over time this does imply a role of alliances in the stability of the hierarchy in macaques and baboons. Secondly, Walters' argument does not explain the sex-difference here, since the same logic applies equally to males, among whom the higher rankers may also achieve greater reproductive success and should similarly defend their rank positions. The evidence from this study was instead that males used alliances to challenge the hierarchy rather than to defend their own ranks.

An alternative explanation for the sex-difference is provided by Dittus (1979). Females of female-bonded troops are more closely related to one another than are the males, who are unlikely to be relatives. Since establishment of dominance relationships confers the greater benefit on the dominant, females are more likely to concede dominance to a related female than are males to an unrelated male, so that kin-selection may have favoured greater acceptance of dominance relationships among females.

In conclusion, it is likely that agonism is more frequent and more often uprank among males than among females because (a) females are more inhibited from competing by the costs of reproduction; (b) males may increase their reproductive success more by direct competition, and by increasing their rank, than may females; and (c) females may be more likely to accept established dominance relationships because they are more closely related, while subordinacy has fewer benefits among males.

CHAPTER 7

The Menstrual Cycle, Sexual Behaviour and Consortship

1. INTRODUCTION

Female baboons undergo a number of ovarian cycles between the end of lactation amenorrhoea and the start of the next pregnancy, manifested by swelling of the perineum. Maximal swelling coincides with sexual activity or oestrus (Heape, 1900) which in most cycles is also the time of maximal fertility. The relations between ovulation, mating, and external signs of oestrus have been intensively studied in macaques (reviews in Rowell, 1972; Keverne, 1976; also Tokuda et al., 1968; Dixson, 1977; Wolfe, 1979) which, with mangabeys (Chalmers & Rowell, 1971) talapoins (Scruton & Herbert, 1970) and chimpanzees (Goodall, 1968), parallel baboons in several respects. Preceding chapters have contrasted the behaviour of cycling and non-cycling females, but this chapter describes changes in behaviour during the cycle itself, and the details of copulation.

2. THE MENSTRUAL CYCLE AND OVULATION

7.2.1 Cyclical perineal changes affect the vagina, clitoris, and circum-anal region; numerous authors have documented these changes in captive baboons (Zuckerman & Parkes, 1932; Gillman & Gilbert, 1946; Hendrickx & Kraemer, 1969; Rowell, 1970 ; Stevens, 1978) and their findings are confirmed in the wild (Hall, 1962; DeVore, 1965; Rowell, 1967a; Saayman, 1970; Hausfater, 1975; Seyfarth, 1978a). After menstruation, the sex-skin swells gradually due to buildup of oestrogen in the follicular phase, maintains full size around midcycle, and then deflates rapidly as progesterone antagonises this effect of oestrogen (Gillman, 1940). The sex-skin remains deflated until the next menstruation. Underlying hormonal changes are described by Stevens et al. (1970) Hagino (1974), Stevens (1978) and Wildt et al. (1977).

In order to assess the relation between males' mating activity and reproductive success (Chapter 8), it is important to know which is the most fertile part of the cycle, since sperm viability is limited (Restall, 1967). Zuckerman and Parkes (1932) and Wildt et al. (1977) concluded that ovulation occurred close to the first day of deflation.

In contrast, Gillman and Gilbert (1946) and Hendrickx and Kraemer (1969) found that matings were more successful earlier than this, respectively two days, or between two and eight days, before deflation-day. The contrast between these two sets of results probably reflect differences in methodology. Zuckerman and Parkes (ibid) examined corpora lutea of females several of whom had been killed in fighting (Zuckerman, 1931, cf. 1932 pp. 218-228): Wildt et al., used laparoscopy on anaesthetised females. Since deflation may be induced prematurely by aggression or injury (DeVore, 1965; Rowell, 1970; Ransom, 1971) or by laparotomy (Gillman & Gilbert, 1946; Hendrickx & Kraemer, 1971), these estimates of ovulation in relation to deflation may be less reliable than estimates based on timing of successful matings. Hendrickx and Kraemer found that mating success did not vary significantly between the eighth and the second day before deflation, but was highest on the third day beforehand.

7.2.2 Cycle-stages at Ruaha

The stages of the perineal cycle have been defined in 2.IIIb. The ten cycles during observations at Ruaha (Fig. 7.1) were similar to those described for yellow baboons elsewhere (Hendrickx & Kraemer, 1969; Hausfater, 1975). The follicular and luteal stages of the ovarian cycle correspond approximately to the two halves of the perineal cycle: turgescence (swelling increasing or full) and deturgescence (perineum deflating or flat). The correspondence is not exact in that deturgescence may persist for a few days after menstruation, and turgescence may persist after ovulation for about three days (or implicitly up to seven, in Hendrickx & Kraemer, 1969).

Because the onset of deflation is easily recognised it is used here to name the days of the cycle, as in Hausfater (1975). The onset of deflation is d-day, the following days d+1, d+2 etc., the preceding days d-1, d-2 etc. This notation defines a week of potentially fertile mating (7.2.1) from d-7 to d-1, referred to as full swelling. Inflation extended from 9 to 31 days before this ($\bar{x}$ 16.7), deflation took 2 to 7 days ($\bar{x}$ 4.4) and the subsequent flat stage from 13 to 16 days ($\bar{x}$ 14.7). The summed length of turgescence was therefore 16 to 38 days ($\bar{x}$ 23.7) and of deturgescence 18 to 25 days ($\bar{x}$ 20.7). Reliably observed intervals between deflation-days were 34, 36, and 40 days. Menstruation started between 7 and 18 days after d-day ($\bar{x}$ 12.7), that is between 9 days

FIG 7.1 Menstrual Cycles: length of stages, in days.

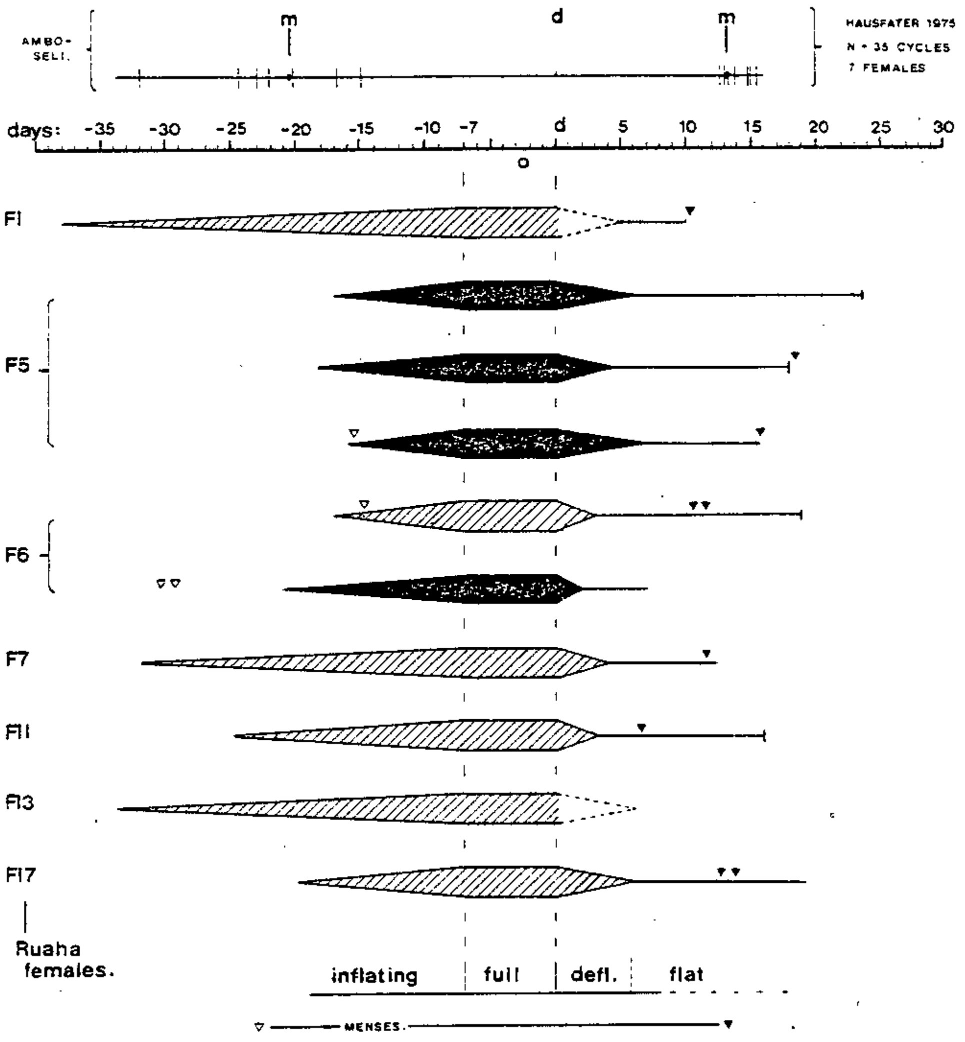


Fig. 7.1. The ten perineal cycles observed in this study. Each is represented by one horizontal line, with the female named on the left and the cycle stages indicated by the width of the line. The six resumption cycles are cross-hatched, the four subsequent cycles are black. Two periods of deflation which were not observed are marked by dotted lines. Some flat stages are terminated by a short vertical bar, indicating the start of the next inflation; but endings without such a bar indicate the end of the study. Days of menstruation are marked twice, as ▽ in relation to the following inflation, or as ▼ in relation to the preceding deflation. For comparison the top line shows the mean lengths of turgescence and deturgescence of seven females at Amboseli, with mean incidence of menstruation (m), from data of Hausfater (1975).

before and 2 days after the start of inflation, and lasted one or two days.

Fig. 7.1 differentiates cycles which were the females' first after lactation amenorrhoea (six resumption cycles) from those which were not (four subsequent cycles). Turgescence tended to be longer in resumption cycles (17 to 38 days) than in subsequent ones (16 to 21). Atypical resumption cycles are also reported by Gillman and Gilbert (1947), Ransom (1971) Hausfater (1975). None of the cycles here resulted in pregnancy, and some may have been anovulatory: according to Hendrickx and Kraemer (1969) 12.9% are without ovulation (cf. 0% in Wildt *et al.*, 1977). It is not impossible for conception to occur in resumption cycles, but unusual (pers. obs. at Gombe).

Rowell (1970) found that the follicular phase was extended if the female received frequent aggression during that time, but over nine cycles at Ruaha (excluding F11) the mean rate of aggression received during inflation was not related to the length of the turgescent phase (r_s 0.033, n.s.). Variability appeared more to reflect differences between individuals, and between resumption and subsequent cycles.

Longer-term cycle-length data are available from Ruaha, collected by P.L.A. Ngatwika and L. Mathias between Sept. 1974 and Feb. 1976. These show that females cycled between 3 and 8 times before conceiving (9 conceptions, $\bar{x}$ 4.3 cycles), and that differences between these females were not related to dominance rank (r_s 0.367, n.s.). The interval between birth and resumption of cycling (first inflation) was between 4 and 17 months (9 intervals, $\bar{x}$ 11.3), but was shorter for higher-ranking females (r_s 0.857, n=9, $p < .01$).

3. RESUMPTION OF CYCLING, AND INTERACTIONS

7.3.1 Females who were observed both in lactation (or motherhood) and during cycling showed contrasts in interaction rate in the two states. The interaction rates of five of these six females (i.e. excluding F11) have been used in statistical comparisons of reproductive states in the preceding chapters, and so cannot be analysed statistically here. However, the changes in interaction rates between lactation and cycling which were shared by all five females were as follows. When cycling, all five showed increases in (a) association with males; (b) grooming of adult males; (c) grooming by adult and subadult males, and immatures; (d) presenting to adult males; (e) unintromitted mounts by adult males and by immatures; (f) intromitted mounts by adult and subadult males and by immatures; (g) avoidance of, and supplants by, adult males (behaviours pooled); (h) aggression from immatures.

4. ANALYSIS OF BEHAVIOURAL CHANGES THROUGH THE MENSTRUAL CYCLE

The following methods were used to document the changes in interaction rate that occurred in each cycle-stage.

7.4.1 Interaction rates of each female

The duration of observation in each cycle-stage is listed in Table 7.I. From this was calculated in each stage the female's interaction-rate with members of each class. Rates were expressed as pooled mean rates (2.XIIc. IV), rather than dyadic mean rates, because when calculated from so few observation-hours the latter were much affected by differences between interaction-partners. Partner-availability comprised 18 females, but the number of males each day varied between 6 and 8 adults, and 3 and 4 subadults. Rates with immatures were calculated as subject-rates (2.XIIc. I), without accounting for partner-availability, since the likelihood of interaction for each behaviour differed according to both age and sex of partner (e.g. compare copulation and grooming).

7.4.2 Mean rates across females

Rates in each cycle-state have been calculated as the mean rates across all females. The two females observed in more than one cycle each contribute only <u>one</u> score per cycle state, obtained by combining all data from that stage of all her cycles to give a single pooled mean rate. F11 was ommitted from this and the following procedure (7.4.3) because of her illness. Mean rates are therefore derived from six females at inflation and full swelling, but only four females in deflation and flat.

7.4.3 Comparison of cycle stages

In contrast to the above, the analysis of cycle changes examined <u>all</u> cycles (except F11's), so that F5 and F6 contribute data for three and two cycles respectively, but the other four females only one each. Analyses gave emphasis to patterns of change consistent over all cycles, rather than to the <u>rates</u> themselves because not all subjects were equally in view. Each stage was compared with the next, although <u>flat</u> was not

Table 7.1: Duration of observation – hours during each stage of each female's cycle.

	Inflation	Full	Deflation	Flat
Females/cycles:				
F1	147.6	33.9	–	–
F5.1	29.5	34.1	30.3	75.6
2	34.1	34.7	22.7	63.4
3	30.3	38.7	24.3	27.9
F6.1	46.3	35.5	18.1	74.1
2	58.7	38.9	6.2	17.4
F7	112.8	40.9	16.6	11.3
F13	128.6	33.9	–	–
F17	63.4	23.5	29.0	68.8
F11	83.8	29.0	16.6	52.2

Female F11 was excluded from all tests and figures (7.4.2), and female F6's deflation of the second cycle was excluded from Wilcoxon tests (7.4.3.).

compared with inflation to ensure independence (except once in 7.7.2). The nul hypothesis was that the change in interaction rate would be random across all cycles in terms of direction (increase or decrease) and magnitude. This was tested by Wilcoxon matched-pairs test, two-tailed. The data from deflation of the second cycle of F6 were ommitted because observation-time was so brief. This left nine transitions from inflation to full, but only six from full to deflation and from deflation to flat.

The fact that the majority of cycles were resumption cycles may detract from the generality of these data, since their cycle-changes were less marked than those of subsequent cycles (7.5.5). However this does lend weight to those conspicuous changes which were found.

5. INTERACTIONS WITH ADULT MALES, and the effect of oestrous females on male-male relations

7.5.1 Changes in interaction between female and adult male during the perineal cycle have been described by Hall (1962), DeVore (1965), Rowell (1967a), Saayman (1970), Ransom (1971), Hausfater (1975) and Seyfarth (1978a). Their findings may be summarised as follows.

During inflation, the female increases her grooming of males, presents often, and may move about conspicuously within the troop. Males may inspect the swelling, mount, or copulate. At full swelling, the female establishes consort relations with one or a series of adult males, and the consort male maintains exclusive mating access. There are three conspicuous differences from the female's interaction at other times: (i) the male maintains proximity to the female, (ii) he grooms her far more than usual, and (iii) he appears to initiate the majority of copulations. The female's grooming is largely devoted to her consort (except in Ransom, 1971), but seldom matches the amount she receives from him. Consort pairs may stray unusually far from the rest of the troop (Bolwig, 1959; Hall, 1962; DeVore, 1965; Saayman, 1970; Seyfarth, 1978a). Consortships begin before or during full swelling, and a female may have several consorts per day (DeVore, 1965; Rowell, 1967a; Hausfater, 1975) or one partner for many days (Saayman, 1970; Seyfarth, 1978a, i.e. in chacma baboons).

Adult males usually lose interest in the female at the onset of deflation or shortly before (Saayman, 1970; Evans, 1974; Seyfarth, 1978a), and consortships cease. Some authors report that during deflation there are transient increases in female presenting (Hausfater, 1975) or in male inspections of the perineum (Hausfater *ibid*.; Seyfarth, 1978a; also in gelada, Dunbar, 1978a).

7.5.2 Association between female and adult male

Females most often had at least one adult male nearby at *full* swelling (Table 7.IIa). Adult male neighbour-frequency increased from inflation to full in 8 of the 9 cycles (T=1, n 9, $p < .01$): and in 5 of 6 it decreased from full swelling to deflation. When males *were* near, however, there did not tend to be more *of* them at full swelling (Table 7.IIb), suggesting that the increased neighbour-frequency at full swelling was caused by particular males. This is generally confirmed in row (c) of the table, in that only 56% of male-female pairs increased association at full swelling: in detail, F7, F1 and F17 experienced as many decreases as increases, the latter two increasing with one male only.

Previous sections have described how high ranking adults were involved more with cycling females in terms of association (4.2.7) and interaction (e.g. 5.4.3). Data were examined for evidence of this pattern in association at each stage of the menstrual cycle. For each male was calculated the percent of its association samples for which an inflating, full, deflating, or flat female was nearest within 15m. The males' rank-order for these variables are compared with dominance rank in Table 7.III, repeating the tests without F1 who was probably attractive to males both as a *mother* and as a cycling female. Higher-ranking adults associated more at full swelling, and tended to do so also during inflation.

7.5.3 Interactions between females and adult males

Table 7.IV shows females' mean rates of interaction with adult males in each cycle state, and the results of statistical comparison of consecutive stages. Comparisons which did not yield significant results, or which were not testable through scarcity of data, are not indicated. The behaviours are as defined in Appendix I, except that (i) aggression combines solo and allied aggression, (ii) female stands next is the converse of male stands next, (iii) male greets rear *includes* inspects. Male mounts are separated into those without

Table 7.II: Females' association with adult males. Mean scores over all females of (a) percent of association samples in which at least one adult male was within 15m. on the minute; (b) mean number of adult males in 15m through the minute during samples in which at least one was near; (c) number of adult-male/female pairs whose dyadic neighbour frequency increased or decreased during each cycle-stage change, from through-minute samples.

			Inflation		Full		Deflation		Flat
(a)	Male(s)	%:	46.5	**	67.3		47.8		53.1
	near.	s.d:	(14.3)		(19.7)		(28.5)		(15.1)
(b)	Number of	$\bar{x}$:	1.3		1.3		1.1		1.5
	males.	s.d:	(.1)		(.2)		(.2)		(.4)
(c)	Pairs increasing:			29		10		14	
	decreasing:			19		15		10	

Table 7.III: Adult males' dominance ranks compared with their association frequency with females at each stage of the perineal cycle. Spearman r_s values ; at n = 8. probabilities * < .05, ** < .01.

	Inflation		Full		Deflation	Flat
r_s, inc. F11.	.786	*	.905	**	.494	.345
exc. F1.	.609		.881	**	.494	.345

Table 7.IV: Pooled mean rates at which cycling females interacted with adult males, per hundred hours. Mean values over all females; standard deviations in brackets. Comparisons between consecutive stages (described in 7.4.3) gave the significant differences indicated at probabilities * <.05, ** <.01. M = male. F = female.

	Inflation			Full			Deflation		Flat	
Agonistic:										
F avoids	.28	(.15)		.09	(.16)		.52	(.82)	.32	(.26)
M supplants	1.51	(1.00)		.94	(.65)		.86	(.66)	1.16	(1.02)
M aggress	.55	(.26)	**	1.23	(.54)		.99	(1.12)	.31	(.25)
M avoids	.02	(.05)	**	.99	(.31)	*	.26	(.41)	0	
F aggress	.12	(.16)		.23	(.51)		.04	(.09)	.09	(.13)
F affiliative:										
F stands next	.10	(.10)		.42	(.28)		.04	(.08)	0	
F grooms	.61	(.17)		2.60	(1.47)	*	.26	(.41)	.16	(.20)
F presents	1.18	(.71)		1.59	(1.30)		1.36	(1.13)	.41	(.28)
M affil./sex:										
M greets rear	1.11	(.66)	*	2.23	(.74)		1.33	(.91)	.94	(.28)
M mounts w'out	.74	(.33)		.90	(.46)		1.70	(1.62)	1.51	(1.58)
M intr.mounts	.65	(.37)	**	9.30	(3.22)	*	2.12	(2.69)	.06	(1.15)
M. consort:										
M grooms	.27	(.16)	**	3.34	(1.13)	*	.30	(.41)	.57	(.55)
M stands next	.69	(.69)	**	3.99	(1.65)		1.33	(1.52)	.64	(.74)
M follows	.27	(.35)	**	1.73	(1.37)	*	.24	(.27)	.24	(.28)
M possessive	.59	(.58)	**	2.23	(.85)		1.16	(1.55)	1.10	(1.06)
M coercive	.18	(.17)		.96	(.78)		.04	(.08)	.12	(.20)

intromission, and intromitted mounts.

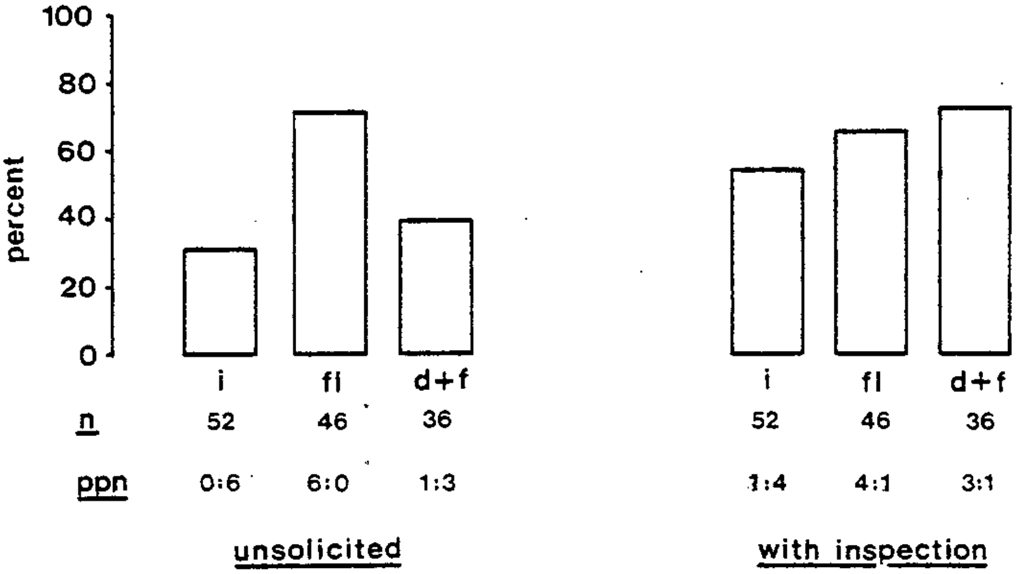
7.5.3a) Agonistic interaction There were no consistent changes in female avoidance or male supplanting over the cycle. However, 67% of the 33 supplants to fully swollen females were by their male consorts, although this was not recorded for the three lower-ranking females. In contrast, the significant increase in aggression received, from inflation to full swelling, was not due to the consort males (< 10%) so much as to rival adults threatening the pair. The increase in avoidance by males at full swelling was because single males generally avoided the advance of a consort pair (6.7.2).

7.5.3b) Female affiliative behaviour In 7 of 8 cycles there was an increase at full swelling in the rate at which females approached and stood next to males (n.s.). Similarly all females except F1 increased their rate of grooming males at full swelling, and all of four decreased it again in deflation in all cycles. Perhaps surprisingly, there was no consistent tendency for females to present more or less at any stage. Consecutive cycles of the same female varied in this respect also. Their rates seemed to reflect the consorting activity of the males. Thus the rate at which females presented at full swelling was greater in those cycles in which males consorted with them least (r_s - 0.831, n 9, $p < .05$). Although females were in consort for an average of 59% of the time at full swelling, only 13% of their presents at this time were to their consorts (n = 32). Female F5 was not seen to present during turgescence in her first two cycles, during which she was consorted assiduously by A1, but she presented during turgescence of the third cycle when A1 did not consort. Similarly, F6 did not present during full swelling in her second cycle, when she was consorted for more of the time than in her first. Finally, females' present rates were not related to their dominance rank, either during inflation (r_s -.543, corr. obs. -.771, n 6, n.s.) or at full swelling (r_s -.657 ± obs. corr., n 6, n.s.).

7.5.3c) Male sociosexual and sexual behaviour

Males gave rear-greetings to females more frequently at full swelling, and rates tended to decrease in deflation (n.s.). 54% of 132 such greetings were in response to presents, and given that females' present-rates did not increase at full swelling, but the males' greetings _did_, it is not surprising that proportionately more rear-greetings were

FIG 7.2 FIG 7.3



Figs. 7.2 & 7.3. The percent of all adult males' rear-oriented behaviours to females in each cycle state which were unsolicited (7.2, i.e. not in response to a present) and which included males' inspection of the female's perineum (7.3). Female cycle states are i - inflation, fl - full, d - deflation, f - flat. The lowest row shows the ratio between the number of females whose percent scores in that state were greater (on left) or less (on right) than their percent overall. Thus 0:6 indicates that six females were below their overall percent.

*un*solicited at full swelling (Sign test, two-tailed $p < .05$, Fig. 7.2). Females also differed in the proportions of their greetings which followed presents: a higher proportion of greetings were unsolicited for higher ranking females (r_s .987, n 6, $p < .05$). This appeared to be a compound of two weaker tendencies; that lower rankers presented slightly more (7.5.3b above) and that higher rankers received unsolicited rear-greetings at slightly higher rates (r_s .571 ± obs. corr., n 6, n.s.).

Rear-greetings in which the male moved his nostrils to within three inches of the female's perineum were defined as *inspects* (Appendix I, XV.c). The proportion of all rear-greetings which included inspection tended to increase later in the cycle, being highest in deflation and flat (which did not differ: Fig. 7.3).

It was shown above (5.5.1) that the presents of cycling females received fewer greetings and more negative responses than did those of non-cycling females. Fig. 7.4 shows the adult males' pooled responses to presents by females in each cycle stage. The proportions do not differ significantly, but it is clear that negative responses were more obvious at full swelling and in all of these the male looked away.

Rates of un-intromitted mounts did not change consistently over the cycles. Only 10.3% of such mounts upon cycling females were in response to presenting, and 0% at full swelling (Table 7.V). The proportion of un-intromitted mounts in which pelvic thrusting occurred varied slightly over the cycle, but not consistently over all females. However, in proportion to *all* mounts, *un*intromitted mounts with thrusting became least frequent at full swelling and in deflation, suggesting that intromission may have been easier at these times (Table 7.VI).

Intromitted mounts became more frequent for all females during full swelling, and decreased again in deflation (Table 7.IV). Only 1.1% of intromitted mounts were seen to follow immediately from the female's presenting, suggesting that males initiated the majority. Although it was shown in Table 5.XVI that cycling females avoided non-intromitted mounts proportionately more than did other females, this tendency was no greater at any particular stage of the cycle; and when these avoidances are considered in proportion to the *total* mounts received (i.e. including intromitted ones) they avoided only 6.4%, considerably less than the equivalent proportion for non-cycling females (19%; Table 5.XVI), and least of all at full swelling (Table 7.VI). This suggests that cycling

FIG. 7.4

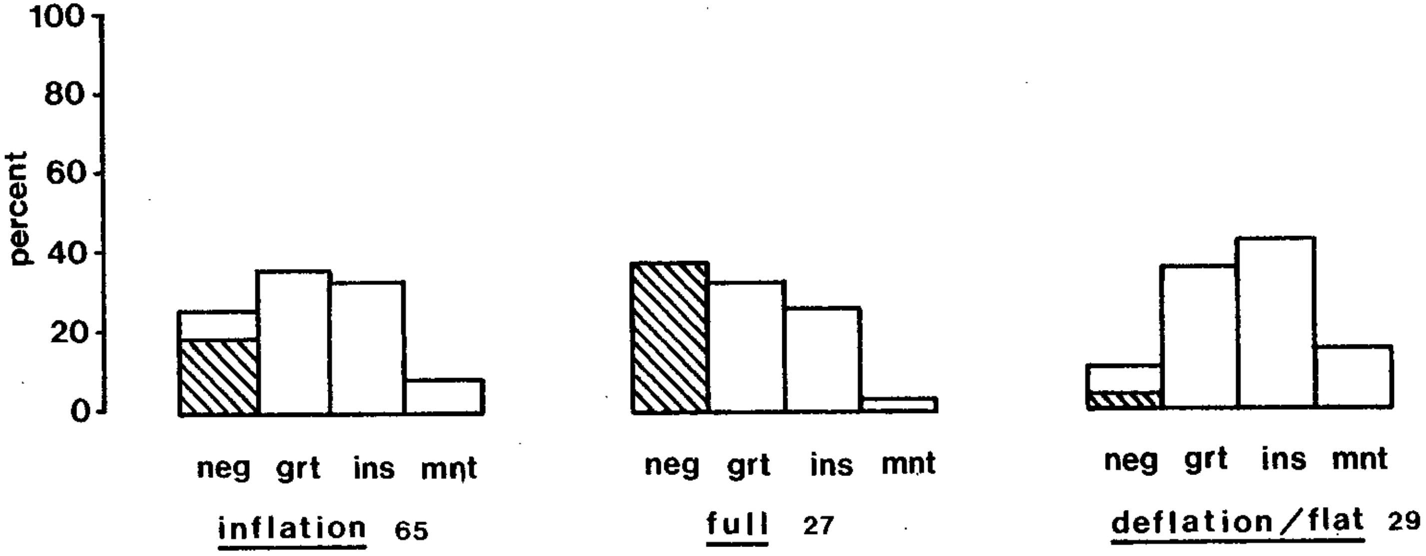


Fig. 7.4. Adult males' percent responses to presents from females in each cycle state. Responses are neg - negative (with, cross-hatched, the minimum proportion in which the male looked away), grt - greets rear, ins - inspects, mnt - mounts. All individuals were pooled; the cycle states are indicated with the number of presents in each case.

Table 7.V: The number of non-intromitted mounts by adult males which were preceded by a present, compared with the number of unsolicited mounts.

	Inflation	Full	Deflation/Flat
With present:	5	0	5
Unsolicited:	32	23	32

Table 7.VI: The percent of three different types of adult male mounts at each cycle stage : and the percent of all mounts which the female avoided.

	Inflation	Full	Deflation	Flat
Total (n) :	69	257	28	27
Un-intromitted:				
without thrusts:	27.5	6.2	32.1	37.0
with thrusts:	26.1	2.7	14.3	51.9
Intromitted:	46.4	91.1	53.6	11.1
% avoided	16.9	3.0	6.7	22.2

females' avoidance of a higher proportion of unintromitted mounts (5.5.2d) was not because they were any less receptive (since they accepted many more mounts overall) but perhaps that they tend to avoid increasingly as mount-rates become very high.

7.5.3d) Consort behaviours Several behaviours characteristic of consort males showed consistent increases at full swelling. Males groomed females, stood close to them, and followed them within arm's reach much more at this time (Table 7.IV), and grooming and following also decreased in deflation. At full swelling there was also significant increase in interactions judged in the field to be possessive. These included a variety of patterns such as herding and shielding (defined in Appendix I, XXI), and a number of instances of mounting, chasing, clasping or holding the female, hurrying close to her, and in some cases grooming her. These were judged to be possessive if they appeared to reduce the likelihood that the female would interact with a second male, as for example when they occurred in response to the arrival of another male, or when the female was moving towards such a male, or (rarely) when another troop appeared. In 85% of cases the components were recorded, with herding and shielding the most frequent (Table 7.VII). The table also reveals that possessiveness was most often shown against adult males, but occasionally against other baboons or other troops.

Finally, coercive behaviours (Appendix I, XX) such as pushing or nipping the side of the female, did not vary consistently over all cycles. These behaviours sometimes preceded mounting.

7.5.4 Percent time spent in consort

One-zero sampling allowed estimates of the percent of time for which each female was in consort with an adult male (2.IX). Consortship was scored if the male showed any two of (a) moving consistently after the female, (b) acting possessively to her against nearby males, and (c) grooming her persistently (Appendix I, E). The mean across females of the percent of their daily 15 min. samples in which they were seen in consort is shown in Fig. 7.5. Resumption and subsequent cycles are compared. It appears that the majority of consortship took place between d-10 and d-1, occasionally earlier. Secondly, females consorted for less of the time in resumption cycles. Thirdly, in both types of cycle consortship reached a maximum between d-4 and d-1, but rather later in the resumption cycles.

Table 7.VII: Behaviours occurring in possessive interactions, as percent of the total, and the contexts of such interactions.

(a) For 86 interactions in which the components were recorded.

Herding	38%	Holding/Clasping	7%
Shielding	23%	Hurrying to female	6%
Mounting	12%	Grooming	2%
Chasing	8%	Miscellaneous	4%

(b) Contexts: for all 112 possessive interactions by adult males, the apparent cause was:

Adult male (s)	76%
Other troop members	7%
Other troops	9%
Unknown	8%

FIG. 7.5

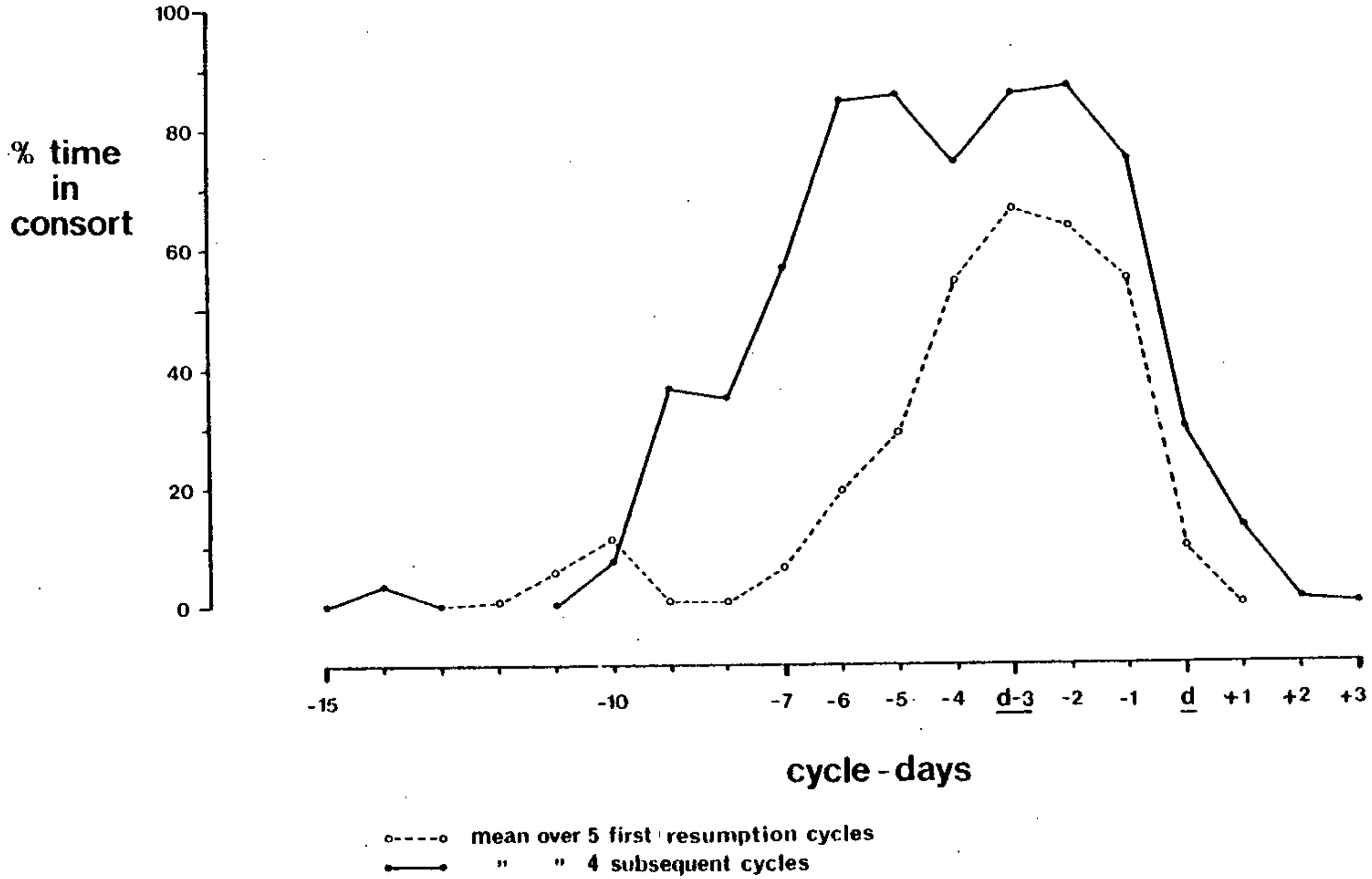


Fig. 7.5. The percent of time which females spent in consort on each day of the menstrual cycle, in relation to the onset of deflation (d-day). The means of the resumption and the subsequent cycles are compared. Estimates made from the percent of 15 min. samples on each day for which the female was seen to consort.

Because *ad libitum* observation was intermittent, and consortship was loosely defined as a result, estimates of the number and duration of consortships can only be approximate. Consortships judged to be continuous lasted between one and 420 minutes; with an average of 99 minutes, but 30% were shorter than 15 minutes. The maximum duration is limited by duration of observations, which on consort-days averaged 313 minutes. Over the week of *full* swelling, females were seen in between 8 and 21 consortships, involving from one to six males per cycle. During *inflation*, consortship only occurred in four of the nine cycles observed, with between one and 13 consortships in each, but involving no more than two males per cycle. Finally, in three of the seven cycles observed in *deflation*, up to four consortships were recorded.

7.5.5 *Interaction rates in resumption cycles*

Resumption cycles and subsequent cycles were compared in terms of the females' interaction rates with adult males. The pooled mean rates of fourteen behaviours (as listed in Table 7.IV, excluding *female stands next* and *female aggression* due to insufficient data, but including percent time in consort (7.5.4)) were compared by Mann-Whitney U-test, and three significant differences were found. In resumption cycles, females were consorted for less of the time (42.3%, cf. 78.4%, $U = 1$, $n\ 5,4$; $p < .05$), and were followed less (1.12 times per 100 hrs., cf. 3.70: $U = 2$, $p < .05$), but they presented more (1.99 per 100 hrs., cf. 0.17: $U = 0$, $p < .05$).

7.5.6 *Initiation of consortships*

When the start of a consortship was seen, it was classified (as in Appendix, I, E) as a *find*, in which a female not consorted during the previous five minutes started to consort, or a *displacement* in which a consort male conceded the female to a nearby male but without aggression, or an *aggressive changeover* in which a male achieved consortship with a female during aggressive exchange with the consort male. The proportions of these three are compared in Table 7.VIII in terms of (a) their distribution at each stage of the cycle, and (b) their incidence at full swelling in *resumption* and *subsequent* cycles separately.

The upper part of the table shows that competitive changeovers (displacements and aggression) were restricted to the period of full

Table 7.VIII: Initiation of consortship. The numbers of three types of consortship, (a) at each stage of the cycle, and (b) distributed between resumption and subsequent cycles at full swelling.

(a)

Cycle-days:	Inflation	d-7	d-6	d-5	d-4	d-3	d-2	d-1	Deflation	% (n = 87)
Finds	21	6	4	8	9	6	4	7	5	71.3
Displacements				1	2	2	1	1		8.0
Aggressive			2	3	2	6	3	2		20.7

(b)

	Resumption cycles					Subsequent cycles				
Female/cycles:	F1	F7	F13	F17	$F6_1$	$F6_2$	$F5_1$	$F5_2$	$F5_3$	% (n = 69)
Finds	7	8	7	9	3	4		1	5	63.8
Displacements			1		1				5	10.1
Aggressive			1			4	6	2	5	26.1

Pooled comparison:

	Resump.	Subs.
Finds :	34	10
Disp.+ Agg:	3	22

x^2 24.8
$p < .001$

swelling, and were most frequent between d-5 and d-2. The lower part shows that completely non-competitive consortships (i.e. finds) were proportionately more frequent in resumption cycles, indicating that competition was more intense in subsequent cycles, in which the chances of conception were probably higher.

7.5.7 The influence of oestrous females on male-male relations

Hausfater (1975) found that on days when one or more females in his study troop were in oestrus, aggression between males became less frequent (although more severe, in terms of wounding rates). He suggested this might be explained if males spread out more at such times. Both aggression-rates and male spacing were therefore analysed at Ruaha.

In Fig. 7.6 are shown the mean rates of aggressive interactions per 100 male-male hours, where records are subdivided according to the number of fully swollen females in the troop on each day, excluding F11. In this calculation an interaction was an incident of aggression between two or more adult/subadult males. The rate of aggression was broadly correlated with the number of fully swollen females (r_s .319, n 84 days, $p < .01$), showing that aggression was more frequent when more females were fully swollen. This result cannot be separated from a possible seasonal difference, since the availability of swollen females and the rates of interaction both increased in the rainy season. However, the aggression rates were not elevated on all days with females fully swollen, but 31% of these 36 days showed aggression above and up to twice the maximum rate on days without swollen females. Finally, days when aggressive interactions were more frequent tended also to have more males involved in each interaction (Median test on 84 days, χ^2 7.05, d.f. 1, $p < .01$).

Two measures were used to estimate whether males spread out more when females were fully swollen. First, for each day of the study was calculated the percent of males' neighbour samples for which a male neighbour was present within 15m. The mean percent on days with none, one or two or more females fully swollen are compared in Table 7.IX(a), Male neighbour-presence decreased significantly when one female was in oestrus, but then increased slightly when more females were in oestrus. Over 83 days considered, mean male neighbour frequency was not correlated with abundance of fully swollen females (r_s -.129,

FIG. 7.6

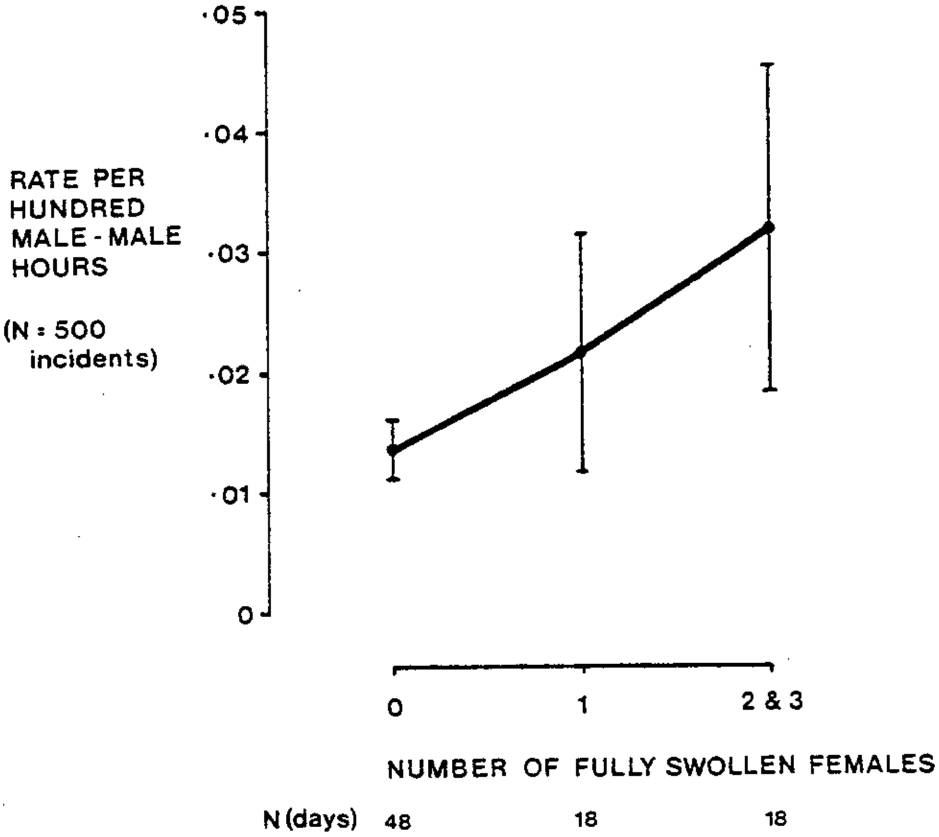


Fig. 7.6. The rate of male-male aggression according to the number of fully swollen females in the troop on each day. Rates calculated as incidents per hour, irrespective of how many males were involved in each incident; graph shows means and 95% confidence limits.

Table 7.IX: Association between males compared with the number of fully swollen females in the troop (excluding F11).

(a) Comparison of days (pooling all males): pooled male-neighbour frequency, mean values across days, with standard deviation in brackets.

Number of females:	None		One		Two or more
N (days)	(48)		(18)		(18)
Mean neighbour frequency	44.3		36.7		42.5
s.d.	(13.4)		(13.3)		(12.8)
t-test: t:		2.06		1.34	
df:		63		34	
p.:		p < .05		n.s.	

(b) Comparison of males (pooling all days): male-neighbour frequencies, by class of subject and neighbour. Means across subjects. The ratio shows the number of males whose neighbour-frequency increased:decreased as more females were in oestrus. Ad = adult. Sub = subadult.

Number of females: Subj. Neighbour.	None		One		Two or more
Ad : Ad.	25.4		18.5		26.5
ratio		1:7		5:2	
Ad : Sub.	16.5		11.5		14.0
ratio		2:6		4:4	
Sub: Ad.	35.2		36.5		35.5
ratio		2:2		1:2	
Sub: Sub.	13.1		11.4		8.4
ratio		2:2		3:1	

n 83, n.s.).

The data were also analysed in terms of males rather than of days. For each male was calculated the percent presence of adult or subadult male neighbours in all of its samples taken on each of the three categories of days. The pattern described above was only evident for adult subjects, and was not common to all of them (Table 7.IX b).

In summary, male-male aggression was likely to be more frequent when one or more females were fully swollen. This is probably more than can be explained by seasonal effects, and is contrary to Hausfater's findings. Secondly, there was only slight evidence that males spread out more when one female was fully swollen, most obvious for adult males: but this again might be a seasonal effect, since days with one swollen female were more frequent in the dry season when the troop was often more dispersed.

7.5.8 Summary of adult-male/female behaviours

These data agree with most details of consort relations at full swelling described elsewhere (7.5.1). One detailed contrast was that females increased their grooming of males at full swelling (cf. Ransom, 1971). The observed pattern of numerous short consortships in each cycle, with agonistic changeovers by males, agrees with the pattern attributed to East African baboons by Seyfarth (1978a), in contrast to the extended and peacable consortships of chacma baboons.

Because consort relationships were exclusive, increases in male-female interaction at full swelling were largely accounted for by interaction with one male at a time (the consort) rather than a generalised increase in interaction with all males at once. The greater association of high-ranking adults with fully swollen females reflects their higher copulation rates (8.3.3). The rate of intromitted mounts by adult males at full swelling was 0.68 per hour (s.d. 0.22; mean subject rates over six females). With observability correction this approximates to 1.22 mounts per hour, and with 54.8% of such mounts ejaculatory at this stage (Table 7.XVI) suggests a rate of 0.67 inseminations per hour.

The most striking finding was the contrast between resumption and subsequent cycles. The higher present-rates in the former, and the greater consorting activity and male competition in the latter, suggest that females' attractiveness was lower in resumption cycles, although swelling size was not obviously less.

6. INTERACTIONS WITH SUBADULT MALES

7.6.1 Previous studies show that subadult males interact increasingly frequently with females through inflation, particularly in copulation, but that their access to fully swollen females is limited by the adult males' consortships (Hall, 1962; Saayman, 1970; DeVore, 1965; Ransom, 1971; Cheney, 1978). Subadults seldom consort, but attempt opportunistic copulation when consort males are otherwise engaged (Hausfater, 1975; cf. Cheney, 1978). Their access to females resumes during deflation (Saayman *ibid*.).

The subadults in this study were old enough to be fertile (Altmann *et al*., 1977; Packer, 1979a). Their rates of interaction were insufficient for comparison with those of adult males.

7.6.2 Association

The frequency with which cycling females had subadult male neighbours was apparently unaffected by cycle state, (Table 7.Xa), as was the number of subadults nearby (b). Furthermore, equal numbers of subadult/female pairs increased and decreased their neighbour-frequency with each cycle-state change (c). Male rank had no effect (Tab. 7.XI).

7.6.3 Interactions

There were no changes in interaction-rates consistent across cycles (Table 7.XII). Although mean rates of interactions and intromitted mounts were higher at full swelling, females varied considerably. Rates of interaction at full swelling in each cycle were compared with the percent of time for which the female was consorted by adult males. The rates of all behaviours pooled (except intromitted mounts) were not related to consort-time (r_s -.548, n 9, n.s.), but intromitted mounts were more frequent in those cycles in which adult males consorted less (r_s -.770, n 9, $p < .05$).

7. INTERACTIONS WITH ADULT FEMALES

7.7.1 It is now generally agreed that female dominance relationships are not affected by cycle-state or consortship (Rowell, 1968; Hausfater, 1975; Nowell & Heidrich, 1978). However, Seyfarth (1978a) noted that consorting females ignored threats more, and were often aided by the

Table 7.X: Females' association with subadult males. Mean scores over all females for (a) percent samples with one (or more) subadults in 15 m on the minute; (b) number of subadults in 15 m during those through-minute samples in which at least one was near; (c) number of subadult male/female pairs whose dyadic neighbour frequency increased or decreased with each cycle-state change, through-minute data.

	Inflation	Full	Deflation	Flat
(a) Subadult(s) %:	10.1	10.3	16.0	9.2
near. sd:	(3.9)	(11.9)	(7.0)	(10.5)
(b) Number of $\bar{x}$:	1.2	1.4	1.0	1.1
subadults. sd:	(.0)	(.3)	(0)	(.1)

(c) Pairs increase:	8	5	4
decrease:	9	6	5

Table 7.XI: Subadult males' dominance ranks compared with association-frequency with females at each stage of the perineal cycle. Spearman rank correlations, n = 4.

	Inflation	Full	Deflation	Flat
r_s. inc. F11:	-.800	.200	-.400	.400
exc. F11:	-.800	-.400	-.400	.400

Table 7.XII: Pooled mean rates per hundred hours at which cycling females interacted with subadult males. Means taken over all females, standard deviations in brackets. S = subadult. F = female.

	Inflation		Full		Deflation		Flat	
S agon	.81	(.59)	1.09	(1.33)	.66	(1.10)	.37	(.46)
F agon	.17	(.28)	.36	(.44)	0		.28	(.33)
Grooming	.79	(.88)	.82	(2.00)	.27	(.55)	.20	(.24)
F presents	.17	(.20)	.18	(.32)	0		.04	(.08)
S greets rear	.26	(.25)	.30	(.47)	0		.78	(1.50)
S mounts w'out	.57	(.56)	.48	(.68)	.85	(1.10)	.86	(1.41)
S possessive	.53	(.55)	.66	(.90)	1.17	(1.16)	.24	(.31)
all the above:	3.18	(1.19)	3.89	(5.13)	2.95	(2.72)	2.70	(2.31)
Intro. mts	3.27	(3.12)	7.20	(5.91)	2.86	(2.52)	.12	(.15)

consort male; and Hausfater (1975) found that fully swollen females conceded defeat less than usual. While some studies suggest that swollen females are involved in more aggression (Bolwig, 1959; Rowell, 1967a), others note the opposite (Saayman, 1972; Seyfarth, 1978a), and Hall (1962) made the curious observation that mating between one female and the α-male caused increased aggression among other females. While oestrus females in some species may encounter competition for access to the male (e.g. Mori, 1979, Ch. 4), yet Seyfarth (1976) found in chacma baboons that such competition was equally frequent at other times in the cycle.

It has also been reported that a swollen female grooms other females less as her attention becomes focussed on the consort male (Rowell, 1968; Saayman, 1971a; Evans, 1974), although Seyfarth's findings were equivocal. Reports of homosexual mounting by swollen females have been mentioned in 5.7.3b.

7.7.2 Association

Females' association was not consistently affected by cycle-state (Table 7.XIII); again, females varied considerably. However, female associates were significantly more frequent in the flat stage than they had been in inflation (Wilcoxon T = 1, n 7, $p < .05$).

7.7.3 Interaction

The rates listed in Table 7.XIV yield only two consistent tendencies. First, females supplanted less at full swelling than they had in inflation; and secondly, rates of all behaviours (pooled) decreased from full swelling to deflation. Other detailed changes which appeared consistent were that at the start of full swelling females were avoided more (6 of 8 cycles), received fewer supplants (6 of 7 cycles), and received more aggression (5 of 7 cycles), but these were not significant. All cycling females gave more grooming than they received in most states, but this characteristic was exaggerated at full swelling. There was no obvious relationship between cycle-state and the tendency to give or receive mounts with other females.

No relation was found between the percent of time in consort at full swelling and either (a) interaction rate with females during full swelling (r_s -.183, n 9, n.s.), or (b) percent change in interaction rate with females between inflation and full swelling (r_s .183, n 9, n.s.).

Table 7.XIII: Cycling females' association with other females in each cycle-stage. Mean scores over all females for percent of samples with one or more adult females within 15m. Standard deviations in brackets.

	Inflation	Full	Deflation	Flat
Female neighbour				
%	52.1	57.6	60.6	68.7
sd.	(20.2)	(18.2)	(7.3)	(19.7)

Table 7.XIV: Cycling females' pooled mean rates of interaction with other females through the cycle; standard deviations in brackets. C = cycling female, O = other females. * indicates change $p < .05$.

	Inflation		Full		Deflation		Flat	
O avoids	.09	(.09)	.21	(.18)	.13	(.22)	.04	(.06)
C supplants	.48	(.26) *	.27	(.28)	.38	(.40)	.30	(.21)
C aggress	.16	(.16)	.21	(.21)	.23	(.20)	.11	(.13)
C avoids	.09	(.10)	.09	(.11)	0		.03	(.04)
O supplants	.21	(.18)	.18	(.38)	.10	(.19)	.13	(.11)
O aggress	.15	(.15)	.30	(.36)	.18	(.21)	.05	(.05)
C grooms	.41	(.19)	.41	(.29)	.13	(.25)	.27	(.18)
O grooms	.27	(.08)	.17	(.13)	.17	(.20)	.33	(.11)
Mounting by C & O	.10	(.09)	.24	(.16)	.15	(.19)	.15	(.14)
All the above	1.94	(.49)	2.06	(.53) *	1.47	(.54)	1.39	(.37)

8. INTERACTIONS WITH IMMATURES

7.8.1 Cheney (1978) noted that immature males tended to interact with cycling females while immature females interacted more with lactating females. Young males mount and copulate during inflation, but as with subadults their access at full swelling is limited by the consortship of the adult males (DeVore, 1965; Saayman, 1970), except to those females least favoured by the adults (Cheney, 1978).

Rates of interaction are presented as subject-rates. They may be approximated to dyadic rates by dividing by 40, or for male immatures only by 20 (e.g. intromitted mounts). Because of small sample-size it has been necessary to pool interactions given and received in agonism, grooming, and sociosexual interaction (the latter includes female presents, male mounts, and male greets and inspects rear).

7.8.2 Interactions

Analysis of the subject-rates of interaction in Table 7.XV showed no changes which were consistent. Most obviously the mean rates of agonism and copulation were highest at full swelling, but not significantly. Immatures showed possessive behaviours like those of consorting adult males quite frequently, but never persistently enough to be declared in consort. The decline in copulation rate after full swelling occurred rather later than it did for older males.

The amount of time the females consorted with adult males at full swelling was not related to their rate of interaction with immatures (all behaviours except intromitted mounts, pooled: r_s .200, 9 cycles, n.s.). However, intromitted mounts were more frequent in those cycles in which the adult males consorted less (r_s -.906, n 9, p <.01).

9. SUMMARY: CYCLING FEMALES' INTERACTIONS WITH SUBADULT MALES, FEMALES, AND IMMATURES

7.9.1 The preceding three sections provide little evidence that cycle-state consistently affects interaction-rate with animals other than adult males. However, females received intromitted mounts from both subadults and immatures more frequently in those cycles in which adult males consorted less. This may explain why there was not a universal tendency for these interactions to occur more at full swelling consistently in all cycles.

Table 7.XV: Cycling females' subject - rates of interaction with immatures, per 100 hours, with standard deviations in brackets.

	Inflation		Full		Deflation		Flat	
Agonistic	5.6	(3.2)	8.8	(4.0)	2.8	(3.6)	8.0	(4.4)
Grooming	4.8	(3.2)	2.8	(2.8)	3.6	(4.4)	.8	(.8)
Sociosexual	15.6	(13.6)	12.0	(8.8)	11.6	(10.4)	6.8	(2.4)
Possessive	4.8	(5.6)	2.8	(2.4)	8.4	(5.6)	.4	(.8)
All the above	31.2	(19.2)	27.6	(5.6)	26.4	(17.6)	16.4	(6.0)
Intro. mounts:	34.4	(22.8)	52.8	(34.4)	32.4	(18.8)	.8	(1.2)

There was no evidence that cycling females groomed less with other females at full swelling, in contrast to studies mentioned above, but they did supplant females less at this time. The evidence that they associated with other females more during the flat stage supports Saayman's findings (1971a). Otherwise females' interactions together were little affected by cycle state.

10. CYCLE STATE AND INTROMITTED MOUNTS

7.10.1 Previous authors have noted that cycle stages vary in the proportions of copulations attained by each male-class (Saayman, 1970; Cheney, 1978), in the females' response to copulation, and in the male's likelihood of ejaculation (Saayman *ibid*.; Ransom, 1971). The interaction of these factors is investigated in the following section.

7.10.2 General findings

Although all male classes mounted with intromission at higher *rates* at full swelling, yet only adult males achieved most of theirs at this stage (Fig. 7.7). All male classes also showed the ejaculatory pause more often when mounting fully swollen rather than inflating females (Table 7.XVI). However, this finding from pooled data may be biassed by over-contributions from particular females in particular cycle states, because (a) male classes did not copulate equally with all females in all cycle states (Table 7.XVII, Appendix II) and (b) the likelihood the male showed the pause was affected by the identity of the female (Table 7.XVIII, Appendix II). This last was partly because adult males showed the pause more with females F5 and F6, both of whom underwent *subsequent* cycles, than with females who were only seen in resumption cycles.

A further complicating factor was that the females' response to copulation was related to the occurrence of pausing by the male. When a male dismounted from intromission, the female would often run ahead (the "withdrawal response") giving the distinctive copulation call. During observations, the females response to intromitted mounts was classified as in Appendix I, xvii. Locomotory response was categorised in 89% of intromitted mounts, from 0 - no movement - to 2 - a full run. Vocal response was categorised in 97% of copulations from 0 - none audible - to 2 - the full copulation call. Table 7.XIX

FIG. 7.7

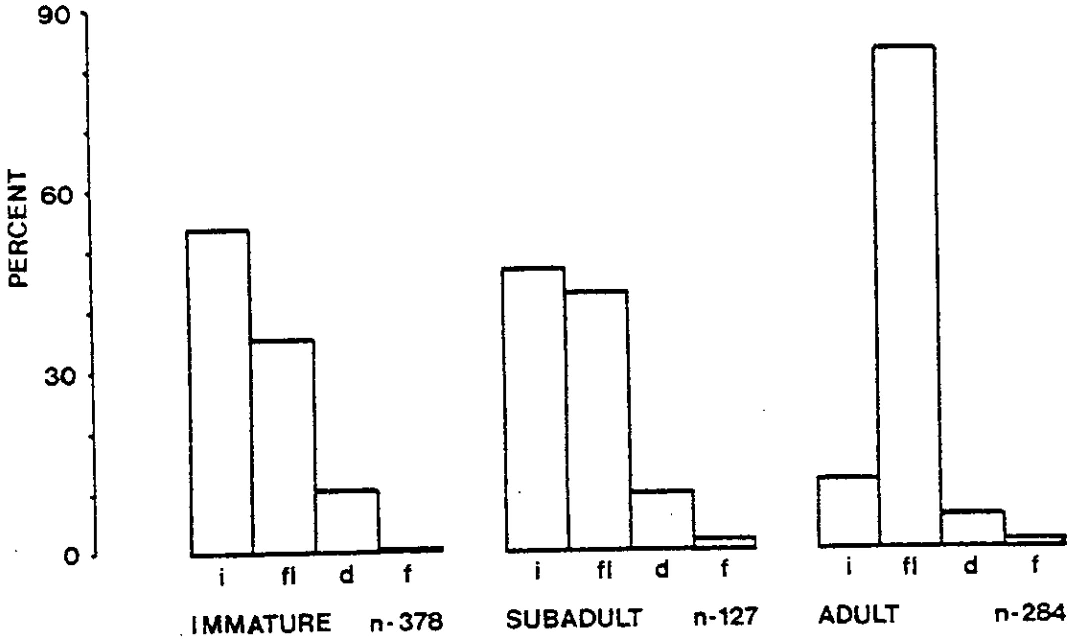


Fig. 7.7. Male classes compared for the percent of their intromitted mounts which occurred with females in each stage of the perineal cycle. Stages labelled i - inflation, fl - full swelling, d - deflation, f - flat. Note that although all classes interacted at highest rates at full swelling (7.5.3, 7.6.3, 7.8.2), yet due to the greater length of inflation the immatures and subadults acheived the greatest number of their intromissions at that time.

Table 7.XVI: The proportion of each male-classes' intromitted mounts in which the ejaculatory pause was seen, as percent of those in which it could be scored present or absent.

Males:	Inflation	n	Full	n	Deflation	n
Immature:	12.1	(91)	26.6	(35)	41.7	(12)
Subadult:	8.3	(24)	41.7	(24)	0	(3)
Adult:	20.8	(24)	54.8	(93)	80.0	(5)

Table 7.XIX: All intromitted mounts, classified by vocal and locomotory response.

		Vocal:				
		0	1	2	%	
Locomotory:	0	25	23	14	8.7	
	1	45	137	161	48.3	x^2 188.47
	2	3	37	265	43.0	df 4. $p < .001$
	%	10.3	27.8	62.0		

Table 7.XX: Intromitted mounts: vocal response compared with incidence of ejaculatory pause:

	Vocal response: 0	1	2	
No pause:	60	80	76	x^2 43.21
Pause:	8	17	74	df 2. $p < .001$

FIG. 7.8

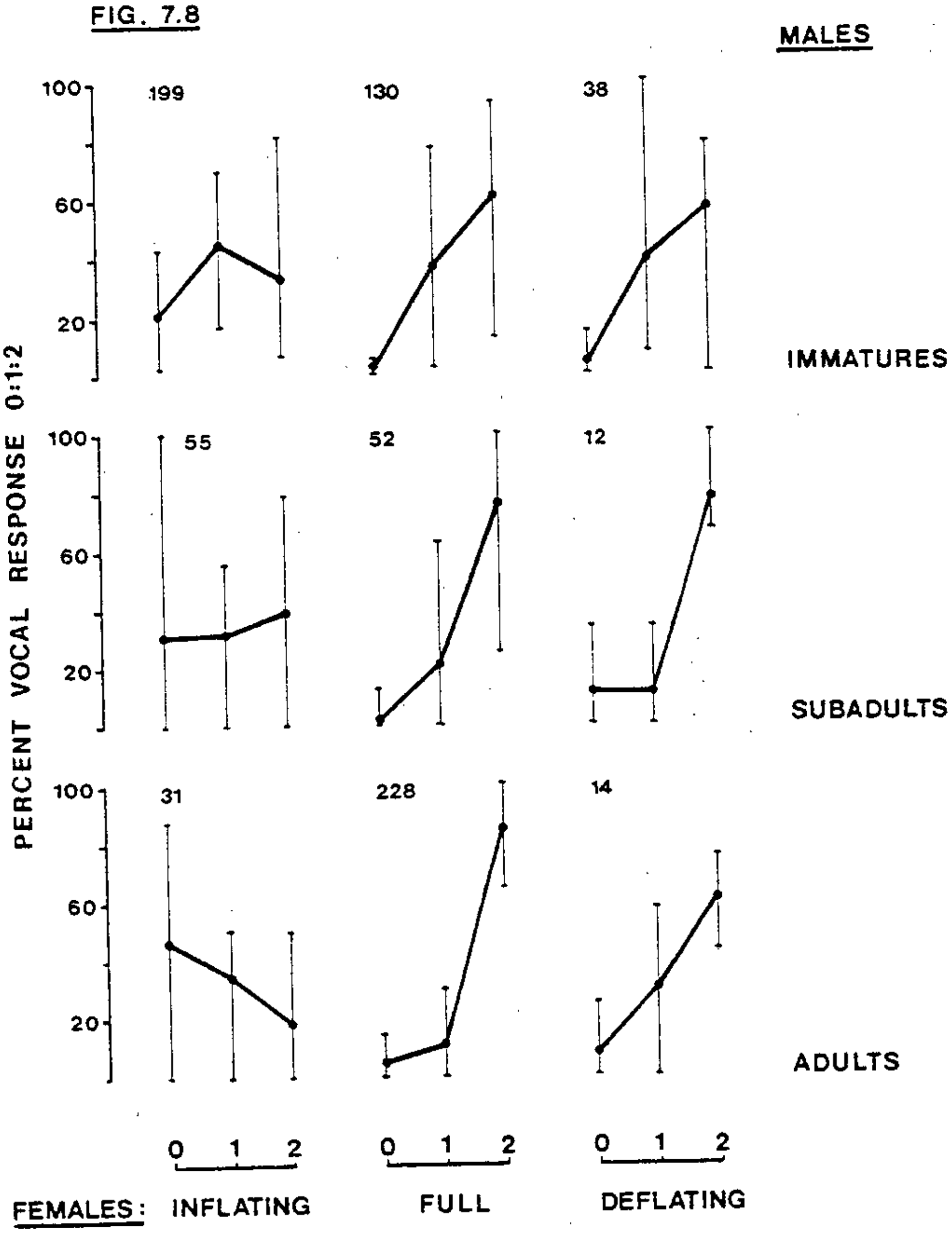


Fig. 7.8. Females' vocal response to intromitted mounts, subdivided according to female cycle state and the class of the male partner. For each female was calculated the percent of her intromitted mounts with each response from 0 (no response) to 2 (full copulation call). These results are portrayed as mean values across the six females, with range, in each combination of cycle state and male partner. Females appeared to respond most at full swelling and in deflation.

shows that these gradings coincided in 60.1% of cases, and because they were not independent only vocal response is considered below. The female vocal response appeared more intense in those intromissions in which the male showed the pause (Table 7.XX). However, not only was vocal response linked to the pause, but so also was it affected by cycle-state (Fig. 7.8): all classes of male received greater response at full swelling. The considerable variance in this figure is because females varied widely in responsiveness, even under the same conditions (Table 7.XXI: Appendix II).

These pooled data therefore suggested that cycle state, male ejaculation, and female response were related variables. But the pooled data could not be analysed since they comprised different contributions in each cycle state from particular females who varied in responsiveness and whose identity affected the probability the male would ejaculate. For analysis therefore, the data were broken down into subsets, separating _all_ variables except the two being compared, and treating each subset as an independent sample. For example, the relation between male pause and female response was examined within every possible combination of female identity, cycle-state, and male-class. The nul hypothesis in each case was that the independent variable would be in constant proportion in the two conditions of the dependent variable: for example, that females would show full vocal response equally in mounting _with_ or _without_ the ejaculatory pause. This was tested in every subset of female/cycle-state/male-class for which data were available, and variations scored merely _greater_ or _less than_ expected. Then the proportions of subsets greater or less than expected were compared with 50:50 expectation by sign test, two-tailed.

7.10.3 Detailed findings

All the data here described are shown in Appendix II, Tables 7.XXII to 7.XXVI.

Hypothesis 1: Male classes differ in the proportion of intromitted mounts in which the ejaculatory pause occurs. From data in Table 7.XXII, adult males paused more than did subadults in 4 of 9 cases (n.s.), and adult males paused more than did immatures in 9 of 11 cases (n.s.).

Hypothesis 2: The likelihood of ejaculatory pause differs in each cycle state. The data in Table 7.XXIII show that males paused proportionately more with fully swollen than with inflating females in 9 of 13 cases (n.s.), and that males paused more with deflating than with fully swollen females in 4 of 9 cases (n.s.).

Hypothesis 3: Females' response to intromitted mounts is affected by the class of the mounter. Table 7.XXIV shows that adult males received greater response than subadults in 3 of 8 cases (n.s.), and that adult males received greater response than immatures in 7 of 15 cases (n.s.).

Hypothesis 4: The intensity of female response differs in each cycle state. It is evident in Table 7.XXV that females gave full response more often at full swelling than in inflation, in 16 of 19 cases ($p < .01$). However, full response was only more frequent at deflation than full swelling in 2 of 6 cases (n.s.).

Hypothesis 5: Female intensity of response is affected by the presence or absence of the ejaculatory pause. Table 7.XXVI shows that full response was more frequent in copulations with the pause in 16 of 20 cases ($p < .02$).

Conclusions: By the procedure of holding constant all variables and then comparing two at a time, there is evidence that females' full vocal response was more likely (a) at full swelling than in inflation, and (b) in those mounts in which the male showed the ejaculatory pause. It seems likely also that other relationships would have been found (e.g. ejaculation/cycle state) with more data.

7.10.4 Discussion of intromitted mounts

Hall (1962) and Saayman (1970) noted that the females' response to copulation appeared to be involuntary, and Saayman suggested that it was consummatory and led females to prefer adult males as sexual partners. Chacma baboons give the copulation call in the majority of intromitted mounts (92%, Hall, 1962; 100%, Hamilton & Arrowood, 1978), but olive baboons do so less frequently (10%, Ransom, 1971; 30%, Hall & DeVore, 1965). The yellow baboons at Ruaha appeared intermediate between these two extremes: the full copulation call was given in 62% of intromitted mounts, and no call at all in 10% (Table 7.XIX). As elsewhere, the females' response appeared involuntary; there are reports of females giving the call during defecation, and when an adult male walks close by. The latter was seen several times for the sick female F11: she also gave the call when wading in leg-deep water, and as she sat on a branch, suggesting it was elicited by tactile stimuli (also Deputte & Goustard, 1980).

The proportion of adult males' intromitted mounts which included the ejaculatory pause (54.8% at full swelling, 50% overall) compares with 18% for chacma baboons (from Saayman, 1970), 60% for olive baboons (Ransom, 1971; Owens, 1976) and 74 to 78% for yellow baboons at Amboseli (Hausfater, 1975). Female cycle-state did not consistently affect the proportion of ejaculatory mounts (despite the pooled data in Table 7.XVI) which is as reported for gelada by Dunbar (1978a). The fact that immature males showed the pause in 18% of intromitted mounts aligns them again with olive baboons, which show this pattern (0-25%, Owens, 1976) rather than chacma, which do not (Saayman, 1970). This difference may therefore reflect the series-mounting which is reported for chacmas in contrast to the single-mount copulations of olive baboons (Hall & DeVore, 1965).

Females' vocal response seemed unaffected by the age of the male (cf. Hamilton & Arrowood, 1978), but was more intense at full swelling (as found for younger males, but not full adults, by Saayman, 1970; and Ransom, 1971). However, the most striking finding was that females were more likely to give full copulation calls after those mounts in which the male had ejaculated (also Deputte & Goustard, 1980). Macaque females also show a clutching response which coincides with male ejaculation (Slob _et_ _al_., 1978) which some consider may represent orgasm (Zumpe & Michael, 1968; Chevalier-Skolnikoff, 1974; Wolfe, 1979). Thus female responses may _well_ be called consummatory: for example, Zumpe and Michael(1977) found that females solicited males _more_ after the male had ejaculated.

Even though call and ejaculation may coincide, it is not necessarily true that ejaculation causes the female response. There may be changes in the female which promote both the ejaculation (Allen & Lemmon, 1981) _and_ the female response. Although adult males did not ejaculate more at full swelling, they _tended_ to ejaculate more with the two females who underwent _subsequent_ rather than resumption cycles (Table 7.XVIII), although the two types of cycle did not differ significantly in this (U = 6, n 4,5, n.s.), nor did these females call more (Table 7.XXI). Also, the clutching reaction of rhesus females begins _before_ ejaculation (Zumpe & Michael, 1968) and there is recent evidence that orgasm may be accompanied by uterine contractions in stumptail macaques (Goldfoot et al., 1980). Against all this, however, Evans (1974) found that olive baboon females gave the call more in mounts when males did not ejaculate, and Saayman (1970) considered response to be independent of ejaculation.

11. DISCUSSION

7.11.1 Physical features of the female cycle

a) Can males detect ovulation? Neither male nor female gametes remain viable in the female reproductive tract for very long: in humans, sperm survive up to 48 hours, ova only for 24 (Restall, 1967, Thibault, 1972). If males could recognise the time of ovulation, their reproductive effort would be more efficient and more successful; but what cues might they use? Absolute swelling size, which varies between females, can be discounted, but there is a transient lapse in swelling-size around d-3 or d-2 (Gillman, 1937; Gillman & Gilbert, 1946; Hendrickx & Kraemer, 1971; MacLennan & Wynn, 1971; Evans, 1974) apparent in three cycles at Ruaha (d-4 & d-1). In some females, the vagina showed a whitening of the lower lip, or a tendency to open, which in some cycles coincided with increased consortship.

Olfactory cues might also be available. Vaginal fatty acids which affect mating in rhesus monkeys (Michael & Keverne, 1968) also occur (albeit at lower concentrations) in baboons, peaking at midcycle (Michael et al., 1972). Internal changes near ovulation, which males might detect, include epithelial shedding (Zuckerman & Parkes, 1932), increase in leucocytes (Gillman, 1937) and mucus (Hendrickx, 1967), and release of glycogen (MacLennan et al., 1971) which may be converted to lactic acid (Katzberg, 1967). Bacteria may play a large part in the production of these acids (Michael et al., 1972), so that they are not true pheromones in the strictest sense. However, males do sniff the vagina (Hall & DeVore, 1965; Ransom, 1971), especially in deflation (7.5.3c, also below); and they often stop consorting a female before the onset of deflation (Saayman, 1970; Evans, 1974; Seyfarth, 1978a, pers. obs. at Gombe and Ruaha), both of which suggest an awareness of olfactory state.

However, males do not behave as though they recognise ovulation exactly. Hendrickx and Kraemer (1971) found that conception probabilities were quite high between d-7 and d-1, and Seyfarth (1978a) observed conception in several cycles which were not consorted at all on d-3. Although α-males may tend to consort more on this day (Hausfater, 1975; Packer, 1979a), and secondly males appear to consort more in those cycles in which conception occurs (Seyfarth ibid.; Packer ibid.) yet in all studies, males willingly consort and compete on many days and indeed in whole cycles in which conception did not occur. Overall, it appears that males behave according to the broad probability of ovulation, but cannot detect it exactly.

Adult males therefore tend to restrict copulation and consortship to fully swollen females, and this selectivity appears to be learned because subadult males mounted inflating and deflating females at higher rates than did adults. This raises the question of what reinforces mating nearer full swelling: is it merely the willingness of the female to mate, or are there tactile cues during copulation (e.g. Erikson, 1967)? Either of these could become associated with particular olfactory stimuli.

7.11.1b) The function of the swelling If swellings do not signal ovulation, but merely bracket its occurrence very widely and indicate a probability which is at no time very high, what then is their function? The strongest evidence may be found in their distribution among Catarrhines: although swellings are more common in some lineages, yet their distribution coincides more closely with social organisation. They more frequently occur in species that usually live in multi-male groups (Clutton-Brock & Harvey, 1976; Short, 1979; Sadler, 1980). Struhsaker and Leland (1979) suggest that this is in part because swellings would facilitate the α-male's monitoring of female reproductive state, allowing him to tolerate other males as group residents (for other benefits). Conversely, without swellings the α-male would have to exclude rivals, forming a one-male group. However, there is convincing evidence that social organisation is determined primarily by the feeding strategy and dispersion of females (Wrangham, 1980), and that if this permits formation of multi-male groups, swellings will then be favoured as a device for mate-selection. That is, they may attract a range of males for comparison and active selection by females (Harcourt & Stewart, 1977; Tutin, 1979a) or they may induce competition between males in which stronger or higher-ranking males would be favoured (Clutton-Brock & Harvey ibid.; Cox & LeBoeuf, 1977).

Two other functions may be suggested. First, swellings might attract immigrant males from other groups, enhancing outbreeding and intensifying male-male competition. This is supported in that adult males migrate into troops containing more cycling females (Packer, 1979a), and in that cycling females may move so as to maximise the chances of encountering other troops (Packer ibid.; Rasmussen, 1979). Reduction of inbreeding might also explain the presence of swellings in the one-male groups of hamadryas; females transfer between units and between bands (Sigg, Stolba et al., in press), and the presence of swollen females increases the chances of male-male conflict in which female transfer may occur (A. Stolba, pers. comm.). This does not however explain their rarity in other species living in one-male groups, unless the probability of male takeover is there determined more by the strength of the unit-male than by the number of females in the unit (e.g. Dunbar & Dunbar, 1975, p.112).

Finally, the extended period of swelling may even have been selected to conceal the time of ovulation. If males bias their protectiveness to the infants of females with whom they have mated (Altmann, 1980; but cf. Seyfarth, 1978b; Packer, 1980; also Angst & Thommen, 1977) a female may secure more protection for her infant by mating with a variety of males (Hrdy, 1979b), and this would be facilitated by the attractiveness and duration of the swelling. Such behaviour might also reduce the likelihood of infanticide (Altmann et al., 1978) as suggested for the pseudo-estrus of Hanuman langurs (Hrdy, 1977, p.284).

7.11.1c) Why repeat cycles? Two of these arguments, (active mate-selection, and the possibility of inducing male protectiveness) may also offer advantage in the fact that females cycle several times before conceiving (Means of 4.3 times at Ruaha, 4.4 at Gombe (unpubl. data), c 4.0 at Amboseli (Altmann et al., 1978)). However in proximate terms this may merely indicate that the reproductive system must cycle a few times before it is ready to conceive. First, hormonal feedbacks might not at first be fully expressed: which is supported in that the resumption cycles showed less consortship, suggesting that females were less attractive and their oestrogen levels perhaps lower (Keverne, 1976).

Secondly, early cycles might be anovulatory if prolactin levels are raised by persistent suckling (Short, 1976 & refs. therein; Bowman et al., 1978). Thirdly the nutritional drain of lactation (Altmann, 1980) may affect reproductive cycles (Frisch & McArthur, 1974; but cf. Huffman et al., 1978): this is suggested by the fact that five females resumed cycling within one week after the onset of the rains, although it is not certain that food availability had sufficiently increased by then. Overall, hormonal and nutritional explanations for repeated cycling are equally supported by the fact that females who miscarry or lose young infants resume cycling sooner, and take fewer cycles to conceive, than those who do not (Altmann et al., ibid.).

7.11.1d) The copulation call The female copulation call is typically restricted to the period of swelling. It indicated here (a) that a female had just been mated, and (b) a probability that the female was near ovulation (i.e. fully swollen) and had been inseminated; it also probably revealed her identity (Hamilton & Arrowood, 1978). Because it may clearly inform males of these details, it might also induce male-male competition (as in Cox & LeBoeuf, 1977). Although rival males seldom responded immediately to this call, yet their interventions in mating pairs were anyway seldom direct (Chapter 8). Therefore the copulation call may share this function with the swelling; Struhsaker (1975, p.111) noted that calls and large swellings were found in the same subspecies of red colobus. The rarity of copulation calls in hamadryas (Stolba, pers. comm.) is also consistent with this hypothesis, but the copulation-call of gelada cannot be explained in the same way (Dunbar & Dunbar, 1975; Mori, 1979, Ch. 7).

7.11.1e) Summary Overall, the lack of an exact index of ovulation, the conspicuousness of the swelling, the information content of the copulation call, and the duration and repetition of oestrus, all appear to increase the costs of mating for males. That is, they were associated with much consortship and some aggressive competition, at times when conception did not occur. The arguments above suggest that this may benefit the females in terms of mate-selection and possibly protection for their infants.

7.11.2 The behaviour of male and female

a) Female behaviour Laboratory studies of macaques have isolated three components of female mating behaviour. These are proceptivity (Beach, 1976), receptivity and attractiveness (Keverne, 1976). The Ruaha females gave evidence of greater receptivity at full swelling in that they avoided fewest mounts at this stage. This suggests that they were behaviourally more receptive, or that intromission was easiest at this time. However, males sometimes showed laboured pelvic thrusting, and sometimes problems in intromitting, even on fully swollen females. Conversely, a male intromission attempt on d+2 caused a female to shake as though in pain. Attractiveness also appeared greatest at full swelling. At this time adult males gave more rear-greetings, (of which more were unsolicited), and showed more consort behaviours, time in consort, and agonistic takeovers; and mean rates of intromitted mounts were particularly high. However, males' responses to presents were <u>not</u> greater (also Chalmers & Rowell, 1971), perhaps suggesting that they were more inhibited from response to fully swollen females (5.7.3c). Finally, males' inspection of the swellings became proportionately more frequent in deflating and flat stages (also Hausfater, 1975; Dunbar, 1978a; Seyfarth, 1978a) as though the condition of the female was less evident than it had been at full swelling (also Goodall, 1968).

Two patterns which appear proceptive (standing next to, and grooming the male) were most frequent at full swelling. However presenting, which is often interpreted as a proceptive pattern (Beach, 1976) was not generally more frequent at this time (7.5.3b). Rather, it was more frequent in resumption cycles, that is, cycles in which males consorted less. And for female F5 it was most frequent in the cycle in which her usual male consort did <u>not</u> consort her. This pattern agrees with Seyfarth's (1978a) observation that swollen females <u>desist</u> from presenting once they are in consort, true also of olive baboons at Gombe (pers. obs.). Evans (1974) also noticed a decline at full swelling. Presenting obviously emphasises the visual stimulus of the swelling, and possibly olfactory stimuli: but females did not always accept mounts they had elicited by presenting, and since it was so seldom responsible for initiating copulation (5.5.1, 7.5.3c) it may instead function to solicit male possessiveness and consortship. It may also express preferences for particular males (8.4.5a).

The cycle of the sick female F11 was unusual in that although she showed a normal swelling, presented quite frequently, and was responsive (by copulation call) to tactile stimuli, yet she received few mounts and no possessiveness, and appeared to be unattractive.

7.11.2b) Male behaviour A male can increase his relative mating success by fertilising as many females as possible, and by preventing other males from doing so. If ovulation-probability can only by roughly estimated, males might be expected to circulate among swollen females, mating frequently, and reproductive success would depend on gamete output. There is indeed some evidence that selection has favoured high sperm production in males (Collins, 1978). Two factors however would militate against the success of this. First, it is often the case that only one female is in oestrus at a time, in which case mating success would be assured for any male who could both copulate and guard her, at no cost in terms of opportunities lost to mate other females. Secondly, if competition was only at the level of mating frequency, the success of a male would be affected less by his ability to produce sperm than by the number of his competitors. If there were many males, each male's chance of fertilising any one female by completely promiscuous mating would be so low that he would gain less by searching for other mates than he would by staying to guard any female with whom he had just mated: i.e. monopoly would be more important than inseminating ability. Consortship is therefore comparable to the female-guarding discussed by Parker (1974).

The behaviours whereby male baboons monopolise swollen females constitute extreme social possessiveness (Kummer, 1973). The consort relationship is less reciprocal than that reported for macaques (e.g. Carpenter, 1942a), in that the male follows the female and initiates most interaction. His behaviour appears to achieve monopoly in three ways.

1. by reassuring the female; e.g. grooming.
2. by preventing her interacting with other males; e.g. by herding, shielding, and by grooming which causes her to stay close.
3. by advertising the consortship to rival males; e.g. any of the behaviours above makes it obvious that a pair are in consort, and this may inhibit rivals (8.5.2). For example mounting was quite often an apparent response to the presence of rival males or other troops.

Male consort behaviour includes less aggressive or coercive behaviour, to shape the responses of the female, than is reported in macaques (examples given by Carpenter, 1942a; and Lindburg, 1971, p.66) and chimpanzees (Goodall et al., 1979, p.50; Nishida, 1979). Possibly the greater sexual dimorphism in baboons dictates that the male's priority is to overcome the female's fear of him rather than to enforce her co-operation. However, coercion was seen during herding, and occasionally preceded mounting.

Overall, consortship was the means by which higher-ranking males attained greater mating success (Ch. 8), and it also excluded the subadult and immature males from access to mate with some fully swollen females. Their consortship also was selective (8.4.2).

7.11.3 Comparison with the hamadryas mating system

Hausfater (1975) has pointed out that the short-term relationships within consort pairs of savanna baboons (i.e. chacma, yellow and olive) are very similar to the long-term relationships whereby hamadryas males monopolise females of their units. Many of the possessive and coercive behaviours which savanna males direct especially to their consorts are used by hamadryas males to shape the behaviour of females in all reproductive states (also Cheney & Seyfarth, 1977). The male neck-bite and female following response have been given particular prominence in this respect (Kummer, 1968), but they are less often given when the hamadryas female is in oestrus, at which time the unit-male follows and grooms the swollen female and generally behaves much more like a savanna consort male than usual (Kummer ibid.). Thus the main contrast in the species' behaviour is in males' relationships to non-swollen females.

The mating pattern of the savanna males is apparently permitted by the females' tendency to form female-bonded groups which can monopolise patches of high-quality food (Wrangham, 1980). Males reside temporarily or permanently in these groups, establishing comparatively loose, non-exclusive relationships among a wide range of females, which become exclusive only at oestrus, to preclude sperm competition. These relationships also permit males to protect possible offspring, but paternity is uncertain due to promiscuous mating.

In contrast, because of the sparser pattern of food availability, hamadryas females do not form female-bonded groups (Wrangham, 1980). Although in theory the males might associate loosely with a large number of females, consorting opportunistically, they do not. Instead, they establish long-term exclusive relationships with a small number of females, which include mating. Similar long-term bonds <u>may</u> occur in savanna baboons, but they are seldom as exclusive (Seyfarth, 1978b). It is not clear why hamadryas males do not consort at random, but two arguments favouring long-term bonds with fewer females are as follows. First, hamadryas have a much longer day-range (Kummer, 1968; cf. Altmann & Altmann, 1970), and it may be too costly energetically for a male to compete with others for consortship over the entire week of oestrus (by analogy with Dunbar, 1978a). Secondly, if hamadryas females naturally tend to disperse in very small groups (as implied by the patterning of their food), males who associated and mated widely among such females would reduce their opportunity for protecting their offspring, and increase the risk of infanticide. Therefore longer-term bonds assure both mating access and certainty of paternity, allowing male protection of offspring.

CHAPTER 8

Mating Competition and Mate Selection

1. INTRODUCTION

8.1.1 The theory of sexual selection predicts that male baboons may increase their reproductive success by maximising the number of their fertile matings, and that this will lead to competition between males. In contrast, female's reproductive success is more directly affected by energetic efficiency and parental care, but they may improve the quality of their offspring by selecting mates of high quality (1.3). Female baboons spend only a small part of their lives in the fertile stage of the menstrual cycle, and show no strong tendency to cycle in synchrony nor to breed seasonally. This means that in a multi-male troop there are usually very few females receptive at once, but that all the resident males are available to mate; the scope for both male competition and female choice is therefore intensified. However, competition between females and choice by males may still be expected but to a lesser degree.

There are several reports emphasising mating competition between males, notably from Zuckerman (1932), Maxim et al. (1963), DeVore (1965), Hausfater (1975) and Packer (1979a & b), although in other studies it was not evident (Hall, 1962; Rowell, 1967a; Saayman, 1970; Seyfarth, 1978a). Secondly, most authors have at least suggested that females may show preference for particular males (Marais, 1939; DeVore, 1965; Rowell, 1967a; Hausfater, 1975) and data are provided by Saayman (1970), Seyfarth (1978a,b), Packer (1979a,b) and Rasmussen (1980). There is also some evidence of female competition (Hall, 1962; Seyfarth, 1976): and males are reported to consort selectively (Ransom, 1971; Packer, 1979b) or occasionally to refrain from consorting with particular females (Saayman, 1970; Seyfarth, 1978a; Packer, 1979b).

The following sections document the pattern of non-random mating in the study troop. This is described first in terms of competition within each sex (part 3), examining in particular whether male dominance rank was related to mating success, and why. Secondly, an attempt is made to identify which pairs mated particularly frequently, and to see how such partnerships were formed (part 4) to estimate the importance of mate selection. Initially, however, it is necessary to determine how mating is to be quantified (part 2).

2. QUANTIFYING MATING: mounting, copulation, and consortship

8.2.1 In this study, the male's rigid pause at the end of thrusting during intromitted mounts was used as an index of ejaculation (as in Saayman, 1970; Evans, 1974; Hausfater, 1975; Packer, 1979a). The pause usually coincides with ejaculation during masturbation (Ransom, 1971). Because adult males only showed the ejaculatory pause in 54.8% of their intromitted mounts with fully swollen females, each male's rate of intromitted mounts would have provided an overestimate of mating success (in terms of possible inseminations). In their incidence of ejaculations per mount, the Ruaha baboons were intermediate between olive and chacma baboons (7.10.4). This reflects the fact that they sometimes ejaculated after only a single mount, as do olive baboons (Hall & DeVore, 1965; Ransom, 1971), but at other times only after a number of mounts, as do chacmas (Hall, 1962; Saayman, 1970; also hamadryas, Kummer, 1968). In many intromitted mounts it was not possible to see clearly whether the pause had occurred or not, and so in order to assess whether ejaculation might have occurred it was necessary to examine their distribution in time.

8.2.2 Intervals between mounts and between ejaculations

Table 8.I shows that only in a minority of cases were non-ejaculatory mounts caused by the female leaving or by other animals interrupting: in the majority, the male appeared to withdraw voluntarily. Fig. 8.1 shows the length of intervals between intromitted mounts of particular pairs of animals: mounts were very often repeated within 10 minutes, but with a second peak between 40 and 50 minutes later. This second peak was not found for subadult males, but data were scanty. Fig. 8.2 confirms how particular pairs tended to mount between one and four times at intervals of just under an hour.

The few reliable records of inter-ejaculation intervals of particular males are given in Table 8.II: most fell within 20 and 60 minutes, and if those greater than 140 minutes are excluded (because individuals were not continuously observed) the mean interval was 45.1 minutes, coinciding well with the second peak in Fig. 8.1 and the main intervals in Fig. 8.2. Only one interval was less than 20 minutes. The implication is that males may ejaculate about every 45 minutes, but that several mounts may accompany each ejaculation.

Table 8.I: Termination of mounts. The number of intromitted mounts at full swelling by adult and subadult males in which the termination was visible : the percent of each type.

	Incomplete			Complete	Total
	Male dismounts	Female leaves	Other Interrupts.	Male attains pause	
Adult males:	32.3	10.8	2.2	54.8	93
Subadult males:	54.2	0.0	4.2	41.7	24

Table 8.II: Males' intervals between successive ejaculatory pauses, in minutes.

4, 24, 24, 40, 43, 45, 50, 50, 54, 57, 57, 60, 78, 142, 173, 210, 297.

Table 8.III: The single- and multiple-mount copulations of each male, with female partners at full swelling. In brackets are shown the number of intromitted mounts which contributed to the multiple-mount copulations.

	Copulations.			Percent of copulations which were multiple-mts.
Males	Single	Multiple.	(mounts) (contrib)	
A1	26	7	(22)	21.2
A2	11	5	(10)	31.3
A3	33	9	(25)	21.4
A4	19	18	(43)	48.6
A5	12	3	(10)	20.0
A6				
A7	11	4	(10)	26.7
A8	3			0.0
S1				
S2	9	1	(2)	10.0
S3	13	4	(12)	23.5
S4	11	3	(6)	21.4

Fig. 8.1

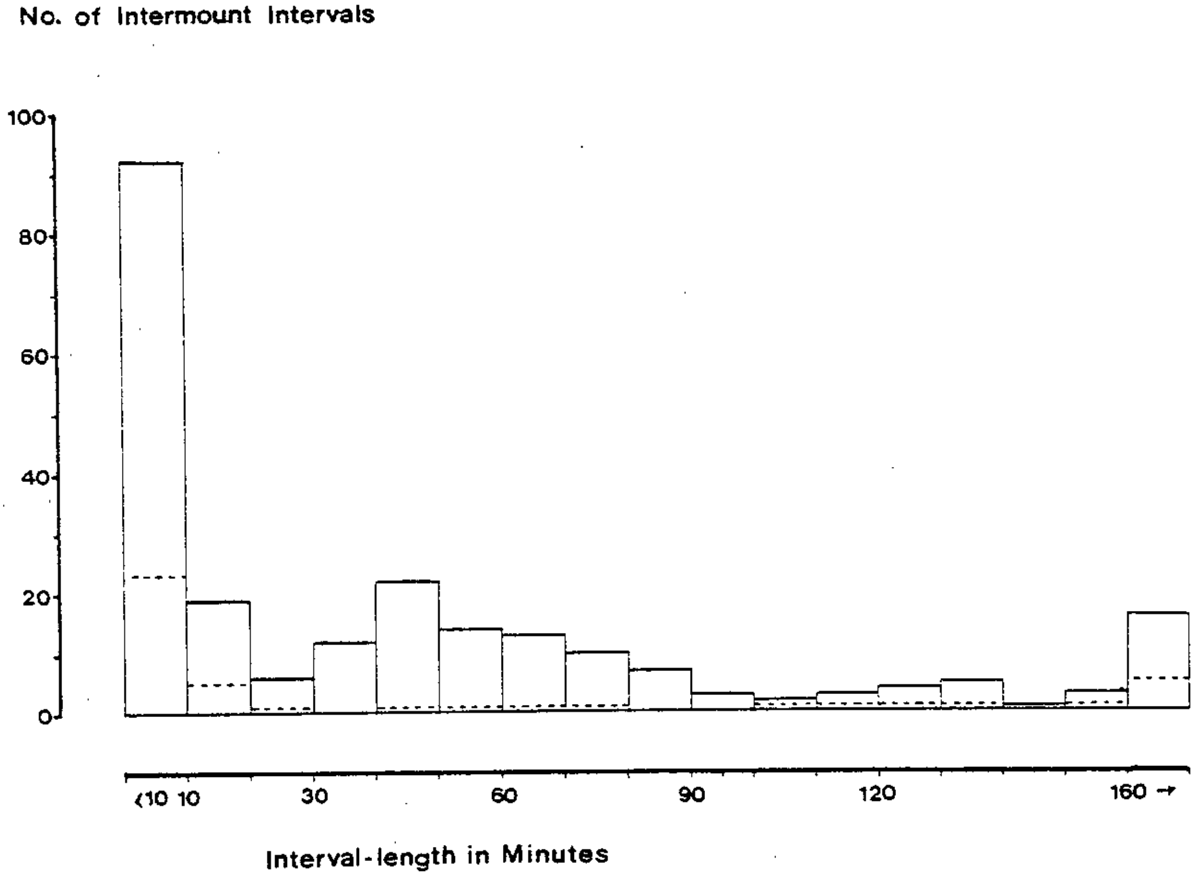


Fig. 8.1. Intervals between mounts. The number of intervals of different lengths between consecutive intromitted mounts within the same pairs of animals. The dotted line shows the proportion contributed by subadult males. The mean duration of observation on the days concerned was 340 minutes. N = 232 intervals.

Fig. 8.2

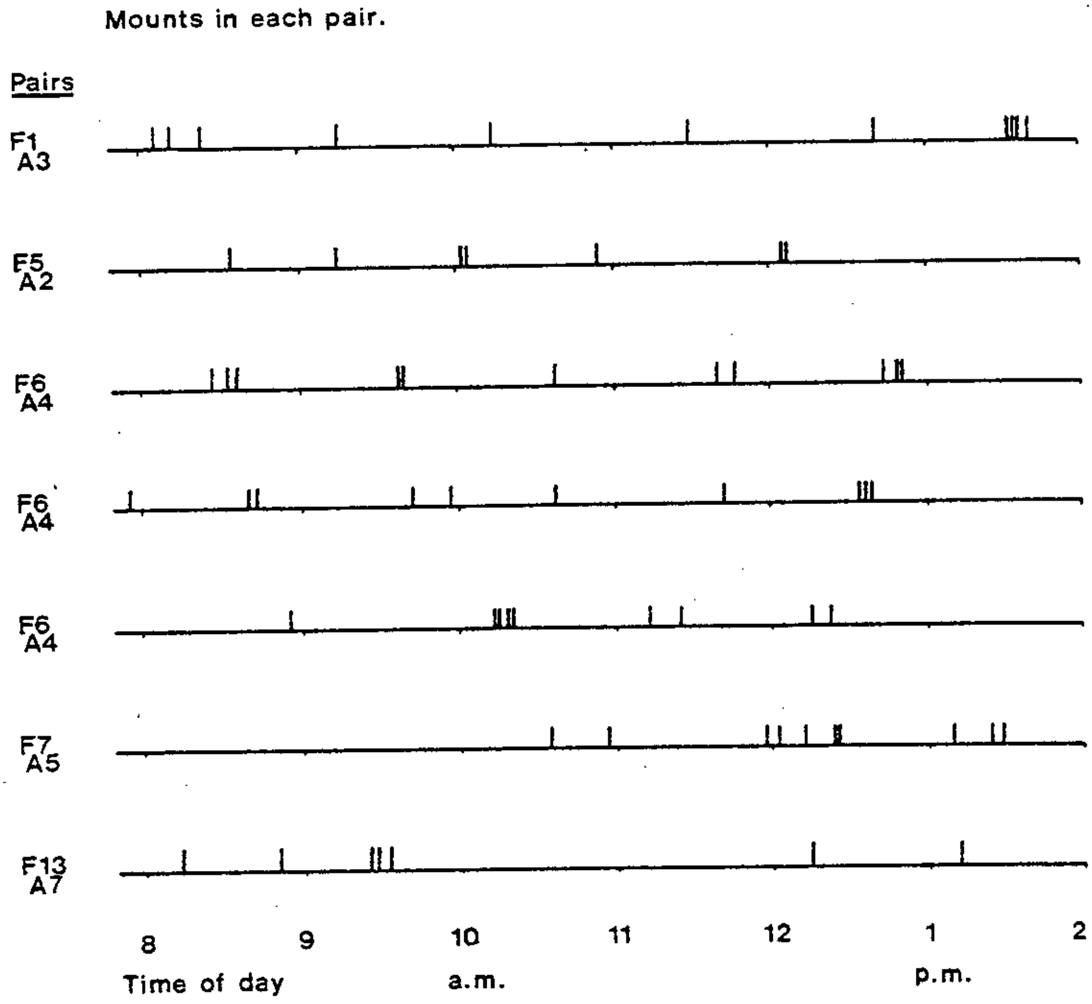


Fig. 8.2. The distribution in time of intromitted mounts between particular pairs on several days of the study. The pairs were not continually in view, so that more mounts probably occurred than were seen.

Therefore a copulation (or possible insemination) was defined as one or more intromitted mounts between any pair, separated by an interval of 20 minutes or more. If mounts were closer in time, they were included within the same copulation. Table 8.III compares the males for the proportion of their copulations so defined which included multiple mounts, with females at full swelling. Adult males showed multiple mounts in an average of 24.2% of their copulations, accounting for 51% of their intromitted mounts, while subadult males did so in 18.3% of their copulations, accounting for 38% of their intromitted mounts.

8.2.3 Grouped mounts compared with single mounts

There were up to five mounts within each group/copulation ($\bar{x}$ 2.7 for adult and 2.5 for subadult males). When copulating with fully swollen females, all seven adult males testable showed the ejaculatory pause less often in grouped mounts than in single ones (32% of 50 mounts in groups, cf. 76% of 46 single mounts: Sign test across seven males, $p < .02$). For subadults, in contrast, the pause was equally likely in mounts isolated or grouped (i.e. in 37% of 27 mounts of both types).

8.2.4 The incidence of the pause within a series

Within any pair's sequence of grouped mounts, the ejaculatory pause was more often seen in the final mount (Table 8.IV), although data for subadults are inconclusive. In only two of 20 well-observed groups of mounts by adult males was the pause seen twice - at intervals of 4 and 24 minutes. Continuous observation of particular pairs also confirmed that ejaculation tended to be in the final mount of a series.

8.2.5 Copulation and consortship

As many as 78.9% of the copulations between adult males and fully swollen females occurred during consortship (n = 162). During inflation, only 11.4% were in consort (n = 32), and during deflation 27.3% (n = 11). In contrast, subadult males achieved most copulations without consorting; the percentages in consort were 2.1% in inflation (n = 47), 2.4% at full swelling (n = 41), and none in deflation (n = 11). This difference between adult and subadult is confirmed in that the number of copulations seen between any pair was related to the amount of time they spent in consort for adult males (r_s .826, over 48 pairs, $p < .001$) but not for subadults (r_s .134, over 24 pairs, $p > .20$ n.s.).

Table 8.IV: The incidence of ejaculatory pause within any multiple-mount copulation, according to whether seen on the first, last, or any intermediate mount.

	First	Intermediate	Last	
Adult males:				
Without pause	18	16	7	
With pause	4	1	15	χ^2 20.2 df 2. $p < .001$
Subadult males:				
Without pause	7	2	6	
With pause	1	0	3	no test

Considering the six adult males who consorted and copulated most frequently, 34.0% of their copulations in consort comprised multiple mounts (n = 126 copns.) but only 8.3% of copulations between non-consorting pairs did so (n = 34 copns.). All six males showed this tendency. Multiple mounting was not obviously a characteristic of any particular cycle-state, or male or female subject, but was conspicuously frequent between A4 and F6 (64% of 22 copulations: the maximum of any other pair was 33%).

8.2.6 Conclusion

These data suggest that the best estimate of males' mating success is their rate of copulation (as here defined) rather than consortship. Although copulations in consort are probably more effective against sperm competition, yet because males achieved a substantial number of copulations outside consortship (particularly subadult males) and because consortship was anyway loosely defined, copulation rate at full swelling provides the most accurate measure of mating success in this study.

3. MATING COMPETITION

8.3.1 Male competition over females is generally expected to favour the mating success of higher-ranking males. Most strictly, Altmann (1962) proposed that a male's access to females would be directly proportional to his dominance rank. For example, a third-ranking male would only be able to mate on days when three or more females were simultaneously receptive; on other days, the first and second rankers would monopolise the females. Although studies of multi-male troops do not reveal such a linear relationship, yet most of them show that in the short-term at least, higher-ranking males achieve more matings. This has been repeatedly demonstrated in macaques, by Carpenter (1942b), Tokuda (1961-2), Conaway and Koford (1964), Kaufmann (1965), Suarez and Ackerman (1971), Hanby *et al*. (1971), Lindburg (1971), Stephenson (1974), Taub (1980a) and others. A weak association between rank and paternity (determined biochemically) was found by Duvall *et al*., (1976: further described in Symons, 1978, p.162) and a stronger relationship by Smith (1981). Only a few studies report that rank has little or no effect in macaques (e.g. Loy, 1971; Drickamer, 1974a; Eaton, 1978).

Relatively high mating success has also been found for higher ranking male langurs (Curtin, 1980), red colobus (Struhsaker, 1975), vervets (Struhsaker, 1967), and weakly for mangabeys (Struhsaker & Leland, 1979); but not for lemurs (Jolly, 1967). It is also reported for chimpanzees at Mahale Mts. (Nishida, 1979) but not at Gombe (Tutin, 1976; Bygott, 1979).

Several studies of baboons describe competition among males whereby the higher-rankers attain more matings (DeVore, 1965; Hausfater, 1975; Packer, 1979b; Rasmussen, 1980), and even when competition is minimal the highest ranker may still do better (Hall, 1962; Seyfarth, 1978a). Also among immatures, high rankers may mate more (Cheney, 1978). However, both Hausfater (1975) and Packer (1979b) concluded that lower rankers did better than expected (compared with Altmann's model), and DeVore (1965) and Saayman (1971b) also observed low ranking adults who mated particularly often.

In interpreting such findings, four caveats are important. First, in some early studies, male access to females was used as a criterion of dominance (e.g. Bolwig, 1959), so that some relation between dominance and mating success became inevitable. Secondly, the apparent success of high rankers in some studies may have been because the lower rankers tended to mate more under cover: thus Drickamer (1974a) found that the correlation between rank and mating success was removed when the males' scores were corrected for their observability differences (2.XIc). Thirdly, just as levels of competition may vary between troops (Maxim *et al.*, 1963; DeVore, 1965; Paterson, 1973), so also the relation between rank and mating success may change with time: thus Eaton (1974) was unable to find such a relationship in a macaque troop in which it had been earlier demonstrated by Hanby *et al.* (1971). Finally, a relationship between rank and mating success may be merely an effect of age: this is not only true of correlations which include immature animals, who tend to be low rankers *and* infrequent maters (Loy, 1971), but also among adult males. Adult baboons' ranks are related to age in a ∧- shaped way (Packer, 1979a), and rank turnovers may be quite frequent (Hausfater, 1975). There is yet no evidence that individual differences in mating success, related to rank, persist throughout life although a recent simulation by Saunders and Hausfater (1978) suggests that they would.

The following section compares the males' mating success in terms of their dominance ranks and thereafter in relation to other details of competition. Finally, female competition is briefly examined.

8.3.2 Individual differences in number of copulations

Individuals were compared for their number of copulations, involving only females at full swelling. Expected numbers were calculated in accordance with differences in their availability of copulation partners, measured in partner-hours.

Females did not differ in the amount they copulated with adult males (χ^2 5.26, d.f. 5, n.s.), even accounting for their observability differences (χ^2 5.53), although those who were only observed in resumption cycles copulated slightly less than expected. However, females did differ in their copulations with subadult males (pooling scores of some females, χ^2 25.76, corr. obs. 25.40, d.f. 3, $p < .001$). As noted in 7.6.3 this was because those consorted less by adults mated more with subadults.

Conversely, adult males differed markedly in their copulation scores (χ^2 82.08, corr. obs. 118.33, d.f. 7, $p < .001$), but there were no differences between subadults (χ^2 3.99, corr. obs. 5.70, d.f. 2, n.s.). The patterning and possible reasons for these differences are examined in parts 3 and 4.

8.3.3 Male dominance rank and mating success

8.3.3a) Altmann's model The predictions of Altmann's (1962) model, described above (8.3.1) were tested using consortship as a measure of access, since that is the means by which males monopolise females and restrict the access of others. Table 8.V compares the number of study days for which each male was present on which he consorted with a fully swollen female, compared with that expected from his rank according to the proportion of study days for which one, two, or more females were simultaneously at full swelling. It is clear that in this short study the model does not fit, specifically in that males A1 and A2 consorted less, while five others consorted more, than expected.

8.3.3b) Time spent consorting As a measure of reproductive investment, Fig. 8.3 compares the percent of time which each male spent consorting with females in each stage of the menstrual cycle, estimated from one-zero samples (2.IX). It is clear that (i) adult males consorted far more than did subadults, (ii) only A1 consorted much with inflating

Table 8.V: The number of days each male consorted with a fully swollen female compared with the number expected from his rank and the availability of simultaneously swollen females(8.3.3a).

Male:	A1	A2	A3	A4	A5	S1	A6	A7	A8	S2	S3	S4
Consort - days:	13	11	27	12	9	-	-	8	3	-	1	-
Expected:	49.1	28.5	5.2	1.3	-	-	-	-	-	-	-	-

Kolmogorov-Smirnov one sample test, $N = 84$, $D = 0.636$, $p < .01$

Table 8.VI: Males' rates of copulation with females on the third day before deflation in the cycle. Rates expressed as pooled mean rate per female - hour.

Adult males:	A1	A2	A3	A4	A5	A6	A7	A8
Rate (n = 33 copns.):	.15	.02	.10	.17	.13	-	.02	.04

Subadult males:	S1	S2	S3	S4
Rate (n = 4 copns.):	-	.02	.04	.02

Fig. 8.3

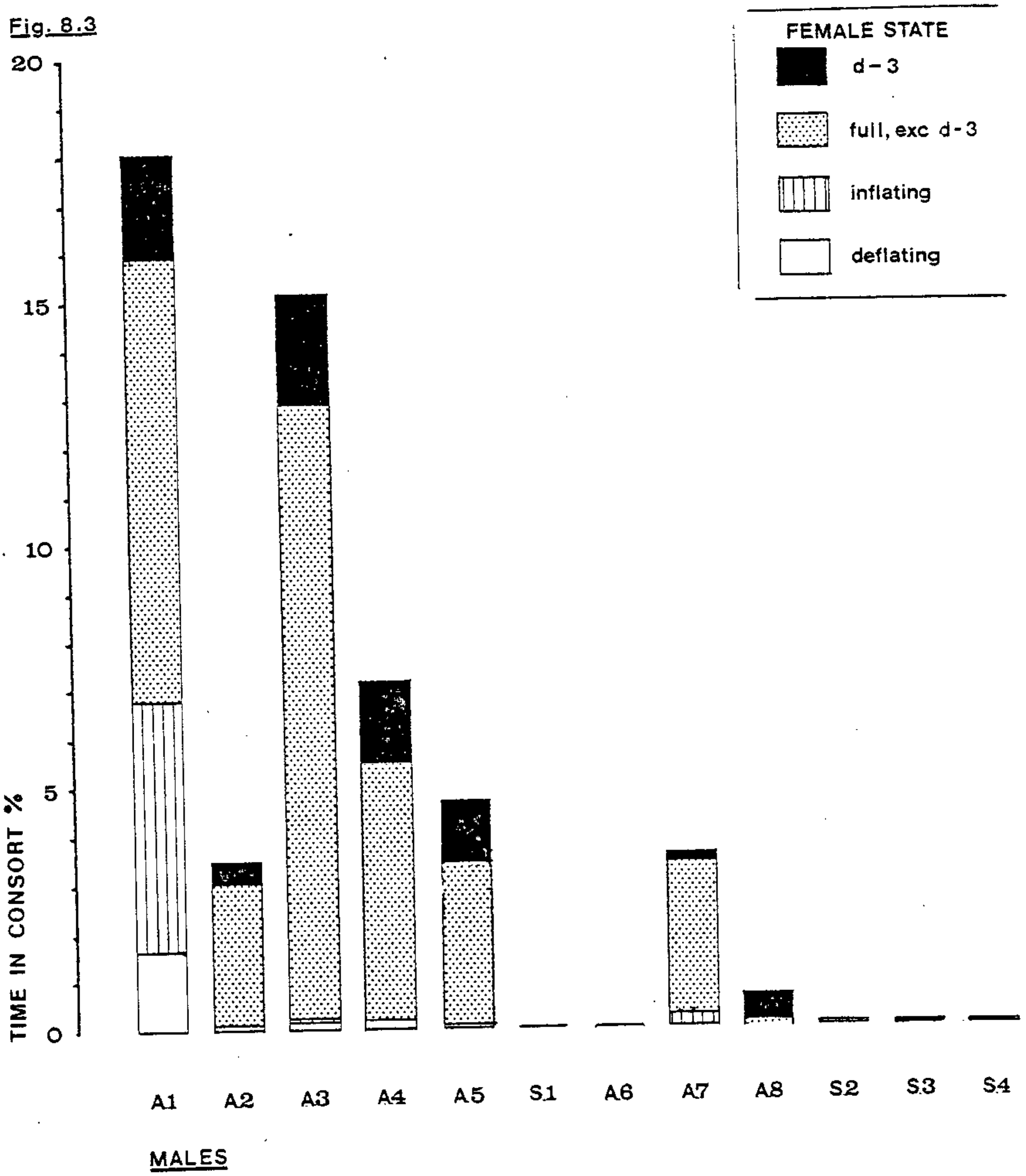


Fig. 8.3. The percent of time for which each male was seen in consort with females of each cycle state. Estimated from the percent of all 15 minute time blocs through the whole study in which the male was seen to consort (n 1860 samples). Males in order of dominance rank descending from the left; A - adults, S - subadults.

Fig. 8.4

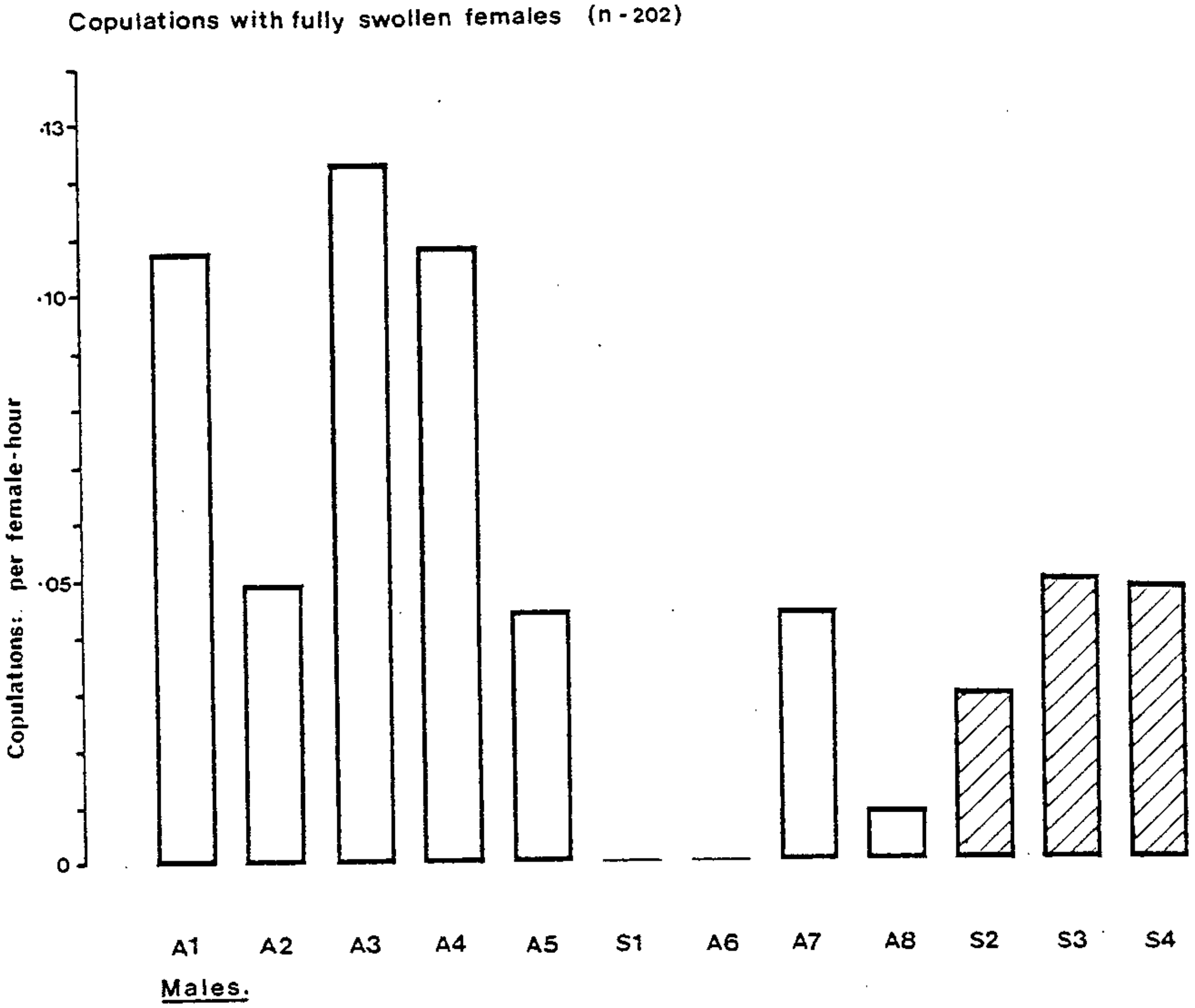


Fig. 8.4. Males' rates of copulation with fully swollen females, as pooled mean rates per partner-hour. Subjects in order of dominance rank, descending from the left; subadult males cross-hatched.

and deflating females, and (iii) with the exception of A2 and A6, the adults consorted in linear relation to their dominance rank. A6 fell ill and died, while A2 is discussed below (8.3.5).

8.3.3c) Copulation rate with fully swollen females As a measure of mating success was calculated each male's pooled mean copulation rate with fully swollen females, per partner-hour (Fig. 8.4). Among adults, copulation rate was approximately related to dominance rank (r_s .719, n 8, $p < .05$), a relationship which persisted when the males' scores were corrected for observability (r_s .810). There was no relationship for subadult males (r_s -.800 ± obs. corr., n 4, n.s.).

The same comparisons were made using only copulation rates with females on d-3 of the cycle (Table 8.VI), but these yielded no significant results either for adults (r_s .419, corr. obs. .548, n 8, n.s.) or for subadults (r_s -.632, corr. obs. -.800, n 4, n.s.), although the number of copulations underlying these data was very small.

8.3.4 Factors affecting mating success of particular males: Introduction

Although male dominance rank was related to mating success, the relationship was not linear: rather, the high- and middle-ranking adults mated more than did low rankers. Even then, A1 and A2 still consorted less than expected from their rank alone. Several authors have proposed reasons for the success of middle- and low-ranking males, and these will be referred to as they arise below. One of the reasons, female choice (Saayman, 1971) will not be discussed until part 4 of this chapter. Another factor which allows lower rankers opportunity to consort is that high-ranking males sometimes refrain from consorting with swollen females who appear to be available to them (Hall, 1963; Saayman, 1970; Hausfater, 1975; Seyfarth, 1978a; Packer, 1979b). Such abstinence might result from lack of attractiveness in the female (8.3.9), male fatigue or injury (Packer, 1979b; 8.3.12), selectivity by the male (Hausfater ibid.; Packer, 1979b) or female's preference for another male (Seyfarth ibid.; Bachmann & Kummer, 1980) both of which are discussed in 8.4.8, or asymmetry of contest (Packer ibid., discussed in 8.5.2). The following sections examine the reasons for the males' differences in mating, while admitting that these were short-term differences which might have been found to be more closely related to rank in a longer study.

8.3.5 Time of day of consortship

Hausfater (1975) found that females tended to consort with males of lower rank in the afternoon than they had in the morning. Because most observation in this study was made in the morning (2.XId.1), there may have been a bias against observing the mating of lower rankers. Fig. 8.5 suggests that this may apply only slightly to males A5 and A7, but not enough to explain their relatively low consort scores in Fig. 8.3. What is more striking is that A2 consorted much more before 9.00 a.m., and this may explain his relatively low score in that figure. Fig. 8.6 shows that 11 of his 16 consortships were in progress at the start of observations, but only three continued after 1.00 a.m. Data from all other males show 23 consortships in progress at the start, and 44 at the end of observations. It appears that he may have consorted more at night, a pattern also characteristic of a particular male at Gombe (pers. obs., male JNH in Packer, 1979b). This is probably because as a young adult he would have been more mobile in outmanoevring competitors in the sleeping trees; he was also seen to take over consortship of a female single-handedly in the evening (Oliver & Lee, pers. comm.).

8.3.6 Day-selection in consortship

Both Hausfater (1975) and Packer (1979b) found that high-ranking males concentrated their mating around the probable day of ovulation, d-3, a tendency which would give lower-ranking males the opportunity to mate at other times during full swelling. Each male's copulation rate per female partner-hour is illustrated on every day of full swelling in Fig. 8.7. While there is some evidence that higher rankers mated more on d-3 (notably A1, A3, A4 & A5), it is not entirely clear that low rankers were forced to mate earlier and later in the cycle. A3 and A4 show peaks before <u>and</u> after d-3, but this is most extreme for A7: he had eight consortships on d-1, and <u>four</u> of these were with females who had been deserted by their high ranking consorts prior to deflation.

8.3.7 Details of male-male competition: Introduction

The prediction that high-ranking males would achieve more copulation was derived from the assumption that males do compete (Altmann, 1962). Two manifestations of competition in baboons are harassment of copulations,

Fig. 8.5

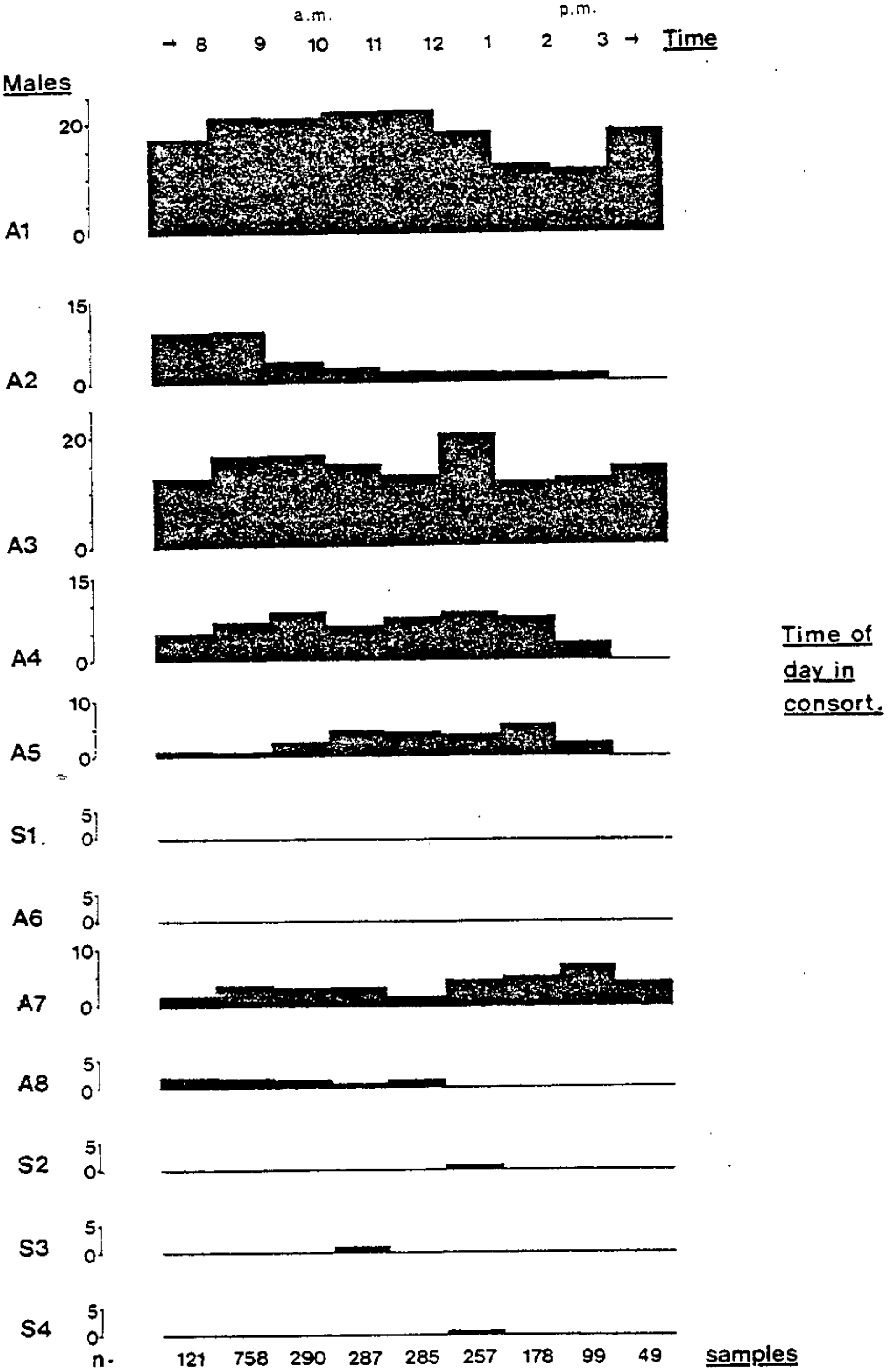


Fig. 8.5. The percent of observation time for which each male was in consort at different times of day, estimated from 15 minute one-zero samples (2.IX). Males arranged in descending order of dominance rank from the top.

FIG. 8.6

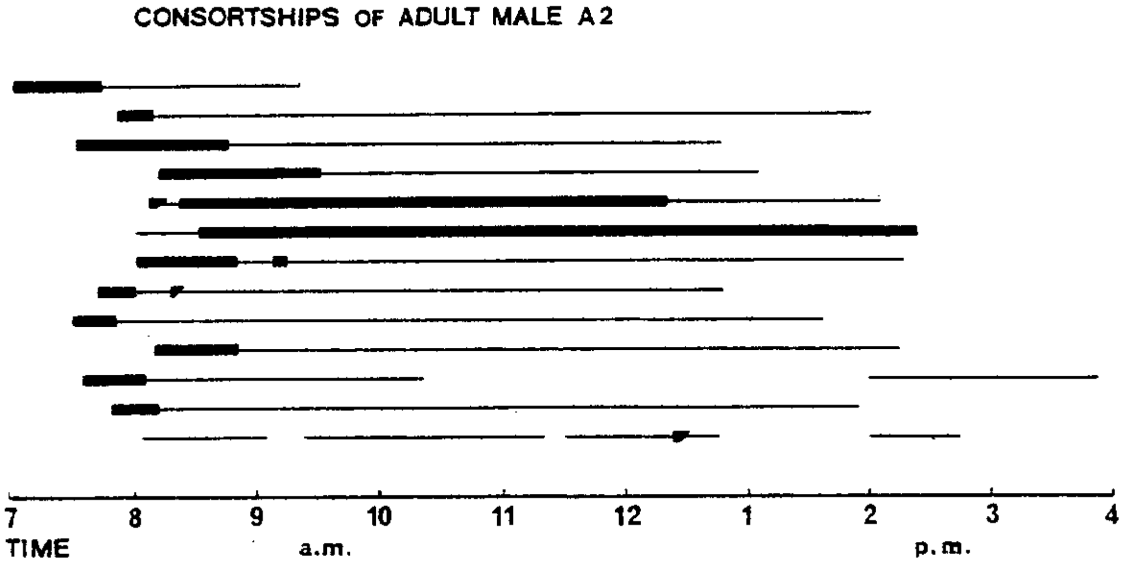


Fig. 8.6. The time of day of A2's consortships. For each day on which this male consorted, the thin line indicates the duration of observations, the thick line shows when he was in consort.

Fig. 8.7

Males' copulation rates with females on each day of full swelling

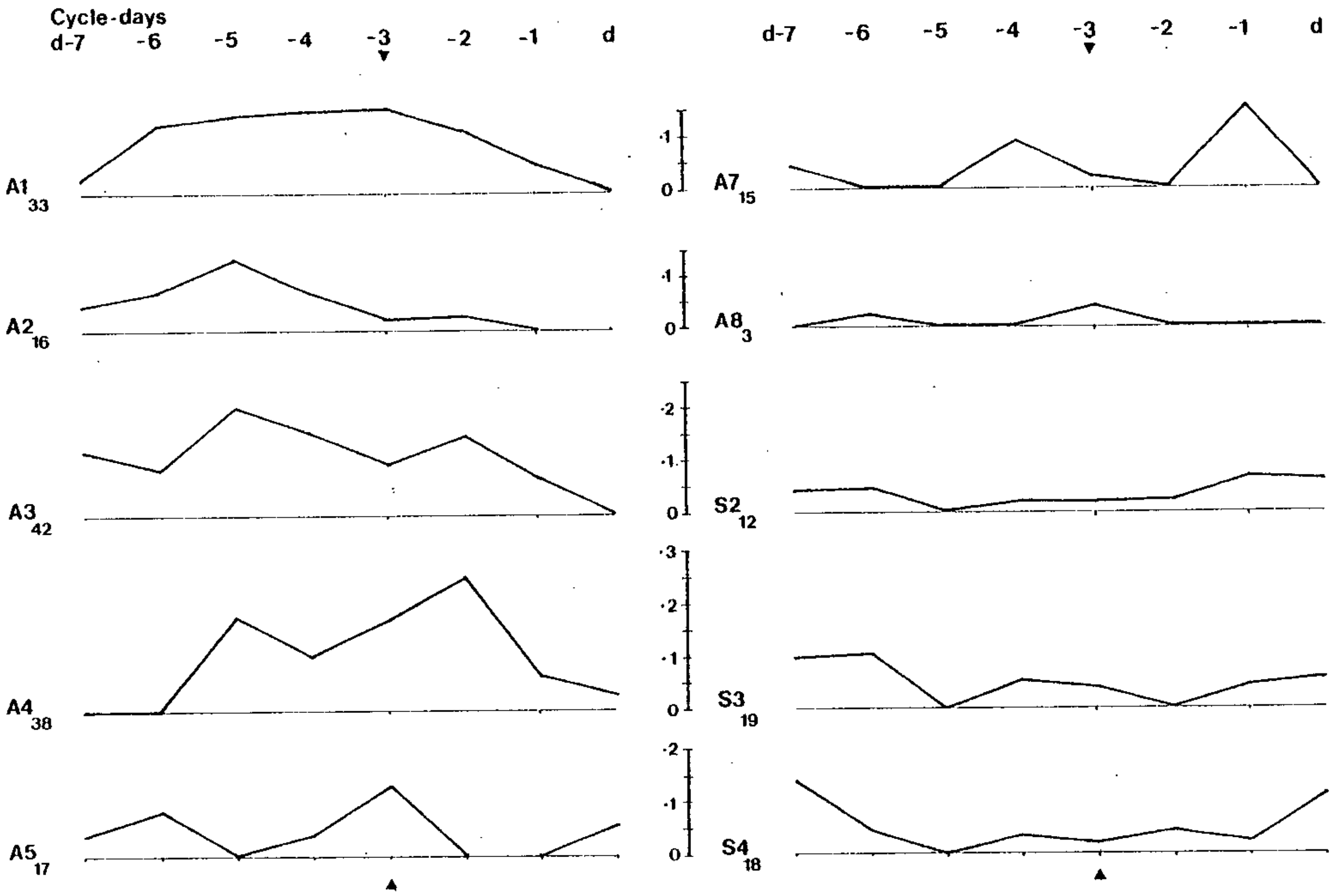


Fig. 8.7. Males' pooled mean rates of copulation with females on each day of full swelling, expressed as rate per female per hour. Below each male's name is the number of copulations involved. The highest probability of conception is on d-3.

and agonistic competition for consortship (DeVore, 1965): these are described in turn below.

8.3.8 Harassment of copulations

When two animals mounted or copulated, onlookers occasionally responded by running towards or directing aggression at the pair. Aggression of this sort, directed at one or both of the pair, was recorded as harassment. Harassment of copulation is seen in other species, either by adult males, or by immatures often the offspring of the mated female (Rowell, 1972). It occurs in lemurs (Jolly, 1967), langurs (Jay, 1965; Hrdy, 1977), red colobus (Struhsaker, 1975), vervets (Struhsaker, 1967), patas (Hall, 1965a; Loy & Loy, 1977), macaques (Gonzoules, 1974; Stephenson, 1974), and chimpanzees (Goodall, 1968; Tutin, 1979b). Studies of baboons report considerable variability, from no harassment at all (Saayman, 1970; Seyfarth, 1978a) to occasional (Hausfater, 1975) or frequent harassment (DeVore, 1965). DeVore saw that it was frequent in one troop but absent in the troop adjacent.

All cases of harassment of copulations and mounts, and other onlookers' responses, are tabulated in Fig. 8.8. Harassment of intromitted mounts was only seen 17 times, or in 2.74% of such mounts in which it could be scored present or absent (n 261). In only four of these did it cause the male to dismount, so that harassment at Ruaha had negligible effect on the success of copulation attempts. Aggressive harassment was mainly directed at pairs which included a fully swollen female, although onlookers sometimes ran towards or threatened mounts on partially swollen females.

The majority of responses were by immatures against consort males. In four of these the harasser was known offspring of the mated female (including one daughter), and one infant responded with distress and whimpering to its mother's mating. Lee and Oliver recorded frequent offspring-mother harassment (pers. comm.).

Consort males also harassed mounts between young males and the consort female, consistent with other patterns of possessiveness shown by adult males. In only two cases did an adult male harass a consort male, and in both the harasser had himself consorted the female concerned earlier in the day. A subadult also harassed a mount upon a female with whom he had groomed and mated shortly beforehand.

Fig. 8.8

Harasser/Responder \ Mounter	Consort male	Adult male	Subadult male	Imm.	Other
Consort male			●	●● ■■ ○○ □	
Adult male	●●	■	●	○	
Subadult male				●	■
Immature	●●● ●●● ●●●	■	●	□□	
Other				○	

	Inflating	Full	Deflating
Harassment	3	18	1
Other response	3	4	

Fig. 8.8. Onlookers' responses to mounts without intromission (□ & ■) and to intromitted mounts (○ & ●). Black symbols represent aggressive harassment, the open symbols refer to other responses. The lower panel subdivides all responses according to the cycle state of the mounted female.

Anecdotal evidence suggests that a male may be inhibited from copulation by the presence of other males, possibly because of the risk of harassment (Hausfater, 1975, p.118). Twice, a male looked around furtively before copulating with a deflating female; and on four occasions an adult male initiated copulation as soon as other baboons had moved temporarily out of sight. But rival males may also be inhibited from harassment: twice a mounted male threatened away a juvenile harasser after dismounting; and on two occasions when a nearby pair started to copulate, a male (A2) chased animals nearby as though in redirected aggression.

Thus although mounting sometimes elicited tense, possessive, or aggressive responses by nearby animals, it was never seen to spark off multipartite aggression such as often leads to consort changes at Gombe (pers. obs.). There was also very little shadowing of consort pairs, which is prominently associated with harassment elsewhere (Ransom, 1971; Hausfater, 1975; Packer, 1979a). These data suggest that male-male competition at Ruaha was of relatively low intensity.

8.3.9 Competition and consort-formation

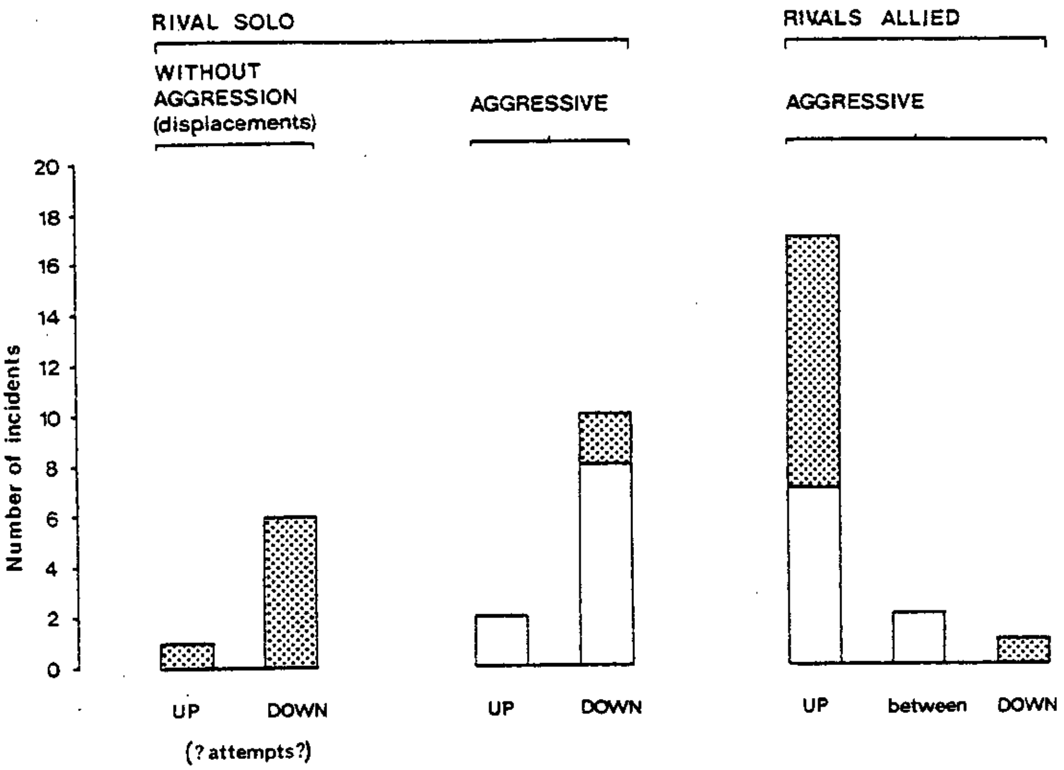
In section 7.5.6, the onset of consortships were divided into non-competitive *finds* and two types of agonistic takeovers: these were *displacements* (without aggression), and *aggressive* changeovers. Table 7.VIII showed that males started consorting without evident competition in 61% of consortships with fully swollen females. While this was partly because of the high proportion of resumption cycles, in which competition was significantly less frequent, yet even in subsequent cycles 31% of consortships at this stage began as finds. This is further evidence that male-male competition at Ruaha was not generally very intense.

8.3.10 Agonistic consort changeovers

Males who attempted to gain access to a swollen female by directing agonism to the consort male are here referred to as rivals; only changeovers at *full swelling* are described.

8.3.10a) *Solo displacements* On seven occasions the consort male conceded the female to a rival without exchange of threat. In six of these the successful rival was of higher rank than the deposed consort male (Fig. 8.9). In the seventh, the arrival of a lower-ranking rival apparently caused the consort male to chase a nearby

Fig. 8.9

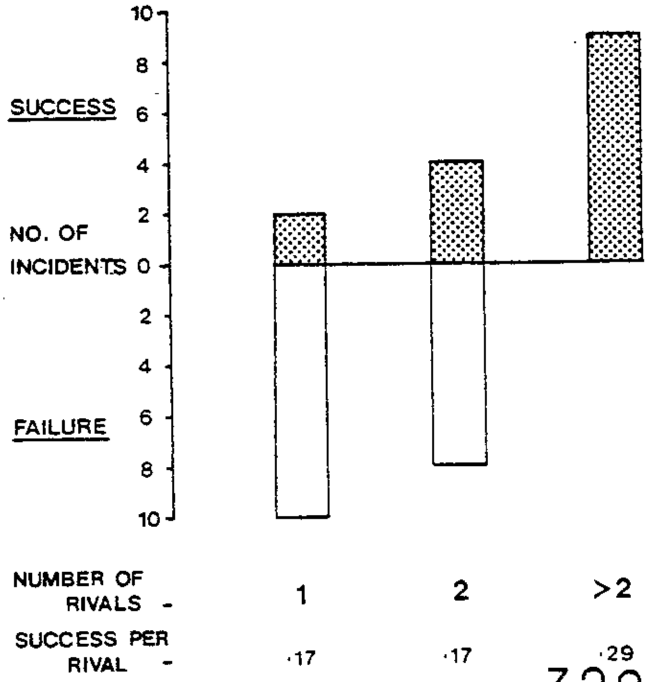


NUMBERS OF ATTEMPTED (▭) AND SUCCESSFUL (▨) CHALLENGES AGAINST CONSORT MALES DOMINANT (UPRANK) AND SUBORDINATE (DOWN-RANK) TO THE RIVAL(S).

Figs. 8.9. & 8.10. The number and success of rival males' challenges to consort males, in relation to the relative dominance ranks of consort and rivals (above), and in relation to the number of rivals (below). It was not possible to recognise attempts to displace (Fig. 8.9.).

Fig. 8.10

SUCCESS OF MALES' AGGRESSIVE CHALLENGES IN RELATION TO THE NUMBER OF RIVALS INVOLVED



female, thus conceding the swollen female to the rival. Three successful displacements appeared to have been facilitated by aggression from the rival shortly beforehand (up to 8 minutes earlier). On three occasions the displaced consort interacted with a black infant as soon as he had deserted the female. It was not possible to recognise attempted displacements.

8.3.10b) Solo aggressive changeovers The few attempts to gain consortship by solo aggression were not usually successful (Fig. 8.9). Most attempts were against consort males of lower rank than the aggressor, only two of ten being successful. In three of the unsuccessful attempts the consort male (A3) enlisted the alliance of another (A5) in defence against the rival (A1). Once an infant was carried by the defeated consort male, and once by the consort male's ally in defence. As mentioned above, three unsuccessful aggressive attempts were followed by successful displacements shortly afterwards.

8.3.10c) Allied aggressive changeovers Previous studies indicate that subordinate males may obtain females from dominant consorts by forming coalitions (DeVore, 1965; Packer, 1979b; Rasmussen, 1980). Packer suggests that males' ability to benefit from coalitions reflects their mobility, their experience, and possibly their tendency to reciprocate alliance.

Incidents of multipartite aggression between the consort male and others were considered to be potential takeovers. Occasions when the consort male enlisted alliance in defence of the female have been included above. In the remaining cases, between two and four rival males were involved ($\bar{x}$ 2.6 adult males) and in five cases included animals other than adult males as well. These were subadult males (twice), cycling females (three times) and an infant (once). In addition, infants were twice carried by males, once by the successful rival, once by an ally of the successful rival.

Fig. 8.9 shows that the majority of allied challenges were directed against consort males of higher rank than the rivals: significantly more so than in solo aggressive challenges (χ^2 18.76, d.f. 1, $p < .01$). Secondly, these allied challenges were proportionately more often successful than were solo aggressive challenges (χ^2 4.61, d.f. 1, $p < .05$).

Fig. 8.10 compares the success of aggressive challenges according to the number of adult male rivals involved (i.e. excluding subadult

Table 8.VII The adult males compared for the number and success of their solo and allied challenges to consort males. A successful challenge was one in which the male concerned gained consortship of the female.

Male:	Solo.			Allied.		
	Failure	Success	ppn.	Failure	Success	ppn.
A1	2	2	.50			
A2	3	–	–			
A3	2	–	–	10	7	.41
A4				5	5	.50
A5	3		–	17	1	.06
A6				1	–	–
A7				7	–	–
A8				2	–	–

male and female allies, etc.). Solo attempts were only successful in 0.17 of male attempts. Attempts with two rivals were more often successful, but because there were more rivals the success remained at 0.17 per male attempt. However, those with more than two rivals were all successful, and the success rate per male attempt rose to 0.29. Thus although the addition of extra rivals might have diluted each male's chance of success, this was over-ridden by the greater likelihood that changeover would occur. However, it is shown below that males did not benefit equally from this effect.

Table 8.VII compares the adult males for the number of solo and allied aggressive challenges each one made, and their success. Solo attempts were only successful for A1, (although solo displacements also benefitted A2, A3 and A5, see 8.3.14), while allied aggressive challenges worked in favour of A3 and A4. Despite frequent involvement in allied incidents, A5 and A7 seldom gained females as a result. In the thirteen allied takeovers, the highest-ranking of the rivals gained the female in nine cases.

8.3.11 The mechanism of agonistic changeovers

The quantitative data above miss much contextual information. Agonistic changeovers were often confusing to watch, but some patterns recurred sufficiently to be described.

Although rival males generally appeared inhibited from interaction with the consort pair, often avoiding them (6.7.2) and seldom attempted solo takeovers even when dominant to the consort male, yet consort males often appeared unsettled by the proximity of rivals. Thus three times a higher ranking rival gained consortship by slowly working his way between consort and female. Consort males occasionally made unprovoked chases on nearby rivals, and on eight occasions deserted their females apparently because a large number of other males were gathered nearby.

On the three occasions when a consort male resisted a solo aggressive challenge by enlisting the help of an ally, this was because the rival chased the ally. Once the rival briefly overcame this by chasing the consort male instead, but he still did not take the opportunity to consort. Another time a rival gained consortship by chasing the female rather than the male.

Allied challenges usually followed aggressive exchanges among rivals. A rival might initiate this by being assertive to another (e.g. mounting, cheekchewing, supplanting) but more often did so by threatening and chasing near the consort pair. Such initiations often appeared purposeful and manipulative, because although they sometimes petered out in chasing elsewhere, they more often led to one rival soliciting another against the consort male, or chasing him towards the consort pair. At this the consort male might intensify his possessive behaviour towards the female, by grooming and herding, but he more often became separated from her as consort and rivals chased back and forth. One of the males would try to work back to the female: in most cases, the consort male chased a lower ranking rival, freeing the higher ranking rival to move after the female. Whichever male reached her would act possessively, and sometimes mount, establishing consortship. However, chasing was often prolonged, and males appeared to miss opportunities to regain the female, for example by resuming chasing _after_ they had reached her. Juvenile and subadult males sometimes copulated opportunistically while the adults were chasing, and in four instances an adult male who was not involved came in and established consortship. After aggressive changeovers the females sometimes appeared agitated and uncooperative to the new consort, by walking rapidly (sometimes towards other males), or by refusing his mount-attempts.

Adult females were occasionally implicated in causing changeovers in two ways. In seven cases, the consort male without provocation chased a female nearby, apparently redirecting aggression elicited by the presence of rivals, and in five of these another male gained consortship as a result. In three other cases the consort female herself chased a nearby female, becoming separated from the consort male and in two of these a rival male was able to gain the female.

8.3.12 Short-term changes in consorting activity

One of the assumptions of Altmann's model (8.3.1) was that all males consort at every opportunity in accordance with their rank. However, males may differ in consort motivation independently of rank (Conaway & Koford, 1964). Secondly, high ranking males sometimes refrain from consorting (refs. in 8.3.4) in some cases through injury or fatigue (Packer, 1979b). This was borne out at Ruaha in that some males showed short-term lapses in consortship after losing a female as a result of combined aggression from other males.

Fig. 8.11. (overleaf). The time-course of each male's consorting activity. The upper row shows the number of females at partial or full swelling on each day of the study; partial swelling includes inflation and deflation, but F11 is excluded from the figure. Below that the letters A to F refer to particular events described in the text of 8.3.12. Beneath those are twelve rows depicting the consort activity of each male, in order of dominance rank descending from the top. The height of the vertical bars on each row show for what percent of the day that male was in consort with a female at partial or full swelling (open and dark bars respectively), estimated from 15 minute one-zero samples (2.IX); 100% of the day would coincide with the base of the row above. The numbers below the bottom row refer to periods of days which have been ommitted from the diagram, either because no observations were made (15 days) or no consorting was seen (30 days).

FIG. 8.11

CHANGES IN CONSORTING ACTIVITY of EACH MALE:

compared with availability of females at partial (○) or full (●) swelling.

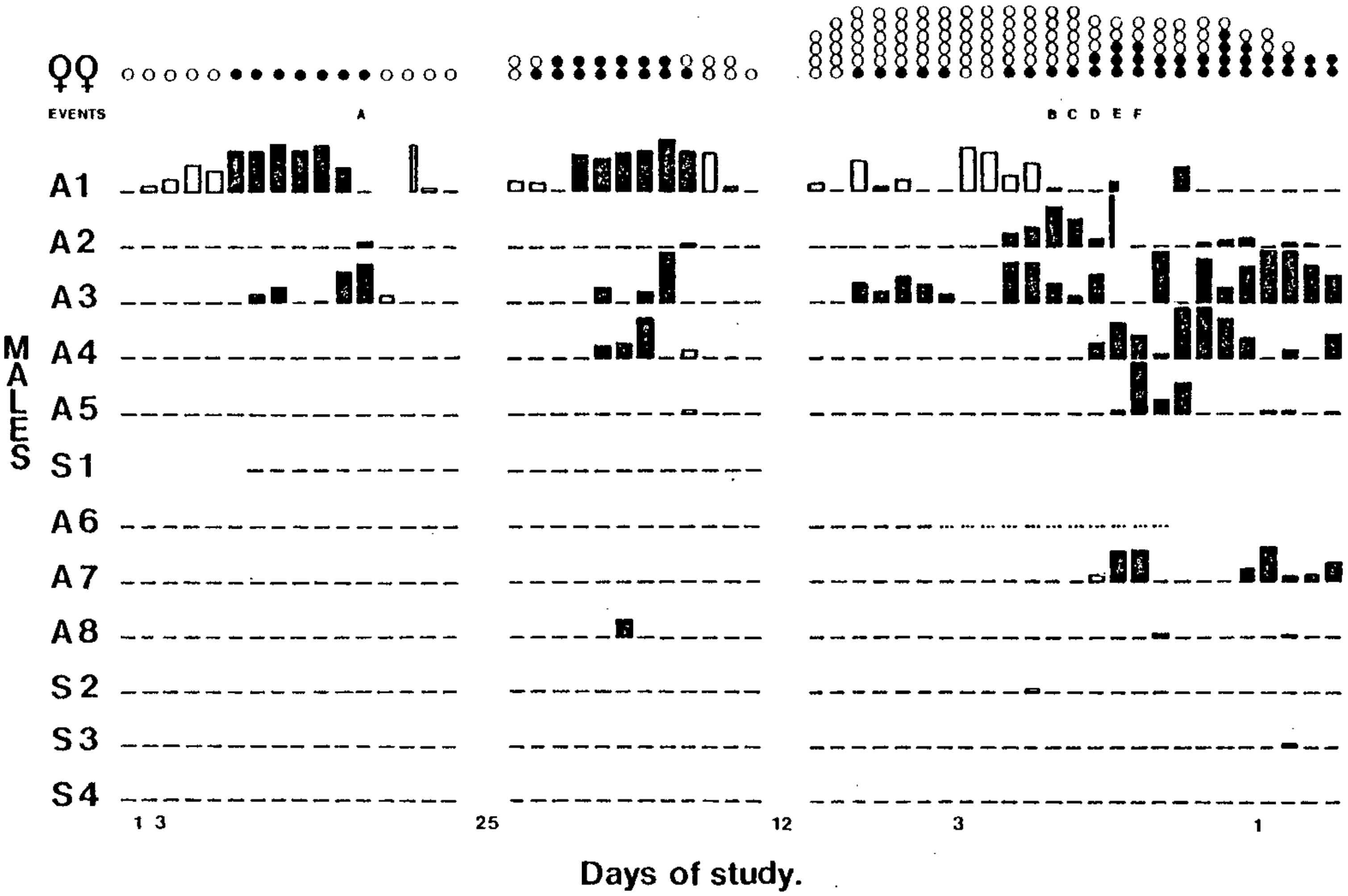


Fig. 8.11 shows the time-course of each male's consorting activity with partially and fully swollen females against a backdrop of female availability. The absences of S1, and the illness and death of A6, are indicated. The letters denote events referred to below.

The general pattern agrees loosely with Altmann's model, in that middle and lower ranking males consorted more when more females were fully swollen. However, the fit is not exact: for example, when only one female was available, adults ranked 1, 2 and 3 consorted: and conversely, when most females were available, male A1 consorted least of all. Finally, the marked increases in consortship by A4, A5 and A7 (at time c) were apparently because A1, A2 and A3 were not consorting for reasons described below.

Incidents in which a male's behaviour was altered, apparently through competition for males, may be described under four headings.

1. Injury: During the night of Oct. 25th (a on fig.), A2 obtained consortship of F5 from A1, but sustained a bad face wound. He soon conceded the female to A3, and for the next three days frequented the periphery of the troop, his face considerably swollen, at times appearing ill.

2. Decreased consorting: In F5's third cycle, A1 consorted on d-9 and and d-8, but on the morning of d-7 he had lost her to A2 and appeared unwell (b on fig.). For the next four days he formed loose consortships with F7 (d-10 to d-7) but usually moved to the periphery of the troop after 1.00 a.m. He made no attempt to regain F5 despite their mutual preference at other times (8.4.6).

During the same cycle, A3 consorted F5 on d-5 and d-4, but lost her on d-3 as he was chased to the edge of the troop by A4, A5 and A7 (c on fig.). He remained there, interacted little that day, and did not consort on the next two days despite the presence of three fully swollen females, interacting instead with mother-infant pairs. On the third day he resumed consortship.

3. Absences from the troop: Male A1 left the troop four times, during which he was seen and once slept within one mile of them. In F5's first cycle he consorted her from d-11 to d-2, but lost her overnight to A2 (a on fig.), with evidence of fighting given above. A1 was absent for 1½ hours that day, and again left on the following day, returning 1½ days later and immediately resuming consortship with F5

(d+1). Similarly, during his 'unwell' period described above, he was absent for $1\frac{3}{4}$ hours (*c* on fig.), and on the fourth day of this period, after losing consortship of F7 when chased to the edge of the troop by A3, A4, A5 and A7, he left and was not seen again till over 50 hours later (*e* on fig.). Finally, A2 was absent for at least $4\frac{1}{2}$ hours after losing consortship of a female (*e* on fig.).

4. *Increased consortship*: Male A4 showed markedly increased consortship and competitive activity after his takeover of F5 from A3 (*e* on fig.).

8.3.13 Discussion of short-term changes

Other authors have reported both lapses in consortship (refs. in 8.3.4) and temporary absences by males (Hausfater, 1975; Seyfarth, 1975). The temporary lapses seen here appeared not to result from the accumulated costs of *maintaining* consortship, such as vigilance or decreased feeding time (Packer, 1979b; cf. Rasmussen, 1980), or repeated mating (Carpenter, 1942a). Rather, they all followed *loss* of consortship, with evidence of coincident aggression received and at least one case of wounding. These factors, with also possibly internal injury not visible to the observer, appeared to cause short-term decreases in motivation. Such changes may be mediated hormonally, because testosterone levels may fall after defeat (Rose *et al*., 1972) and affect sexual behaviour (Phoenix, 1974). However the behavioural changes were so immediate that cognitive processes must also be involved. Whatever the mechanism, the fact that these setbacks were concentrated on high-ranking males clearly allowed the middle-rankers numerous opportunities to consort. The increase in consorting activity by A4 suggests also that achievement may have a converse effect, again perhaps with an hormonal component (Bernstein *et al*., 1974).

8.3.14 Individual differences in males' competitive behaviour

Table 8.VIII summarises how each male's consortships with fully swollen females began and ended, emphasising that most did so without competition. The pattern of agonistic changeovers was that A1 and A2 tended to gain consortships single handed, but to lose them against alliances, while the reverse was true of resident males. This probably reflects the fact that A1 and A2 were newcomers rather than that they were of highest rank.

Table 8.VIII: Each adult male's consortships with fully swollen females, subdivided by the ways they began and ended, as described in 7.5.6, 8.3.9, and 8.3.10.

	Beginning					End				
	not seen	Finds	Displaces	Aggressive		not seen	Deserts	Displaced	Aggressive	
Males:				solo	allied				solo	allied
A1	(14)	2	–	2	–	(11)	2	–	–	5
A2	(10)	1	4	–	–	(2)	5	1	–	7
A3	(9)	22	2	–	8	(22)	14	3	2	1
A4	(3)	5	–	–	5	(8)	5	–	–	–
A5	(1)	6	1	–	3	(5)	4	2	–	–
A6										
A7	(2)	6	–	–	–	(4)	2	1	–	1
A8	(1)	2	–	–	–		3	–	–	–

8.3.14a) Newcomers A1 and A2 Male A1 lost the majority of his consortships to the alliance of A3 and A5, but often regained them from A3 when A5 was not at hand (circumstantial evidence suggested that this occurred more than is shown in the Table). As already described, A2 established most of his consortships overnight, but was tense in consort by day and tended to desert his females when in the vicinity of other males. However in one three-day period he repeatedly gained consortship of F5 by persistently moving near her consort A3 and causing him to desert her.

8.3.14b) Prime-age adults A3, A4 and A5 Male A3 was responsible for the majority of peacable consortships with undisputed females. Both he and A5 relied more on alliances when challenging higher-ranking consorts than they did against lower rankers. A3 depended conspicuously on A5 when challenging A1 and A2. He was never seen to challenge their consortship, or defend his own against them successfully without the help of A5, (except once using an infant against A2). He would solicit assistance by barking or screaming with tail up when A1 or A2 drew near, often looking around or towards A5.

A4 was never seen to lose a consortship agonistically, and he used alliances with A3, A5 and A7 to gain them. He appeared the most effective strategist, both in the timing with which he initiated challenges, and in his tendency to return to the female rather than be drawn off into fighting and chasing.

A5 was remarkable in his apparent willingness to be solicited by A3, but this was mainly against newcomers A1 and A2. It generally resulted in A5 confronting A1 while A3 moved away with the female. In their twelve allied challenges, he only gained consortship once, while A3 did so seven times. However, he sometimes ignored A3's solicitations.

8.3.14c) Post-prime males A6, A7, A8 The lack of consortship and competition by A6 may be partly explained by his illness. A7 consorted only undisputed females, and never benefitted directly from his alliances with the middle-ranking males. The large, aged A8 occasionally consorted undisputed females, but always avoided confrontation and was even seen to move away from a free swollen female while other males were fighting about her.

8.3.15 Female competition over males

Despite Hall's (1962) report that aggression among females is increased at times when the α-male is mating, subsequent work suggests that females compete over males equally at all stages of the reproductive cycle (Seyfarth, 1976; Scott, 1978; also refs. in 7.7.1). This is in contrast to species living in one-male breeding units, where competition for the male is more obvious, especially between the α-female and oestrus females (Kummer, 1968; Dunbar & Dunbar, 1975; Mori, 1979).

Earlier analyses showed that cycling females tended to exchange relatively more agonism with females than did other reproductive classes (except in supplants: 6.4.4b), but there was insufficient evidence that this involved more competition over males (6.2.3, 6.4.6). Nevertheless in 14 female-female interactions which appeared to be competition of this sort, the recipient was a cycling female in all but one: nine of these were fully swollen, six in consort. Surprisingly, their antagonists were also cycling females in ten of these interactions, five being fully swollen and including four in consort. Most of these interactions were supplants or chases from close to an adult male. While this may be taken as an indication that cycling females do compete over adult males, comparable data on possibly more subtle competitive interaction involving other female classes are not available. Certainly it did not cause females to differ in their interaction rate with males (8.3.2), although it might have influenced females' success in access to a preferred male (8, part 4).

4. MATE SELECTION

8.4.1 Numerous studies of multi-male primate groups report partner-preferences in mating. Selective partnerships in terms of age, social class (central vs. peripheral) or individual characteristics have been observed in macaques (Tokuda, 1961-62; Kaufmann, 1965; Loy, 1971; Lindburg, 1975; Dixson, 1977; Enomoto, 1978; Fedigan & Gouzoules, 1979; Taub, 1980a) and in chimpanzees (Tutin, 1975; Nishida, 1979). The importance of partner-preference in baboons, particularly female choice, was early suggested by Marais (1939). DeVore (1965), and Rowell (1967a) (see also comments by Kalter and Gillman, Symp. Zool. Soc. (Lond.), 17: 1966, pp.157-158). Quantitative studies emphasise three main aspects.

First, females may prefer certain males by their association and affiliative interaction, but avoid others. Adult females apparently prefer adult (transferred) males over subadult (natal) males (Saayman, 1970; Packer, 1979a). Among adults they often prefer high rankers (Hall, 1962; Seyfarth, 1978a; Scott, 1978; Rasmussen, 1980), although not in all cases (Saayman ibid., Packer ibid.); or younger adults (Rasmussen ibid.). Some studies report a preference for newly transferred or unfamiliar males (Ransom, 1971; Packer ibid.), a pattern also shown by adolescent female chimpanzees (Tutin, 1976).

Secondly, males may consort selectively, or abstain from consorting (refs. in 8.3.4). There is some evidence that they are less attracted to adolescent or nulliparous females (Hall, 1963; Rasmussen, 1980 respectively), but beyond this little evidence as to what female characteristics are preferable; apparently not age (Packer, 1979b) nor dominance rank (Packer ibid.; Rasmussen ibid.). However males do prefer females who maintain proximity to them (Packer ibid.), or approach and present often (Rasmussen ibid.), when not in consort; although as both authors show this need not necessarily reflect preference by the female. Finally, Packer found that males favoured females who were not preferred by other males, suggesting that male selectivity is more a device for reducing competition. The primary preferences of the α-males studied by Hausfater (1975) agree with this, as does Seyfarth's (1978a) observation that the α-male did not interfere in the preferred consortship of his β-male.

Finally, mating preferences probably form only a part of the lifetime relationships of the partners (Seyfarth, 1978b). Adolescent females solicit males often but rather indiscriminately (Sugawara, 1979), but with maturity they select older and higher-ranking males (Scott, 1978; K. Rasmussen, pers. comm.). Older adult males, who have been in the troop long enough to father some of the young adult females tend to consort these less, and they are consorted instead by younger adult males (Packer, 1979a). Older or low-ranking males may groom particular females intensively, arguably to increase the chances that females will prefer them as mates (Packer, 1979b; Seyfarth, 1978b).

The data presented below show that the mating success of each male was really the sum of his mating relationships with particular females.

It is therefore important to see how such relationships were established, and whether they reflected preferences by male or female. The following sections investigate changes in interaction within pairs of male and female through the menstrual cycle, and attempt to relate these to mating partnerships at full swelling.

8.4.2 Non-random mating

Copulation did not occur randomly between all pairs, even accounting for differences in the copulation rate of each male. Fig. 8.12 compares the total copulations of each pair with the total expected if each male had copulated at his own rate equally across all partners. In each cycle stage, the males' overall rate provided the total expected with each female, and the pairs' expected totals in all cycle states were then combined. The distribution of copulations was not random for five of the six adults testable (Kolmogorov Smirnov One-sample Test: results on Fig. 8.12), but the three subadults copulated at random. These partnerships reflect the patterns of consortship of the adult males, in contrast to the more opportunistic copulation of the subadults (8.2.5). Only partnerships involving adult males are considered below.

The distribution of the more frequently mated pairs in Fig. 8.12 suggests a pattern in terms of dominance ranks, to whit that higher ranking males tend to mate with higher ranking females. Although correlation coefficients between dominance rank and mean rank of copulation partner were not significant in either sex (r_s .679 over 7 males, 0.406 over 6 females), yet in the 48 cases where two consortships were in progress simultaneously, the higher ranking female consorted the higher ranking male in 36 (i.e. 75%. Binomial Test, $Z = -3.32$, $p < .001$). This was especially due to the pairings of F1 with A3, and of F5 with A1 and A2, so that further data are required to prove its generality.

8.4.3 Methods used in investigating mating partnerships

The formation of mating relationships was investigated by comparing the distribution of each fully swollen female's copulations among the various males with the distribution of her interactions with them during lactation, inflation, and deturgescence (i.e. the deflating and flat stages combined). The following measures were selected as indices of affiliation or aversion: they are fully defined in Appendix I.

Fig. 8.12

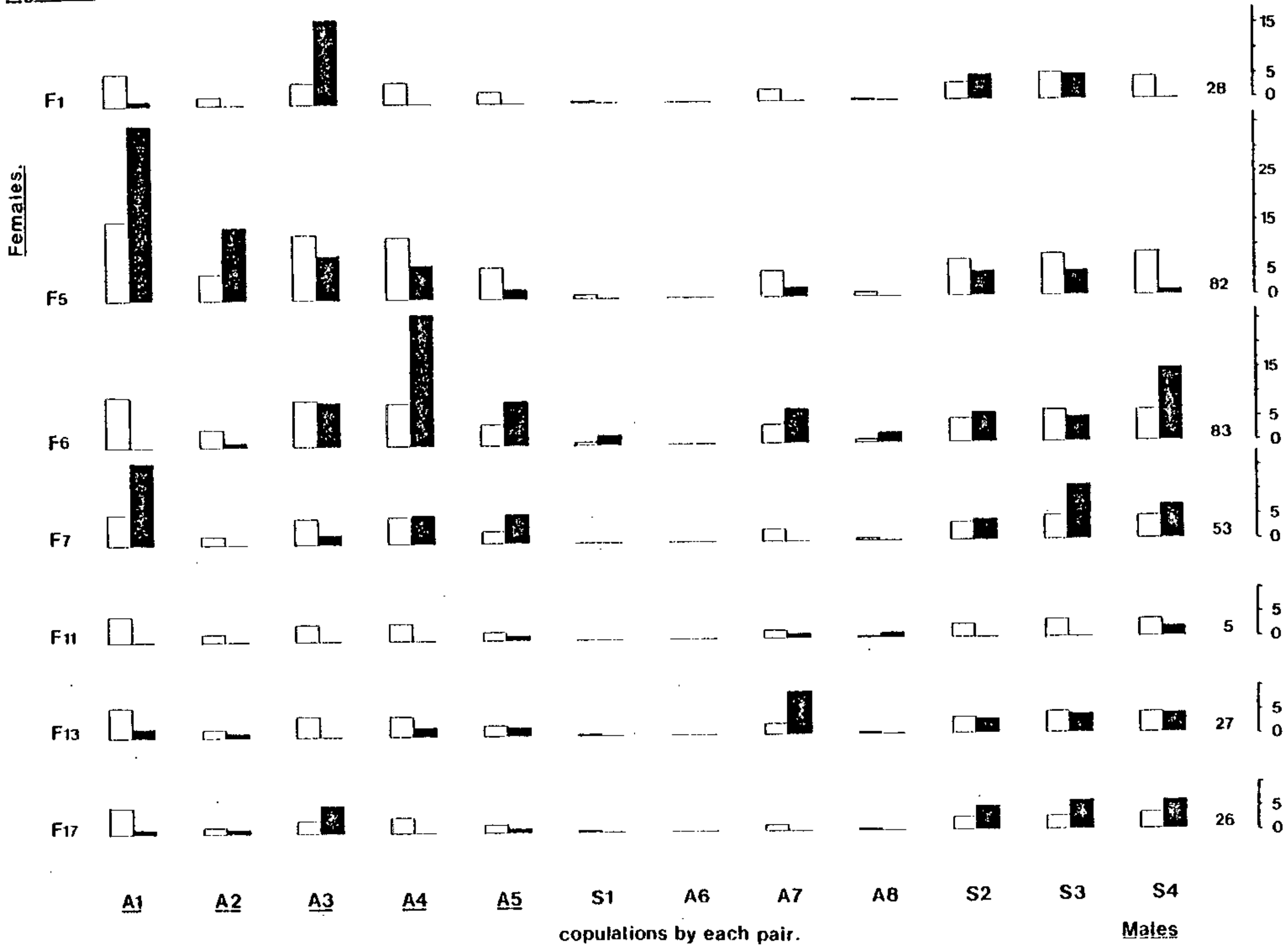


Fig. 8.12. The number of copulations within each male/female pair (dark bars) compared with the number expected if each male had copulated at his own rate equally with all females (open bars). Calculation of expecteds is described in 8.4.2. Males who did not mate at random are underlined (α .05); similar tests on A7, S2, S3, and S4 showed their mating to be random. 66% of these copulations were at full swelling, but the percentage was higher for all adult males except A1.

I. Outwith full swelling

(a) Association: The percent of the 1-minute focal samples on the female in which each male was seen within 15 metres (2.VIIIa).

(b) Affiliative behaviours by the female: (i) grooming, and (ii) presenting.

(c) Affiliative behaviours by the male: (i) standing or following within 1 metre, (ii) greeting the rear, including inspection, (iii) grooming, (iv) mounting without intromission, (v) possessive and coercive behaviours, including herding.

(d) Agonistic interactions: (i) the female moves away, i.e. is supplanted by, or avoids, the male (ii) female aggression, (iii) male aggression.

While all these behaviours were examined for inflation and deturgescence, some were omitted for lactation because they were rare or because they had not been recorded for non-cycling females.

II. At full swelling

(a) Male proximity to the consort pair: the percent presence of each male within 25 metres of the consort pair, estimated from 15 minute one-zero samples (2.IX). Males who were in consort with another female were by convention omitted.

(b) Copulation: as defined in 8.2.2.

(c) Male avoidance of the consort pair (6.7.2-3).

(d) Number of consortships observed.

Several indications of preference used in other studies were not used here: for example, the 'eyeface' or NEEF gesture (Saayman, 1970; Packer, 1979a), because not reliably recorded *ad libitum*; and female avoidance of mounts, for which there were too few mounts per dyad to investigate proportionately. Mounts which were elicited by presenting have been omitted, but first reciprocations of grooming have been included, as in 4.3.2.

The formation of mating partnerships was investigated first by comparing the relationship between *each behaviour* and copulation, across all females (8.4.4); and secondly by pooling behaviours and examining the interactions of *each female* in turn (8.4.5 & 6). The sick female F11 was not included.

8.4.4 Comparison between copulation at full swelling and behaviours occurring at other times

(a) Methods: In each stage of each cycle, the males were ranked in descending order of interaction rate with the female, separately for each behaviour. Males who interacted equally (often not at all) were given the median of their tied ranks; males absent for more than 20% of any stage were excluded, and the ranks of the remaining seven corrected up to their equivalent among eight. These ranks identified the first, second, third etc. copulation partner in each cycle. For each such partner was found its interaction rank for every other behaviour separately, and these ranks provided the mean interaction rank across all females for each copulation partner. Females who cycled more than once contributed only one set of interaction ranks, their means across all cycles.

If mating at full swelling had been universally associated with high rates of any particular behaviour at any other cycle stage, the more frequent copulation partners would have shown higher mean interaction ranks for this behaviour. This possibility is investigated in bloc (a) of Tables 8.IX to XI. As a check on these measures, the proportion of all interactions seen which occurred with first, second, third etc. copulation partners was calculated for each behaviour in each stage, pooling data from all pairs. These proportions are compared with those expected from the availability of such pairs in bloc (b) of Tables 8.IX to 8.XI.

(b) Results: The mean interaction ranks of the first copulation partner tended to be higher than those of the less frequent copulation partners (2nd - 8th in the Tables), indicating some correspondence between interaction and copulation, but it was not exact since the mean rank of the first partner was never as high as 1. The Spearman r_s values also indicate that the correspondence was not usually a linear one. Furthermore, a higher proportion of interactions generally occurred with the first copulation partners than expected (bloc (b) of tables). However the patterning of these results was much dictated by whether those few pairs who interacted particularly frequently either did, or did not, mate; because interaction data from other pairs were very scant. The only conclusions from this analysis are as follows.

Table 8.IX: Female-male partnerships in lactation compared with mating partnerships in the resumption cycle.

	(a) Mean partner-ranks				(b) Proportion of interactions. (N = 38 pairs)					
		Mating partners				Mating partners				
	n (females)	1st	2nd – 8th	r_s	n (interactions)	1st	2nd	3rd	4th	non - mating
					exp:	.13	.11	.08	.05	.63
F grooms	4	4.0	4.5 – 4.9	–.22	5	.20				.80
F presents	5	2.7	4.0 – 5.5	.61	20	.30	.15	–	.15	.40
M mounts	4	3.4	3.0 – 5.0	.79	14	.29	.14	.07	.21	.29
F moves away	5	4.0	3.3 – 5.2	.51	66	.15	.14	.05	.06	.59
F aggress	2	5.3	4.2 – 4.7	–.91	4					1.00
M aggress	5	4.5	4.1 – 5.5	–.28	33	.09	.15	.03		.73
Association	5	3.2	4.1 – 5.1	.69	$\bar{x}$ Assocn. %	8.5	7.5	8.5	5.2	7.0

The males' copulation-ranks at full swelling are compared with their ranks in lactation for the social interactions listed on the left (F = female, M = male). In bloc (a), from left to right, are listed: the number of females with whom mean ranks were calculated: the mean interaction rank of the first mating partner: the range of interaction ranks of the other males: The Spearman coefficient of correlation between the males' ranks for copulation and for interaction. Method of ranking described in 8.4.4.

Bloc (b) shows the proportion of all interactions seen which occurred with the 1st, 2nd, 3rd, etc. mating partners, and with males who did not mate at all, compared with the proportion expected from the availability of such partners (top row). The bottom row lists the mean dyadic association frequency between female and each mating partner.

Table 8.X: Male–female partnerships in inflation compared with mating partnerships at full swelling. Data arranged as in Table 8.IX.

	(a) Mean partner–ranks				(b) Proportion of interactions. (N = 68 pairs)						
	n (females)	1st	2nd – 8th	r_s	n (interactions)	1st	2nd	3rd	4th	5th	non-mating
					exp.	.13	.10	.07	.06	.03	.60
F grooms	6	2.7	4.4 – 5.0	.63	32	.34	.05	.05	.03	.06	.47
F presents	6	4.6	4.3 – 5.0	–.39	57	.26	.04	.08	.04	–	.58
M stands next	6	2.9	4.6 – 5.4	.00	48	.63	–	.02	.02	–	.33
M greets rear	6	2.7	4.6 – 5.0	–.28	12	.58	–	–	–	–	.42
M grooms	5	2.2	4.4 – 5.2	.75	16	.70	.03	.03	.06	–	.19
M mounts	6	4.1	4.0 – 5.2	.34	33	.33	.11	.02	.03	.03	.49
M possess.	6	2.4	4.5 – 5.1	.05	30	.60	.07	–	.03	–	.30
F moves away	6	2.3	4.5 – 5.3	–.27	84	.46	.04	.02	.01	.01	.45
F aggress.	3	3.0	4.0 – 5.0	–.14	6	.33	–	–	–	.33	.33
M aggress.	6	3.9	4.3 – 4.9	.56	25	.28	.10	.10	–	–	.52
Association	6	2.9	4.4 – 5.8	–.12	$\bar{x}$ Assocn. %	21.6	3.9	6.4	5.3	6.4	8.8

Table 8.XI: Male-female partnerships in deturgescense compared with mating partnerships in the preceding period of full swelling. Data arranged as in Table 8.IX.

	(a) Mean partner-ranks				(b) Proportion of interactions. (N = 52 pairs)						
	n (females)	1st	2nd - 8th	r_s	n (interactions)	1st	2nd	3rd	4th	5th	non-mating
					exp.	.13	.13	.08	.08	.04	.54
F grooms	3	1.5	4.8 - 5.1	-.18	8	.88	-	-	-	-	.12
F presents	4	3.0	4.2 - 5.1	.39	28	.32	.05	.09	.07	-	.46
M stands next	4	2.4	4.7 - 5.1	-.10	43	.79	.05	-	-	-	.16
M greets rear	3	1.8	4.3 - 5.1	.30	14	.57	.04	.11	.07	.07	.14
M grooms	3	1.7	4.5 - 5.2	.60	13	.69	.15	.08	-	-	.08
M mounts	4	2.5	3.6 - 5.3	.37	36	.56	.04	.15	.08	-	.17
M possess	4	2.1	4.4 - 5.2	.58	31	.65	.10	.07	-	-	.19
F moves away	4	3.1	4.5 - 5.0	.39	71	.56	.09	.04	.01	.01	.28
F aggress	2	5.0	3.5 - 5.0	.04	4	-	.38	.12	-	.25	.25
M aggress	4	2.5	4.4 - 5.0	.41	17	.59	.09	.03	.06	-	.24
Association	4	1.9	4.3 - 5.2	.83	$\bar{x}$ Assocn. %	36.7	8.8	7.7	10.0	2.1	5.9

1. Behaviour in lactation was not generally related to mating at full swelling. Identification of the first interaction partner would not have predicted identity of the first copulation partner in more than 25% of cycles, using any of the seven behavioural measures.

2. Behaviour in inflation was more closely related to copulation, because in comparison with lactation the mean interaction rank of first copulation partners was higher in five of seven behaviours, and the percent of interactions with first copulation partners was higher in five of six. Knowledge of the first interaction-partner would have allowed correct prediction of the first copulation partner more successfully in several measures: association (56% of 9 cycles), male standing next (56%), greeting rear (56%), grooming (71% of 7) and possessiveness (63% of 8).

3. Behaviour in deturgescence was even more closely related to mating at full swelling. Compared with inflation, the mean interaction ranks of first copulation partners was higher in 9 of 11 behaviours, and the percentage involving first partners was increased in 8 of 12. Similarly, knowledge of the first copulation partner would have allowed better prediction of first interaction partners: in terms of association (correct in 71% of 7 cycles, and dyadic mean frequency very high), female grooming (83% of 6), male standing next, greeting rear, and grooming (66% of 6 cycles each); male mounting (79% of 7), possessiveness (71% of 7) and male aggression (75% of 6).

8.4.5 Selectivity in the distribution of interactions through each cycle

The following section examines the history of each female's interactions with the different males through each cycle. Because interactions in each dyad were quite infrequent, behaviours have been pooled into the general categories given in 8.4.3, namely association, affiliative behaviours by the female, affiliative behaviours by the male, and agonistic interactions. Partnerships of each female are illustrated in these terms in Figs. 8.14 to 8.20, and their pattern is described in the text.

8.4.5a) Measures of preference by the female The data provide two measures suggestive of female preference - presenting and grooming. This interpretation is limited because it was not recorded what proportion of these interactions were actually initiated by the male,

FIG. 8.13

Mean dyadic rates at which each adult male received grooming and presenting from inflating females

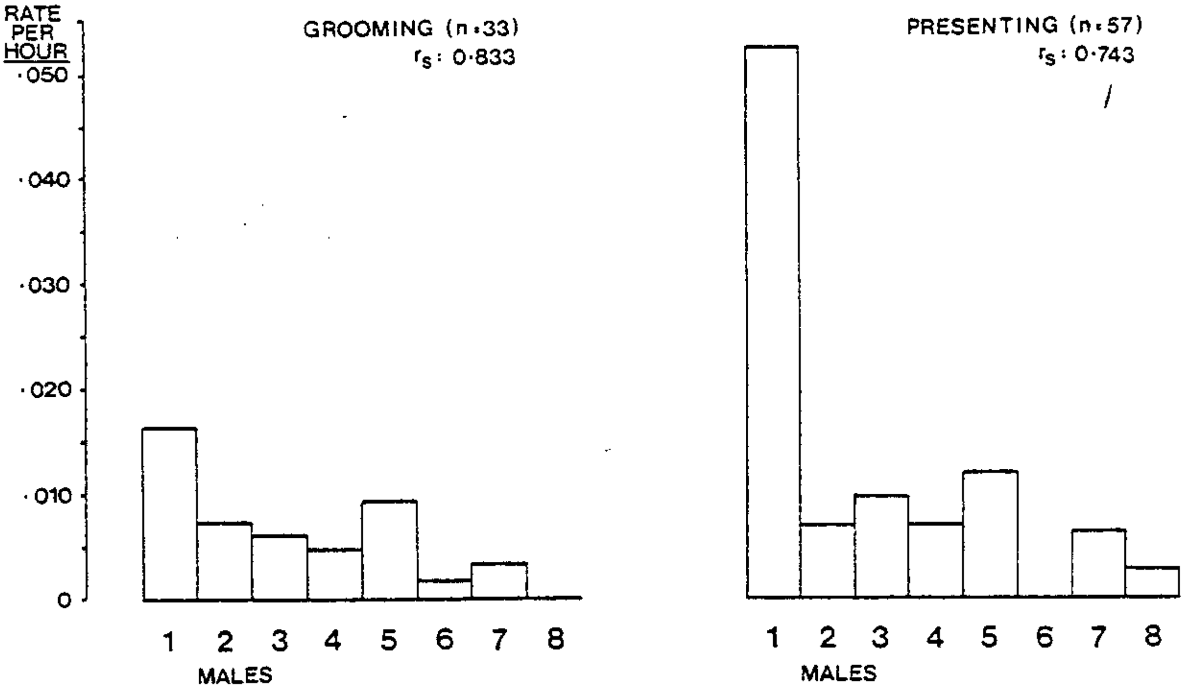


Fig. 8.13. Rates at which each adult male received grooming and presenting from inflating females. Spearman r_s values compare these rates with the males' dominance ranks. The rates at which these males received grooming and presenting from cycling females overall are shown in Figs. 4.10 and 5.3 respectively.

for example by approaching. The data above indicate that grooming was more closely related to eventual mating than was presenting (Tables 8.IX & XI). Fig. 8.13 compares the mean dyadic rates at which each adult male received these two behaviours from inflating females: higher-ranking males received grooming at higher rates (r_s .833, corr. obs. .905, n 8, $p < .05$) and also presenting (r_s .743, corr. obs. .714, n 8, $p < .05$). The result for grooming was also upheld in terms of the males' mean interaction ranks from all females (r_s .833), but not for presenting (.561) apparently because four of the six females gave 50% or more of their presents to male A1. When these coefficients were calculated without the two newcomer adults, the same pattern was apparent for grooming (r_s .771 in all three measures) and for presenting (r_s .657, .514, and .290 respectively), but none of these was significant. It was striking that in four cycles the inflating female did not present at all to her main associate, particularly F5.

When the female was fully swollen, two other measures provided oblique evidence of females' affinities. Males seldom 'shadowed' consort pairs as they do elsewhere, and many cases where males spent much time in proximity to consort pairs were due to the movements of the female. The male most often near the pair was in some cases one with whom the female had shared high rates of interaction, or was also a prominent mating partner in that cycle. Secondly, male avoidance of consort pairs (6.7.2) was often caused by the female moving towards the males, sometimes purposefully. Such movements tended to elicit possessiveness by the consort male, and on two of the 25 occasions preceded a period of proximity by the rival after which he gained consortship of the female aggressively. 40% of such movements were to the male recorded most often in proximity during that cycle, but there was no other evidence that they coincided with other preferences by male or female.

8.4.5b) Measures of preference by the male The measures of affiliation by the male are more likely to have been initiated by male than female (cf. presenting above) especially in possessive interactions against other males. In several of the male-female partnerships during inflation, it was conspicuous that behaviours by the male outnumbered female affiliative behaviours considerably (e.g. F5 with A1; and F1 with A3).

8.4.5c) Agonistic interactions Figs. 8.14 to 8.20 show that agonistic interaction was often very frequent in pairs that exchanged much affiliative interaction. In most pairs these were cases of the female avoiding or being supplanted, (with rather less aggression of which most was by the male), and were presumably a consequence of their association rather than evidence of animosity.

8.4.6 Relationships and mating partnerships of different females

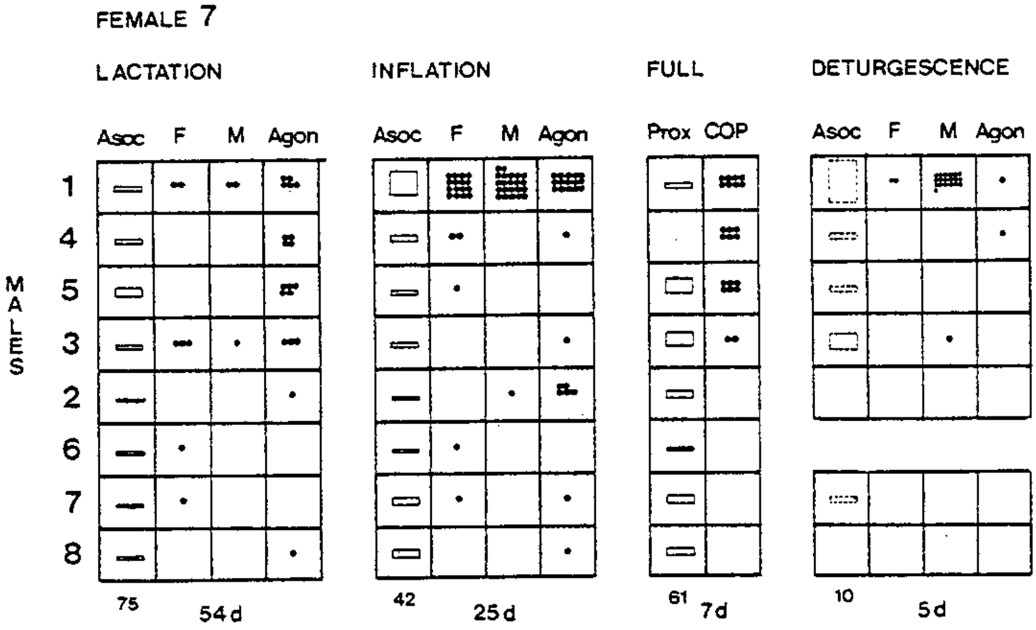
The cycles of the six females are described below under three categories of relationship: those which were apparent beforehand and included mating, and those which did not; and those which only became apparent after mating.

8.4.6a) Relationships which included mating There were two prominent relationships including mating, both of which involved male A1.

Female F7: Her main associate during lactation was A5, although she interacted most with A1 (Fig. 8.14). During inflation, A1 became her outstanding partner: their association became five times more frequent, and interactions by both partners were numerous. In particular, her rate of presents was higher than recorded in any other pair during the study, and he supplanted her particularly often. This exceptionally frequent partnership led to consortship at full swelling. However, other males (A4 and A5) also mated, partly because the female did not appear fully attractive and no competition was seen, and partly because A1 was not motivated to consort, and left the troop, after failure in competition for another female (8.3.12). However this partnership was resumed in deturgescence, while her interactions with other mating partners decreased.

The early cycles of F5: The first two cycles of this female were strikingly similar (Fig. 8.15) because of her consistent relationship with A1 at all stages. Both animals contributed to maintaining their association, although most affiliative interactions came from the male, and he also supplanted her very often. A1 was able to consort her through both periods of full swelling, although in the first one he periodically lost her to A3 (in alliance with A5) who thereby achieved six consortships although she appeared less co-operative to him in consort (A3 had not been an interaction partner at other times). During the second cycle, A3 only established one brief consortship, apparently because F6 was simultaneously in oestrus and he

FIG. 8.14



Figs 8.14 to 8.20 (on this and the following pages).

Interactions of male/female pairs are traced through each stage of the menstrual cycle. The measures in lactation, inflation, and deturgescence are described in 8.4.3: Asoc is the male's percent time within 15m of the female (100% would fill the whole vertical extent of the cell of the matrix); those based on a small number of association samples, as indicated beneath, are drawn with a dotted line. F is affiliation from the female, i.e. presenting and grooming. M is affiliation from the male, including grooming, mounting, and possessiveness. Agon is all agonistic interaction within the pair, mostly avoidance by the female, and supplants and aggression by the male. One dot equals one interaction.

The measures at full swelling are: Prox, which is the percent time the male was within 25m of the female when she was consorting another male; Cop shows the number of copulations as defined in 8.2.2.

The figures in the rows below the matrices show the number of observation days in each cycle stage (e.g. 25d above), while those below the Asoc and Prox columns show the number of samples on which each was based.

The adult males are identified by their dominance rank, and are listed on the left in descending order of their copulation rate with the female at full swelling. This is so that if any behaviours at other times were related to copulation at full swelling, these interactions would cluster towards the top of each matrix, as they clearly do for F7 (above) in inflation and deturgescence.

FIG. 8.15

FEMALE 5 Cycles 1 and 2

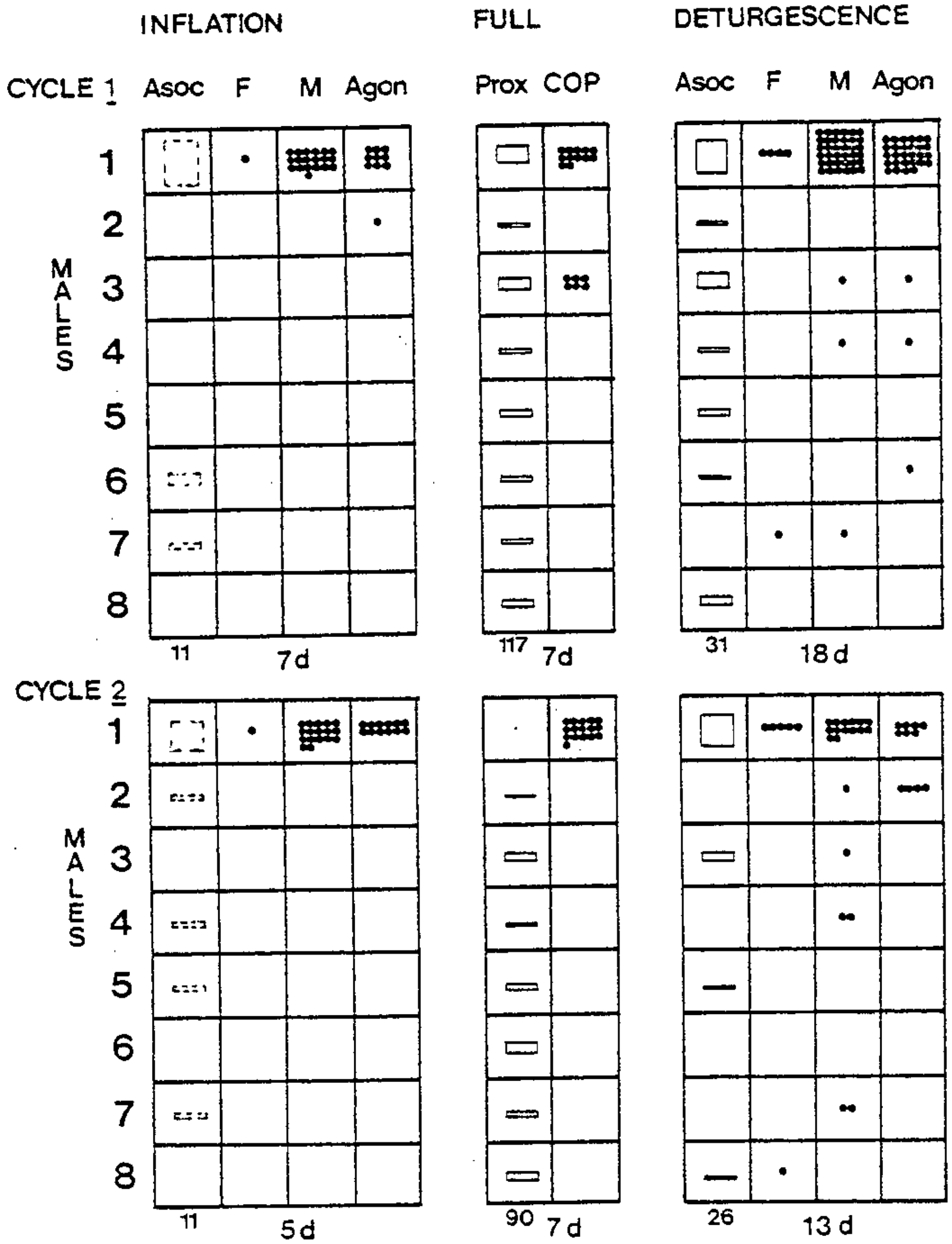


Fig. 8.15 Caption explained as under Fig. 8.14.

was able to consort with her instead. In deturgescence F5's relationship with A1 remained the most prominent male-female partnership in the troop, so much so that they were often in loose consortship. This stage differed slightly in that F5 presented to A1, and she interacted also with other males.

The relationships which these two females shared with A1 appeared to result from affinity by both male and female. They differed in that the partnership with F5 was already well established, while that with F7 was only initiated when she resumed cycling: which may explain why F7 presented so frequently, but F5 hardly at all.

8.4.6b) Relationships which did not lead to mating The four cycles described here provide a number of cases of partnerships which did not result in consortship, and suggest a number of reasons why they did not.

The third cycle of F5: This female's third cycle differed from the two described above only during full swelling (Fig. 8.16). During inflation and deturgescence she maintained the same prominent relationship with A1 as before, although for the first time she was seen to present to him in inflation (perhaps because F7, also inflating, was associating and presenting to him frequently). As in previous cycles, F5 and A1 consorted in late inflation, but at the onset of full swelling A1 appeared to have been defeated in competition for this female (8.3.12) and he neither attempted to consort her nor spent time near her consortships for the entire week; instead he consorted for some of the time with F7. Meanwhile F5 consorted males with whom she had no particular history of interaction, especially in long consortships with A2, who was also nearby most when not in consort. Compared with previous cycles, her rates of presenting and grooming to males at full swelling were more than doubled. A3 achieved seven consortships but fewer copulations (see 8.4.6a). During deturgescence, her partnership with A1 resumed, and her relations with other males were not markedly increased although she had consorted them.

The cycle of F1: During lactation this female was prominently associated with A4, although supplanted by several males (Fig. 8.17). During inflation, however, this male was superceded as an associate by A3, partly because A4 was involved with other females although he still interacted with F1. While she groomed both of these males in inflation, she groomed and especially presented to A1 more than to either of them,

FIG. 8.16

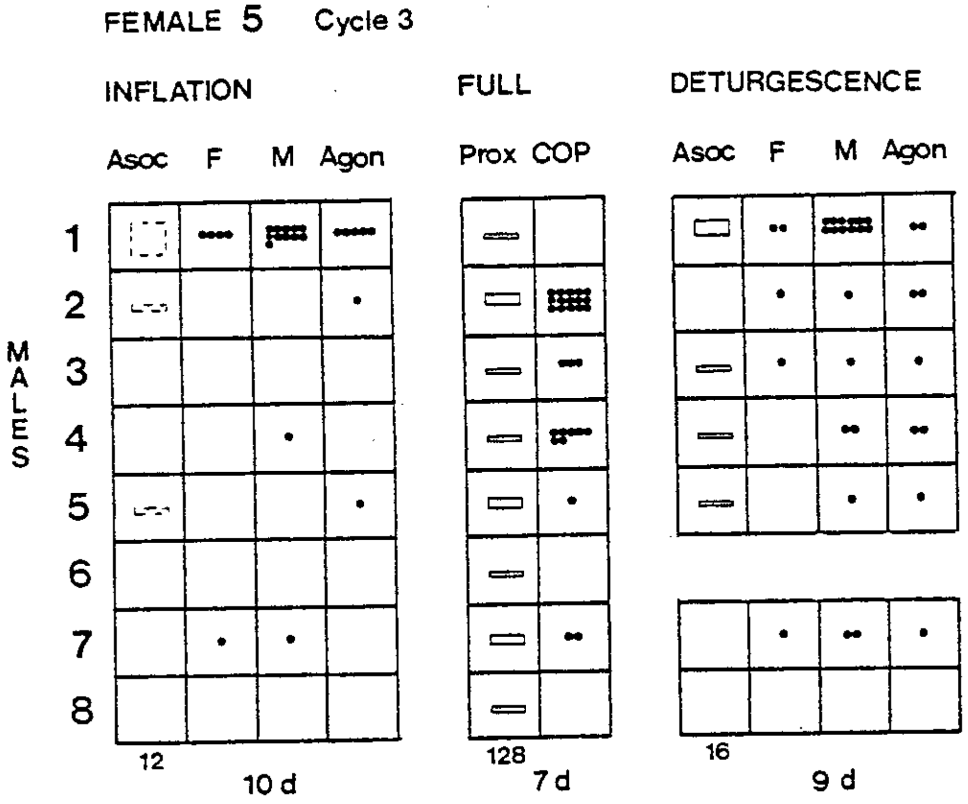
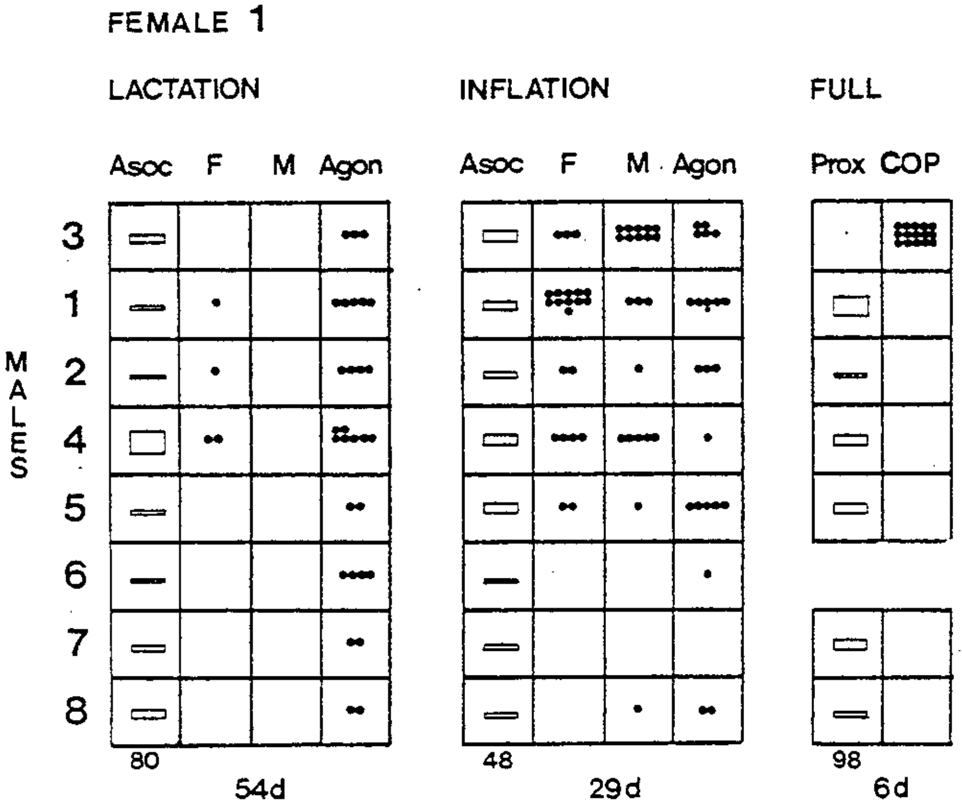


FIG. 8.17



Figs. 8.16 & 8.17. Caption as explained under Fig. 8.14.

and appeared to prefer him. Despite this, A3 gave more affiliative interaction to her than A1 did, and this apparently determined the pattern of consortship at full swelling, which was entirely with A3. Neither A4 nor A1 made any attempt to consort, even though A1 was seen most often near the consort pair, (at least in part because she tended to move towards him). A1 appeared to have been inhibited by A3's behaviour towards the female.

The cycle of F17: This female provides a parallel to F1's relations with A1 and A3 (Fig. 8.18). Although she had no particular partners during lactation, yet in inflation she showed increased association with A3: she interacted with this male and A1, presenting more to the latter, receiving more affiliative interaction from the former. As with F1, this again led to exclusive consortship with A3 at full swelling, perhaps for similar reasons. In deturgescence, however, she associated and interacted most with A5, who had been near most during her consortships.

The cycle of F13: This female had no prominent male partners during lactation, although she associated slightly more with A3 and A7 (Fig. 8.19). During inflation she associated increasingly with A3, but interacted more with A1 and especially A5: however at full swelling none of these three was seen to copulate with her. One reason was that A3 was instead consorting F1, but the main reason was that the female was not fully attractive, since this was a resumption cycle, and most males deserted after consorting for less than an hour. Except for this, it is reasonable to assume A5 would have mated with her; instead he had three brief consortships without copulation, (twice taking over agonistically from A7), and most of the copulation was left to A7, who consorted far more than any other. A5 was therefore possessive to the female independently of his motivation to copulate.

8.4.6c) Partnerships arising after mating

The cycles of F6: F6 was a peripheral female, and during lactation associated most with A1, and received aggression from him and A2: both males at this stage were newcomers and like her quite peripheral. She was unusual in that during inflation no males were particularly prominent partners, except possibly A7 in the second cycle (Fig. 8.20). During the first full swelling, she mated with males with whom she had

FIG. 8.18

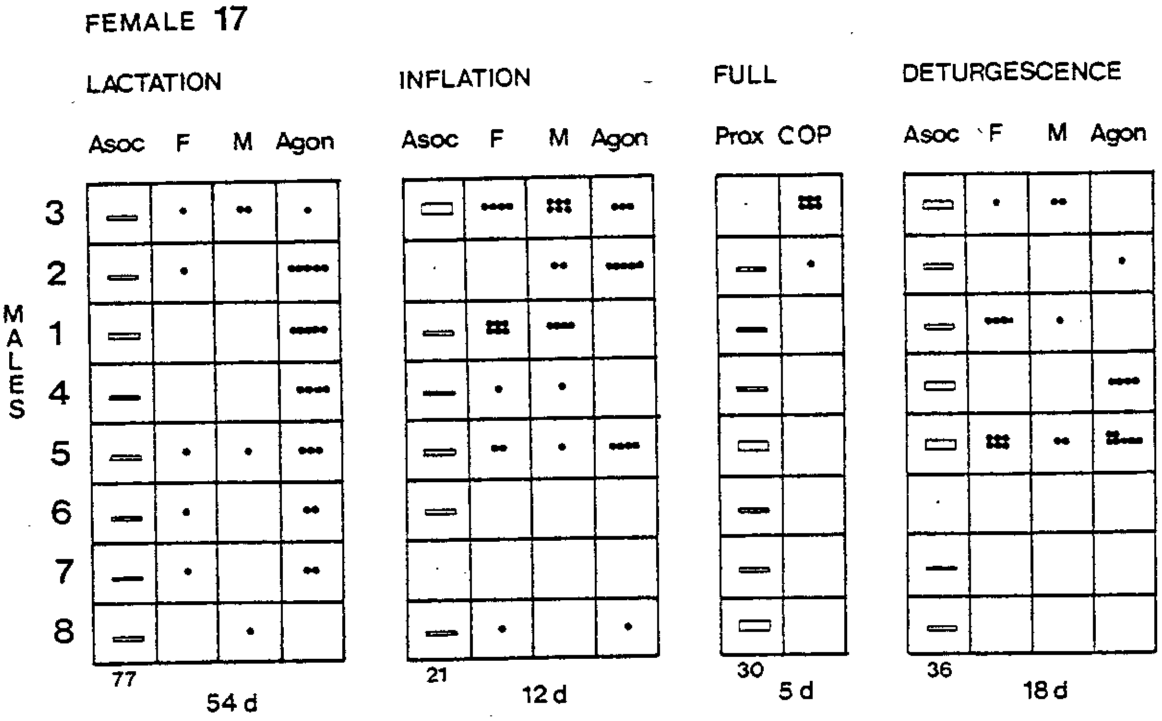
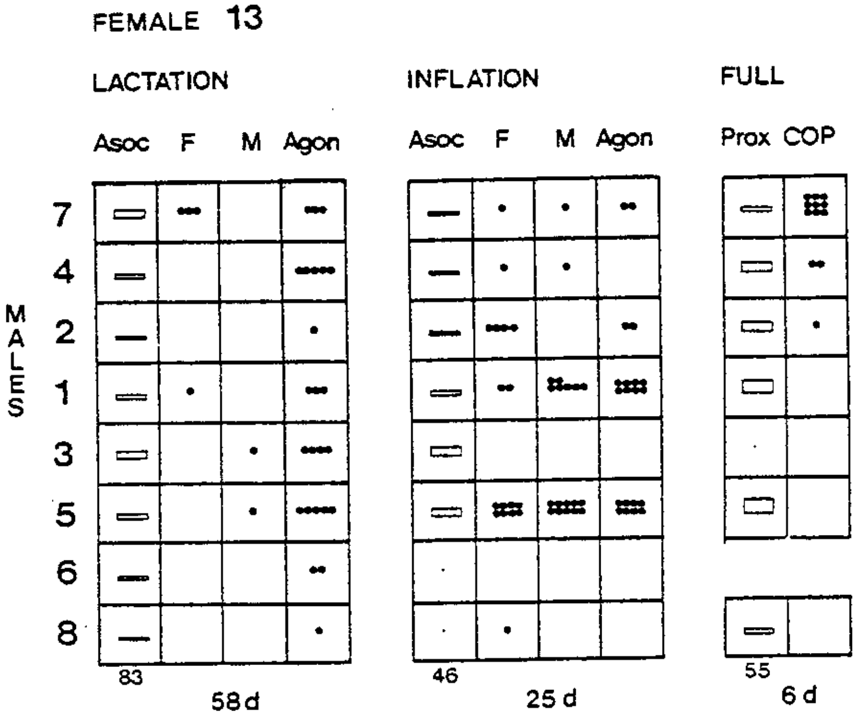


FIG. 8.19



Figs. 8.18 & 9.19. Caption as explained under Fig. 8.14.

FIG. 8.20

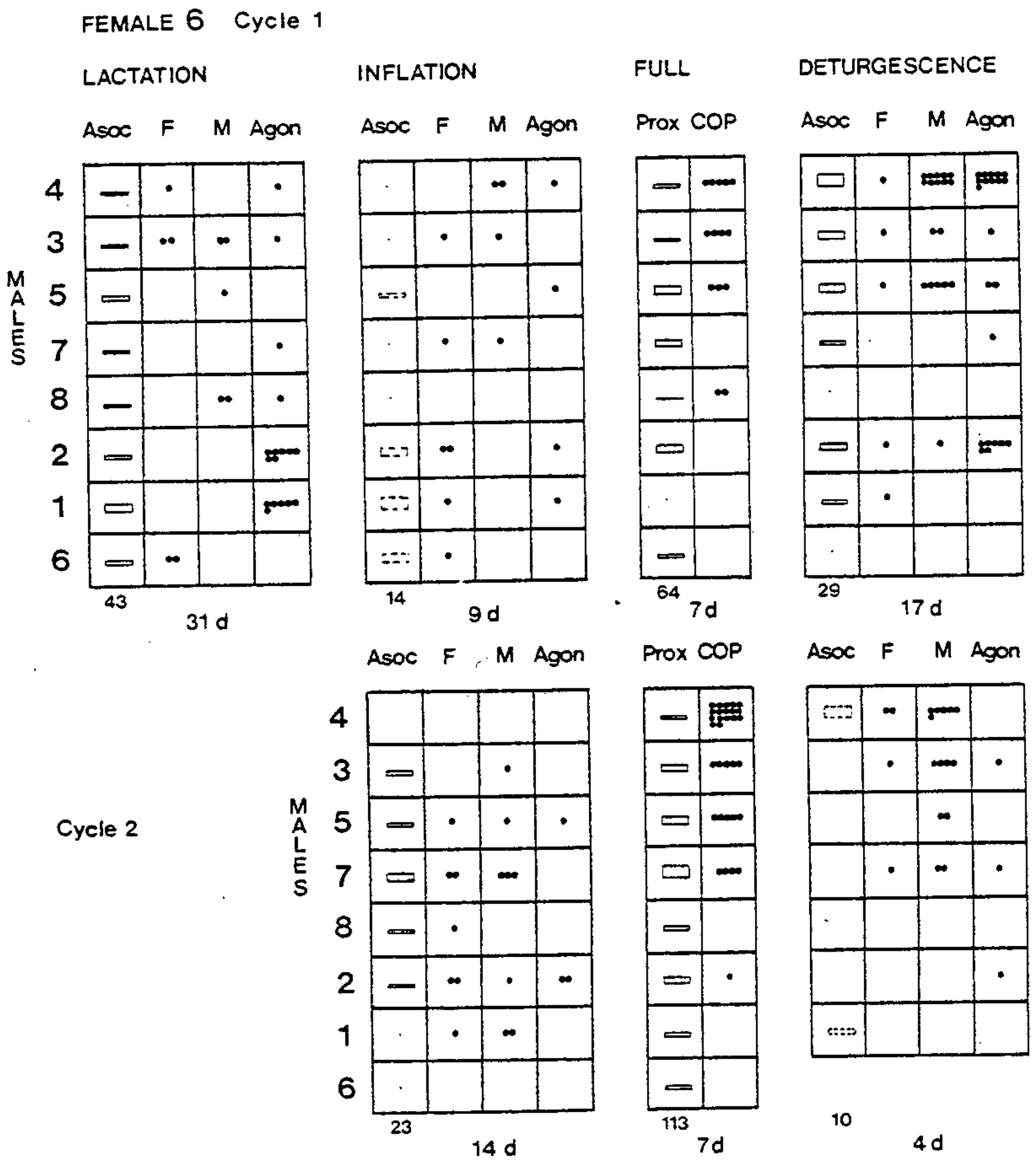


Fig. 8.20. Caption as explained under Fig. 8.14.

no prior relationships, namely A3, A4 and A5; and during the second, she mated with these males and A7. The striking patterns for this female were first that during deturgescence those males who had mated showed marked increases in affiliative and possessive behaviour (and, for A4, supplants); and secondly, that it was these same males who mated in the next cycle, and again interacted more in deturgescence.

These data suggest that relationships may become established as a result of initially opportunistic mating. Although there were a number of initial matings which were not followed by interaction in deturgescence (e.g. F17 and A3: F5 with A2 and A4 in her third cycle), yet the tendency of some males to act possessively to their recent consorts, or even to consort them in deturgescence, was quite striking in the field.

8.4.7 Partnerships in consecutive cycles

There are only three opportunities to compare mating relationships in consecutive cycles of the same female. F6 clearly tended to mate with the same males in her second cycle as she had in her first. F5's second cycle almost exactly repeated her first, but her third cycle differed completely in mating partnerships. These data suggest that partnerships occurring in one cycle tend to be repeated in the next, but not invariably.

8.4.8 Summary: the formation of mating partnerships

In three of the nine cycles, mating partnerships arose between animals who had no observed prior history of interaction (the first cycles of F5 and F6, and the third cycle of F5). However, the majority of partnerships coincided with previous priorities of interaction, by male, female, or both. It was not clear to what extent each sex contributed to the high frequency of association seen in some pairs. Female selectivity among males was apparent through grooming, which tended to be given more to higher rankers, and presenting, which tended more often to be given to the α-male. There was evidence that presenting was used to initiate relationships, but was not especially frequent in established ones: thus F5 presented to A1 far less than did F7, but she presented to unfamiliar consort partners at full swelling more than she did to her usual partner: presenting was also more frequent in resumption cycles (7.5.5). There were insufficient data to show whether consort females' tendency to move towards rivals expressed selectivity for males, or increased the chances of being consorted by them (8.4.5a).

Male selectivity toward females was apparent in their affiliative and possessive behaviour. There was evidence that a male who interacted frequently with a female in this way could inhibit another from consorting her (e.g. A3's behaviour to F1 and F17), even if the other male was of higher rank or was preferred by the female. Finally, pairs who interacted affiliatively also tended to exchange more agonism, apparently a consequence of their frequent proximity.

Only one pair showed mutual and frequent interaction and mated at full swelling (F7 and A1). Other frequently interacting pairs showed a more one-sided relationship, or did not mate at all. There are four reasons for failure to mate: first, because another male had established priority over the female (e.g. A3 over F1): secondly, because the female was not attractive (e.g. F13): thirdly, because the male had been discouraged from consorting by aggressive competition (e.g. A1's failure in F5's third cycle): fourthly, because the male was consorting another female (e.g. A4 during inflation of F1).

Whether mating partnerships follow previous interaction or arise opportunistically, there is evidence they will be perpetuated. First, mating may encourage subsequent interaction during deturgescence, as suggested also by data in 8.4.4. Secondly, there was some consistency between mating patterns of consecutive cycles. It was interesting that in the most consistent partnership in the troop, between A1 and F5, the majority of interactions came from the male.

8.4.9 Contribution of social relationships to each male's mating success

The relationships described above contributed differently to the mating success of each male, as can be seen from Fig. 8.12. Thus A1's success depended primarily on his partnerhsips through the cycle with F5 and F7, both of which included compliance if not preference by the female. In contrast, A2's copulation score resulted almost entirely from his competitive access to F5, and did not reflect any prior relationship with this female. Many of A3's copulations occurred through his possessive monopoly, without overt competition, of F1 and F17; he may also have been developing a partnership with F6, and he also gained competitive access to F5. The majority of A4's copulations resulted from initially opportunistic matings with F6 which he perpetuated in her second cycle, although he also mated opportunistically with F7 and competed to mate with F5. Similarly, many of A5's copulations were achieved because he repeated initially opportunistic matings with F6, although he also mated opportunistically with F7. Finally, A7's matings were entirely opportunistic in that he mated with females who were less attractive, either at the end of full swelling (F5 and F6) or in a resumption cycle (F13).

Overall, the males who achieved copulations concordant with the interactions they gave to females were A1, A3, A4 and possibly A5. Those who achieved copulations with females from whom they had received affiliative behaviours were A1 and to a lesser extent A3: and those who attained copulations opportunistically were A2, A3, A4, A5 and A7.

5. DISCUSSION

8.5.1 Single- and multiple-mount copulations

One unexpected finding was that yellow baboons showed both single- and multiple-mount copulations; although some of the latter reflected difficulties with intromission, the data in 8 part 2, suggest that yellow baboons are intermediate between single-mounting olive baboons, and the series-mounting chacma and hamadryas (refs. in 8.2.1). It is not obvious why such closely-related forms should have diverged so. Series-mounting is the commoner pattern among Cercopithecids, but single mounting is found in bonnet and stumptail macaques (Simonds, 1965; Blurton-Jones & Trollope, 1968, respectively), vervets and mangabeys (in Struhsaker & Leland, 1979). For the male, series-mounting must require more energy (Carpenter, 1942a) and greater risk of harassment (DeVore, 1965), so that if yellow baboons can ejaculate on one mount, why do they not do so always?

Physiologically, variation in the number of mounts to ejaculation may reflect nothing more than variability in male ejaculation threshold (Michael & Saayman, 1967), or physical compatibility within the pair (e.g. it was very frequent between A4 and F6). Alternatively, it might be facultative; if the female provides the consummatory stimuli, (Erikson, 1967; Allen & Lemmon, 1981), she might withold them, or the male might withold ejaculation.

If series-mounting does have advantages, they could be physiological. Because multiple-mounting increased the female's number of copulation calls and locomotory responses (cf. Macaca; Zumpe & Michael, 1968), so it might also increase internal responses which favour conception, such as sperm transport (Buechner et al., 1966; Fox et al., 1970; Adler, 1978), or induction of ovulation. Copulation-induced ovulation has been suggested in humans (Jochle, 1975): if it does occur it is likely to be triggered hormonally, but it is interesting that the baboon ovary is supplied with smooth-muscle fibres (Beck & Blair, 1977), and dual innervation of unclear function (LePere et al., 1965).

Increases in the number of mounts might also have social advantages to the male. First, it may strengthen his bond with the female, and if her response is similar to orgasm (7.10.4) it might also reduce her proceptiveness toward other males. Secondly, it may affect the behaviour of rival males: when mounting (with or without intromission) appeared to be a direct response to social events, these were usually ones eliciting male possessiveness e.g. at risk of challenge from rival males, often with herding; at proximity of other troops; or at establishment of a new consortship. The time-course of incipient mounts in Hausfater (1975) parallels that of behaviours such as herding more closely than that of copulation itself (ibid: Figs. 15, 16 & 17). Mounting unavoidably demonstrates the relationship of a consort pair, and it is argued below that this may inhibit rival males (8.5.2). The contexts separating single- from multiple-mount copulations would repay investigation. It seems plausible that if the pattern is under facultative control by the male, and series-mounting does have social or physiological advantages, males will show series-mounting except in those troops where copulations are frequently harassed: and if the pattern is obligate, that single mounts may have evolved in species where the risk of harassment by males is high.

8.5.2 Consortship and the inhibition of rivals

Female behaviours in consort have been discussed in terms of proceptivity and receptivity (7.11.2a): it was suggested that presenting elicits male possessiveness more than copulation, and data in 8.4.6 show that presents were used selectively. It is necessary only to add that while females usually appeared at ease with their male consorts, yet on occasion they seemed agitated, persistently moving ahead and avoiding the male's mount-attempts, especially when a new male had just taken over. More data were needed to establish whether by such behaviour, or by moving towards other males (8.4.5a), females could discourage consorts or encourage rivals (Bachman & Kummer, 1980; Rasmussen, 1980).

Male behaviours to the female consort were given three possible functions (7.11.2b). First, affiliation (reassurance) to the female. Secondly, possessiveness, to restrain the female or prevent her interacting with other males; and thirdly, advertisement, to demonstrate the male's priority of access to the female. The selective distribution of males' interactions to particular females, described in 8.4.6, provides further evidence in support of this. In the field it is clear that onlooking baboons can discriminate that a pair are in consort, and that males at least alter their behaviour accordingly (6.7.2). It is a necessary complement to the consort male's behaviour that other males respect to some degree his priority of access to the female. On the basis of mainly qualitative observations in this study, and findings from other studies, it is suggested that this respect is analogous with the triadic differentiation which protects pair bonds in hamadryas baboons (Kummer, Gotz & Angst, 1974): indeed, given their congeneric status, it may be homologous. A potential rival male is inhibited from interacting with a female after he has seen her interact with another male, the "owner". The grounds for this suggestion are presented under three headings parallel to those in Kummer _et al_. (1974) pp.75-84.

_1._ Other males avoid interacting with members of a consort pair.

Hamadryas males avoid oestrus females belonging to other units (Kummer, 1968), and in captive experiments show characteristic behaviours of embarrassment and may try to escape from an established pair (Kummer _et al_., 1974). Gelada unit males also respect one anothers' "ownership" of females, but unattached males do not (Dunbar & Dunbar, 1975). Sugawara (1979) and Boese (1975) describe baboon males who consistently avoided their former females who had switched allegiance to another male.

At Ruaha, rival males tended to avoid consort pairs, even if dominant to the consort male (6.7.2). They seldom initiated interaction with either member: in 55 non-aggressive interactions between a consort male and another male, the recipient was in consort in only 22%. Males approaching a female who had recently been in consort sometimes looked around furtively before attempting to mount: negative responses to presents may have had a similar cause (5.7.3c). Males in consort at Gombe become temporarily dominant over other males (Packer, 1979b), and immigrant males gain impunity from resident males by temporarily initiating consortships with inflating females (Packer, 1979a, p.16). At Ruaha, A4 similarly ended a dispute with A7 by consorting a non-swollen female.

2. A male may direct behaviour to the rivals indicating his relationship with the female.

Hamadryas males increase their possessiveness and may threaten rivals when one of the females is in oestrus (Kummer, 1968): and in captivity, the owner's 'notifying' of (presenting to) the rival increases rival inhibition (Kummer et al., 1978). Gelada unit males also interfere with rival males' overtures to the unit females (Dunbar & Dunbar, 1975), and may initiate ritual 'attacks' on the all-male groups which appear to demonstrate their ability to defend their females (Mori, 1979).

Males at Ruaha who were showing possessiveness or consortship to a female sometimes interacted with nearby males assertively, as though to remove them from the vicinity of the female. For example, a consort male dismounted after copulation then immediately moved towards a nearby male who avoided; one male showed a conspicuous increase in non-aggressive contact to other males during consortship with a preferred female; and once A1 herded F5 from A2, then persistently caused A2 to avoid until he had herded him beyond the perimeter of the troop. Males appeared to establish priority over inflating females in this way: thus A3's possessive interactions to F1 were against her main associate from lactation (A4) and the male to whom she presented most in inflation (A1). Ransom (1971) also describes consort males initiating contact interactions with nearby rivals; and Seyfarth (1975, 5.4) describes how the α-male approached the β-male more when the latter was near cycling females.

3. Interactions in the consort pair are enhanced by the presence of rivals.

In hamadryas, the presence of rival males causes significant increase between female and owner in female grooming and male clasping, and lesser increases in male grooming, mounting and herding (Kummer et al., 1974):

herding is particularly frequent if the risk from the rival is high (Kummer *et al*., 1978). Gelada unit males also herd, groom, and mount more after a confrontation with another unit male, or with an all-male group (Ohsawa, 1979, p.36; Mori, 1979, pp.97, 184-185). Both Kummer and these latter authors describe the behaviour as 'demonstration' by the unit male of his relations with the female.

In this and other studies, consort males increase their interaction with the female when rival males are nearby by grooming (DeVore, 1965, Fig. 3; Ransom, 1971) which increases the likelihood the female will stay close. Rasmussen (1980) found that consort males groomed more the attractive females who were subject to more takeover attempts. Alternatively the male may mount (DeVore *ibid*.; Boese, 1975), or herd the female away (Ransom, 1971; Hausfater, 1975; Packer, 1979a). Ransom also recorded consort males attacking females who persisted in moving towards rivals (also Carpenter, 1942a; Lindburg, 1971; and pers. obs.).

These lines of evidence suggest that three kinds of baboons maintain their bonds with females in similar ways, and that they differ only in degree. Quantitative evidence in support of this is required. Kummer *et al*. (1970) consider that the hamadryas male pattern is merely an extreme form of the social possessiveness characteristic of Old World monkeys and apes. However, comparison of hamadryas and olive baboons, and their hybrids, suggest some qualitative differences between them which are apparently heritable.

First, savanna baboon males generally follow their female consorts, whereas hamadryas males train females to follow *them* (Kummer *et al*., 1970). Hybrid males lose this ability, and resort to following females like the savanna consorts (Nagel, 1971; Sugawara, 1979). However, the females do not differ: both types learn to follow hamadryas males, the olive baboons learning within one hour (Kummer *et al*., 1970).

Secondly, rival inhibition is more intense in hamadryas. The average distance between hamadryas males is greater than that between olive or hybrid males, while the latter two do not differ (Nagel, 1971). Also, inhibition in hamadryas is slower to wane, taking perhaps 12 hours (in the experiments of Kummer *et al*., 1974, p.64): whereas a savanna male who loses his female respects the consortship of his successor as soon as takeover is complete, although he may be more prone to shadow the pair (Hausfater, 1975) or harass their copulations (8.3.8).

Thirdly, hamadryas males apply their possessiveness to females irrespective of reproductive state, whereas savanna males usually limit it to fully swollen females. However, savanna males may consort females in other states (e.g. mothers, Altmann, 1980), and some paired relationships which include possessiveness may persist through reproductive changes (Cheney & Seyfarth, 1977; Seyfarth, 1978b).

Finally, why should a male's 'possession' of a female inhibit a rival of higher rank? A similar inhibition occurs in *M. sylvana* (Taub, 1980a), but it does not in chimpanzees, in which the α-male can absolutely prevent a lower ranker from mating, but the reverse is not true (Tutin, 1979a). Packer (1979b) attributes inhibition in savanna baboons to a variety of factors. First, the consort may be more willing to fight than the rival. Secondly, the value of the female may be greater to the consort, because he has already mated, than to the rival who has not: this asymmetry is however slight, and in practice would probably be over-ridden by male differences in reproductive value etc. Thirdly, if the female prefers the consort, the rival may be discouraged from attempting takeover; Bachman and Kummer (1980) subsequently provided support for this in hamadryas; Rasmussen (1980) found that singlehanded takeovers in yellow baboons were achieved more often by males whom the female preferred; and Seyfarth (1978a) observed an α-male who did not challenge the consortship of a female who preferred the β-male. To these it is worth adding that it may tactically be easier for a determined 'owner' to maintain proximity to a female than for a singlehanded rival to come between them.

8.5.3 Why do males consort outside full swelling?

Males sometimes consorted and acted possessively to inflating and deflating females. Ransom (1971) found that resident males consorted earlier in the cycle if a newcomer male had just joined the troop; and that lower ranking adults consorted earlier in the cycle while high rankers concentrated more on the most fertile period (also Packer, 1979b; Hausfater, 1975). Consorting early and late may secure chance fertilisations outside midcycle, and low rankers are undoubtedly forced to consort at such times. However the main consorter outside full swelling at Ruaha was the α-male, and other explanations must be found. First, starting early might be advantageous if prolonged consortship favours conception: for example, chimpanzees tend to conceive on long consortships away from the group (Tutin, 1979a); and baboon females are consorted for longer in conception cycles (Packer, 1979a), but cause and effect are not clear. Alternatively, the three facets of consort behaviour discussed above and in 7.11.2b suggest that the immediate consequences of consortship at other times may be social. First, early consortship may increase the co-operation of the female later on (Packer, 1979b). Secondly, an early consorter may inhibit other males from trying to consort the female subsequently. And thirdly, the consorter may reduce the likelihood that other males will be aggressive to him. The possessiveness which A1 showed to F5 throughout the cycle appeared to achieve both the second and third of these. The first and second reasons, female co-operation and rival inhibition, would also make it advantageous for males to specialise in particular females: Rasmussen (1980) found that males started consorting early with females who they preferred at other times. This suggests that although 60% of consortships at Ruaha began without overt competition, yet the selectivity of many such consortships may represent competition at a subtler level.

8.5.4 Competition and mate selection in this and other studies

The Ruaha study is compared with the results of the main published field studies of baboon mating in Table 8.XII. The findings of Bolwig (1959), Maxim et al. (1963), and Paterson (1973) are excluded, being mainly anecdotal. The table reveals that several features of mating behaviour vary together. Thus the S. African chacma troops have fewer adult males per female; their consortships are prolonged, and initiated with very little aggressive competition; rival males do not shadow consort pairs nor harass their copulations; copulations are series-mounts; and female preferences are evident and effective. In contrast, yellow and olive troops in E. Africa have more males per female, and consortships may be short, changing often with aggressive competition between males; rival males sometimes shadow consort pairs and may harass their copulations; mating is complete within one or two mounts; and female preferences do not obviously determine the formation of many consortships. However some E. African troops incline to the chacma pattern by having proportionately fewer males per female, and these tend to have longer, non-competitive consortships (e.g. SV troop in DeVore, 1965; also Paterson, 1973).

TABLE 8.XII:

Baboon:	Chacma	Chacma	Chacma	Yellow	Yellow	Olive	Olive	Olive	Olive	Olive
Site:	Cape	Transvaal	Mt. Zebra	Amboseli	Ruaha	Ishasha	Gombe 1968-9	Gombe 1972-5	Nairobi	Nairobi
Troop:	S	W	–	Alto's	Msembe	S & V	B	A/B/C	SV	SR
Adult ♂♂	2	3	2	8	8	5 & 17	c. 8.5	c. 7.2	5	6
Adult ♀♀	8	31	8	c.11.5	19	5 & 16	16	c. 13	12	7
Ratio ♂:♀	1:4	1:10.3	1:4	1:1.4	1:2.4	1:1	1:1.9	1:1.8	1:2.4	1:1.2
$\bar{x}$ length consortship:		2.7d	3.5d		<1d					
Range consortship:	2-3d ?	1-15d	1-8d	<1d ?	1-8d	<1d	brief	to 7d	2+ d	few hours to days
Male aggr. competition:	rare	rare	none	some	some	none	much	much	rare	much
Harassment of copulation:	rare		none	some	rare	"interest"	often	often	rare	much
Rivals shadow consort prs.:			no	yes	rare		yes	yes		
Consort ♂ herds vs. rivals:			no	yes	yes		yes	yes	no	rare
Copulation series mount:	yes	yes	yes		24%					
Copulation single mount:				75% ejac	76%		yes		yes	yes
♀ preferences evident:		yes	yes	suggested	yes	possibly	yes	yes	suggested	suggested
♀ preferences effective:		yes	yes		some	possibly	some	some	not very	not very
♂ dominance & mating success:	strongly α♂ 93%	inverse	strongly	approx.	yes		approx.	yes	approx.	approx.
References:	Hall '62 Hall '63 Hall & DeVore'65	Saayman 1970 1971b	Seyfarth 1975 1978a	Hausfater 1975	this study	Rowell 1967a 1967b	Ransom 1971	Packer 1979a 1979b	DeVore 1965 Hall & DeVore 1965	

It is too early to conclude that these differences between chacmas and the E. African baboons are inherited behavioural differences, until we have data from chacma troops containing as many males (absolutely and proportionately) as the E. African troops; for example, those studied by Busse and Hamilton (1981). The most likely species-difference is the series-mount of the chacma, although even that might be a facultative pattern permitted by low levels of competition and harassment (8.5.1). It seems unlikely that the sex-ratio itself is an inherited difference, and it is more likely to reflect habitat quality (Hall, 1965b).

The more convincing hypothesis is that the crucial difference is the number of males <u>per female</u>, so that with more males there will be more competition, shorter consortships, and possibly shadowing and harassment. The effect of this may be modified by other factors. First, if the male dominance hierarchy is not clear-cut, overt competition may be more intense (e.g. DeVore, 1965, SR troop; Struhsaker, 1975, p.60); with a stable hierarchy, competition could be latent; but in both cases it would favour the success of high rankers. Secondly, any tendency for females to become receptive simultaneously would reduce the mating advantage of the highest rankers, who could not monopolise them all, and might at times reduce the intensity of competition (e.g. the change in SR troop, Hall & DeVore, 1965). Thirdly, conditions of visibility in the habitat may affect male competition: in poor visibility, consort pairs might be less susceptible to challenge, and allies less likely to join in, but such challenges as do occur may be more successful because rivals could more easily separate female from consort.

The effectiveness of females' preferences may also vary with these circumstances. Evidence from this and other studies suggests that the results of male competition often over-ride female choice (DeVore, 1965; Ransom, 1971; Rasmussen, 1980;also 8.4.6). If so, female choice will be most effective when more females are simultaneously receptive, and competition reduced. It might also be enhanced if male dominance relations are not clear-cut, such that a female's preference might bias the outcome of competition between two equally-matched males more than between a clear dominant and subordinate. Female choice need not be antagonistic to male competition if both favour the high rankers, as found by Seyfarth (1978a), Rasmussen (1980), and this study.

Comparison between baboons and macaques generally support these conclusions. Most macaques are seasonal breeders, so that females are more likely to be receptive at once than in the non-seasonal baboons. Competition between males is usually less obvious (Conaway & Koford, 1964; Kaufmann, 1965; Lindburg, 1971; Kurland, 1977: but cf. Stephenson, 1976; Dittus, 1979); and females play a prominent role in initiating or changing consortships (Carpenter, 1942a; Lindburg, 1975; Eaton, 1976; Taub, 1980a). Therefore the lesser degree of sexual dimorphism in these species compared to baboons may reflect less intense selection for male competitive ability (Lindburg, 1975; cf. Clutton-Brock & Harvey, 1977, p.24).

8.5.5 Summary and conclusion: mating patterns at Ruaha

8.5.5a) Competition Young adult and prime-age adult males competed, consorted and copulated more than others. Older adults competed little, copulating with undisputed females. Therefore among adults the higher rankers (i.e. younger ones) mated most. In contrast, subadult males mated opportunistically (Saayman, 1970; Hausfater, 1975), the oldest least (Packer, 1979a).

Although competition occurred it was not intense, since over 60% of consortships began without dispute, and harassment was negligible. During competition, a challenger was only likely to obtain a female singlehandedly from a consort male of lower rank. However, the chances were greater for rivals acting in alliance, increasingly so the more males became involved, and such alliances allowed middle rankers to obtain females from higher rankers (also Hall & DeVore, 1965; Packer, 1979b; Rasmussen, 1980). The two highest rankers, as newcomers, did not have the benefit of alliance. After defeat in aggressive competition, males sometimes abstained from consortship or left the troop for a day or so, allowing lower rankers opportunity to consort.

Two males were noteworthy. A2 appeared to consort more at night, arguably because he was more agile in the sleeping trees (8.3.5, 8.3.14). A5 was remarkable for his willingness to aid A3 in consort disputes, although the benefit usually went to the latter (8.3.14). Similar one-sided alliances also occur at Gombe (pers. obs.). There was no evidence as to whether these two were related, or whether A3 might have reciprocated to A5's benefit at other times: during this study, they tended rather to compete. Because ten of their twelve challenges were against newcomers, it is possible that the alliance originated when the newcomers joined the troop but that A3 utilised it later to obtain females. Ransom (1971) also suggested that an ally's willingness to join was affected by his antipathy towards the opponent.

If these patterns of male competition are typical of other troops, it suggests that sexual selection would favour any genetic traits enhancing the following.

(a) High rank in males: because rank appears age-dependent (6.3.8), the crucial factors would be to attain higher rank and to keep it longer than males of similar age.

(b) Competitive ability unrelated to dominance: The advantage of agility in consorting in trees at night might limit the selective advantage of large size (as it affects agonistic ability): very large size may even be a disadvantage on the ground (Packer, 1979b, p.41). Alternatively, social skills such as the ability to establish and benefit from alliances, and to establish possessive relations with certain females, might also be favoured.

8.5.5b) Mate selection Selectivity in mating partnerships has been summarised in 8.4.8. Some pairs who interacted frequently outside full swelling also mated often, others did not. There was evidence that partnerships of mating tended to be repeated (also Goodall, 1975; Fedigan & Gonzoules, 1978) suggesting that relationships may be enhanced by experience of mating. Although females interacted selectively among the males, their preferences were sometimes overridden by male selectivity, or by the outcome of male competition.

There were too few subjects to establish what individual characteristics are favoured by each sex. Females tended to prefer high ranking (i.e. younger) adult males especially the α-male (see refs. in 8.4.1): they would therefore have been choosing males of proven quality. Alternatively, they may have favoured the α-male as a newcomer, a recurrent finding in mating preferences (e.g. Packer, 1979a: refs. also in 9.2.1c): but even among resident adults the higher rankers tended to receive more presents and grooming (8.4.5a). There was no evidence that females favoured particular males because they were either protective to infants, or active in troop defence, (e.g. Trivers, 1972).

Males showed less concensus in the distribution of their interactions among females. Their selectivity seemed influenced by female's preferences (e.g. F7 with A1) and by their availability as determined by (a) the possessive behaviour of other males (e.g. A1 did not consort F3), and (b) the intensity of competition encountered over the female (e.g. A1's failure to consort F5 in her third cycle). Thus F6, with no particular male partners in inflation, consorted with the highest rankers available at the time. The slight correspondence between ranks of mates, although not significant, suggests that males might favour high ranking females, which would be advantageous if they reproduce faster (as in Drickamer, 1974b; Dunbar & Dunbar, 1977; Sade et al., 1977; Wilson et al., 1978; Silk et al., 1980). However the evidence is that female availability is the male's first criterion, agreeing with Packer's (1978b) conclusion that males consort more according to the selectivity of other males than to the particular qualities of the female.

The study was too short to determine whether mating partnerships follow longer-term relationships, as in some pairs of baboons elsewhere (Ransom & Ransom, 1971; Seyfarth, 1978b; Altmann, 1980), or whether they contrast with them as is characteristic of macaques (Enomoto, 1978; Fedigan & Gonzoules, 1978).

8.5.5c) Sexual selection Although these data relate to mate selection and mating success, their relevance to sexual selection is not clear. This is, first, because we do not know what proportion of individual variability in behaviour is inherited, and what proportion acquired during life. Secondly, because adult male rank was related to age, it is not certain that males' differences in mating success would have persisted throughout life; although Saunders and Hausfater (1978) suggest that they would. These data therefore demonstrate mechanisms which contribute to differences in male mating success, but only by comparison with the findings of other studies can we estimate their relative importance and their implications for evolution.

CHAPTER 9

GENERAL DISCUSSION

9.1.1 Comparison with baboons at Gombe and elsewhere

Because no previous studies had been made on the Ruaha population, it is worth reporting some qualitative features of their behaviour. In Appendix III are listed a number of differences between these baboons and the olive baboons at Gombe (pers. obs., data unpublished), with reference to other studies.

While olive, yellow, and chacma baboons are commonly considered a polytypic species (2.IIIa), it is not clear whether they represent forms which have diverged in isolation during the Pleistocene but whose ranges are now contiguous, or whether their differences are currently maintained by local selective pressures. Examples of the latter might be disease (e.g. Wheatley, 1980), or differences in available foods, although there is insufficient evidence yet that they differ in preferred diet or habitat-type. It may be significant that the distribution of the yellow baboon coincides with that of the more erythristic forms of Cercopithecus (Hill, 1970, p.269), suggesting local selection for colour. The yellow baboons' morphology, gracile with an arched tail that appears to act as a counterweight during the stride, looks more appropriate to efficient walking on the ground than does that of the olive baboon.

Whatever past or present selective forces may have separated these baboons, their behavioural differences may have three origins. First, they may be direct responses to different environments: the habitat at Ruaha was less forested than that of baboons studied at Gombe and Ishasha, but with less open grassland than at Amboseli, Mikumi, or Gilgil. The pattern of supplanting may reflect the high intensity of feeding competition (Appendix III, 3). Secondly, they may be inherited differences in behaviour, whose function is not obvious, since those in the appendix seem insufficient to enhance reproductive isolation. Thirdly, they may be pre-cultural differences (e.g. 5.7.3b), and therefore either random or locally adaptive.

The patterns reported in Appendix III place yellow baboons closer to olive baboons but with some features of chacmas. This is surprising since Hill (1970) considered that olive and chacma are taxonomically closer than either is to yellow baboons.

9.1.2 Social relations among adults

9.1.2a) The distribution of social behaviours in this study are summarised in the following paragraphs. Most patterns have been discussed in the relevant chapters, and only more general issues are mentioned here. The data obtained in this study were probably biassed towards the behaviour of males: this is firstly because *ad libitum* sampling had to be limited to conspicuous patterns visible from afar, while relations between females may be better revealed by subtler patterns like friendly contacts, approaches, and coordination of proximity which could not be reliably recorded. Secondly, the choice of behaviours partly resulted from the observer's interest in characterising the males, ultimately in relation to mating: although it does not reflect any belief that males are any more important to social structure than are females (1.1).

9.1.2b) Relations between females Behaviour between females was more affiliative than that between males, in that they groomed one another, while males did not, and they exchanged much less agonism. Patterns of association were characterised by frequent proximity between mothers, attributed to the attractiveness of their infants; patterns of grooming revealed the attractiveness of mothers to non-mothers, and an affiliation between close-rankers which was also reflected in their alliances. The mothers' attractiveness may bring them safety in numbers, and social experience for the infant, but it has its costs in that lactating females are most susceptible to disease (Freeland, 1976, p.15) and in that mothers may receive so much attention as to cause them distress (Altmann, 1980). In all, affiliation was most affected by reproductive state (with pregnant females also more reclusive), and closeness in rank which may reflect kinship (Moore, 1978).

Patterns of agonism between females were primarily affected by their position in the dominance hierarchy, which closely determined the amount of agonism each gave or received. Allied aggression tended to be given to close rankers, possibly concerning maintenance of dominance ranks within or between matrilines. Reproductive state had less effect, although mothers were often supplanted (again because of their infants), and cycling females tended to give and receive more agonism. The fact that pregnant females were supplanted least probably reflects their peripherality.

Overall, these patterns agree with the existence of long-term bonds between females, through kinship or familiarity. The high direction constancy of their agonistic interactions may reflect both their kinship, and that their priorities in reproduction are to feed efficiently and reduce the costs of social interaction, especially of agonism (6.4.6, 6.11.4).

9.1.2c) Relations between male and female Several patterns between the sexes were consistent in most types of interaction. First, adult males were involved more than subadults, both in affiliation and in agonism. Secondly, among female classes, cycling females were more frequently involved with both adult and subadult males, while mothers were involved frequently with adults but very little with subadults.

There was evidence that females who associated and exchanged affiliation with males also received more agonism from them, notably supplants. Thus association with, and agonism from, males tended to be more frequent for high-ranking and for cycling females. Among adult males, high rankers interacted more with females (chiefly because of their high rates with cycling females); but in contrast, among subadults the lower rankers, who were smaller and presumably younger interacted more.

The females' priorities in reproduction - to obtain high quality mates, and to obtain protection for the infants - are exemplified here respectively by the cycling females' greater affiliative interaction to high ranking adults, and by the mothers' association with prime-age resident males. The latter were anyway the males most likely to have fathered the infants concerned (6.9.6). The converse priorities for males, to maximise the number of matings, and only secondarily to provide protectiveness, were also evident. Competition between males favoured the matings of high rankers, at expense of post-prime adults. Although males who have been in a troop for longer might have greater reproductive interest in protecting immatures, this was only evident in the contrast between newcomers and residents, but older residents did not obviously contribute more than young ones. The study was too short to establish whether the males who interacted most with infants did so especially to those of females with whom they had mated (e.g. Seyfarth, 1978b; Altmann, 1980).

The most interesting feature of this pattern is the contrast between cycling females and mothers in their 'choice' of adult males. While both classes were involved with the three prime adults, cycling females also interacted frequently with newcomers, while mothers had hardly any interaction with the newcomers, but interacted frequently with post-prime A7. This contrast may illustrate a general pattern. Other authors report cycling or oestrus females being particularly attracted to unfamiliar males (Ransom, 1971, p.235; Packer, 1979a, pp. 14, 18, 27; Hrdy, 1977). Females in oestrus may range more widely, becoming more likely to meet other groups (Packer _ibid_. p.14; Nash, 1976, p.72; Cheney & Seyfarth, 1977: also in chimpanzees, Tutin, 1976; Nishida, 1979; Pusey, 1980; also see Rasmussen, 1979), and may mate with them. In complete contrast, however, baboon females with young infants _avoid_ unfamiliar males, and may respond to them with fear (Packer, 1979a, p.14; Busse & Hamilton, 1981).

Parallel to this is Seyfarth's (1978b) observation that some females _changed_ their preference among males between lactation and cycling. And there is some evidence that macaque females will not tolerate immigrant males until the onset of the breeding season (Vessey, 1971; Bernstein _et al_., 1974, p.520). Cycling females' preference for the unfamiliar may favour outbreeding (Packer, 1979a), and by attracting immigrants may increase male-male competition and thus the resultant quality of their mates (Clutton-Brock & Harvey, 1976; Freeland, 1976; Packer _ibid_.). However, immigrants may bring diseases, and some risk of infanticide (6.9.6, 6.11.1). It has been suggested that the willingness of langur females to mate with outsiders, and the resumption of cycling by patas females after male takeover (quoted from Loy, 1974: also found in geladas, Ohsawa, 1979) might reduce any newcomers' tendency to infanticide (Hrdy, 1977). However it is the _mothers_ who are most at risk, both from disease (Freeland _ibid_.) and infanticide, and either of these may explain their lack of relations with the newcomers at Ruaha. If females' preferences _do_ gradually change with reproductive state, it would be interesting to know if this is mediated hormonally, or through changes in the mother's protectiveness to the infant.

9.1.2d) Relations between males Interactions between males were usually tense, either assertive or aggressive, and their agonistic rates were far higher than those among females (6, part 4). Individual rates of agonism were determined far less by their dominance rank than were those of females: some males were particularly assertive and aggressive to their subordinates, and many more interactions were given from subordinate to dominant. The pairs who associated and allied frequently also exchanged much agonism, suggesting that relationships even of association and alliance were not 'affiliative' in the usual sense.

The age-range of the males allowed construction of hypothetical life-histories with respect to spatial pattern (3.VIc), affiliation (4.5.6), agonism (6.10.4) and mating (8.3.14). Their individual differences are also discussed in 6.7.12, 6.7.13, 6.9.3, 6.9.6 and 6.11.1.

Overall their differences may be summarised in terms of the contrast between adults and subadults, and the variation among adults in terms of dominance rank, age, and seniority. The latter affected tendency to ally, and to interact with infants, of use in agonistic buffering.

The subadults were not markedly aggressive, even when of quite high rank, and did not compete to mate: two associated often with adults, and received much agonism from them. The other two were more peripheral. All showed particular interest in other troops, moving closer to watch in contrast to adults who tended to herd females away (Cheney & Seyfarth, 1977; Packer, 1979a).

Adult males generally interacted with males more than did subadults, although two of the post-prime adults interacted very little. The two young adults had established few relationships with males or with mothers, apparently because they were newcomers. Therefore without allies or access to infants, they obtained resources including swollen females by virtue of their high rank alone. They were also the most frequent targets of 'gang attacks' (6.11.1). A1's relations with males were partly affected by his persistent association with F5, which appeared to give him some protection against them (8.5.3) and also gave him considerable mating success. A2's relationship with F9 allowed him to be the first of these two newcomers to gain access to a black infant (Ngatwika, pers. comm.): the infant was conceived after A2 had joined the troop, but its paternity is unknown. This suggests one way in which newcomer males may become focal, although Saayman (1972, p.80) provides an alternative example, and it is possible that some males never do (pers. obs. at Gombe).

The social position of the three prime adults was compounded from their high competitive ability (ranks 3, 4 and 5) and because as residents they had allies and access to infants. Alliance and infant-use increased their effectiveness against newcomers and against one another. The position of two of the post-prime males, A6 and A8, suggests that as males age their competitive ability (and thus rank) declines, and females no longer prefer them (Saayman, 1971b, describes an exception, the old male Yogg who was strongly preferred). A7 appeared to be an ageing focal male, compensating for his declining competitive ability by assertiveness to high rankers, by alliance, and by use of infants; and for his decreased attractiveness to females by grooming them very much.

The low rank of the older adults illustrates predictions that old males should rank low in competition for minor resources such as food. However, because an oestrus female is a more valuable resource for an aged male (of low reproductive value) than for a young male, old males are expected to retain high rank in competition for such females. This is predicted by Clutton-Brock and Harvey (1976, p.220), and by Popp and DeVore who cite the example of old male Kovu (in DeVore, 1965) who was a successful mater. The present study does not support this hypothesis (8.3.14c): furthermore Kovu gained matings through alliances, not by his individual ability, and the other example cited by Clutton-Brock _et al_., did so through female choice. The data of Packer (1979b, p.41) _do_ show that older males rank higher for consorting than for dominance, but he ascribes this to _experience_ rather than changing resource value.

The pattern of alliance between resident adults resembled that of the 'central hierarchy' described by Hall and DeVore (1965): the differences at Ruaha were that the males most often involved in alliances were not the high_est_ rankers, and that the allies also competed _against_ each other whereas the 'central hierarchy' males were mutually tolerant. The original descriptions also suggested that central hierarchy males provided most protection for the mothers (but see Altmann, 1980, p.118). In all, the central hierarchy concept combines males' spatial position, dominance rank, alliance, and relations with mothers: thus it is a compound concept, and there are no *a priori* reasons why its components should vary together. In Table 9.1, relevant measures are compared across the eight adult males at Ruaha: these are dominance rank, apparent age, rate of aggression in alliance with males, alliance with males as *proportion* of all aggression given, and (from Table 3.9) percent time with mothers, and percent time in clusters. It is already known that rank is the inverse of age (6.3.8), and that males who spent more time with mothers also frequented the clusters (3.Vd, iii) and interacted more with infants (6.9.3). The remaining pattern is that (a) older, lower ranking males were in alliance for proportionately more of their aggression given, but especially (b) males' rate of aggression in alliance was related to time spent with mothers and to time spent in clusters. Thus spatial position and relations with mothers are related to involvement in alliance with other males: but none is related to dominance rank. This is because the four focal males, A3, A4, A5 and A7 were the top four in all three measures. While it is easy to see a causal link between clustering and time with mothers, it is not clear why they should be related to alliance. It could be that alliance was an inevitable consequence of proximity to the same females, but the frequency of some alliances (e.g. between A3 and A5) suggests that they were more than that. Because the males involved were the three *prime resident* adults, with one post-prime, it is suggested that the keys are *familiarity*, in that longer-term residents will be familiar with one another and with females but newcomers will not, in combination with *rank*, in which low rankers (in this troop the aged males) will be excluded.

9.1.3 The evolution of social skills

Contexts and details of interactions may reveal much that is not apparent from simply considering *rates* of interaction. Contexts have been referred to repeatedly in the text (4.5.3, 5.7.1, 5.7.3, 6.2.3, 6.4.6, 6.8.6, 6.9.2, 7.11.2, 8.3.11, 8.5.2). It was apparent during observations that any one behaviour may have a variety of

Table 9.I: Spearman rank correlation coefficients comparing the eight adult males in terms of dominance rank, apparent age (rank 1 as the oldest), rate of giving aggression when allied with males (repeated with observability correction in brackets), the proportion of aggression given in which allied with males, the percent time with mothers, and the percent time in clusters. The latter two measures are from Table 3.9. A coefficient of .714 corresponds to $p < .05$.

	Age	Allied aggression	Proportion allied	Time with mothers	Time in clusters
Rank:	-.964	-.238 (-.405)	-.857	-.429	-.214
Age:		.222 (.408)	.865	.408	.259
Allied aggression :			.333 (.643)	.810 (.691)	.762 (.429)
Proportion allied. :				.286	.048
Time with mothers :					.833

results according to the context and the way in which it is used. Interactions were sometimes directed to modify the behaviour of others in an apparently purposeful way. Three examples are grooming, male interaction with infants, and male consort behaviour. Each may be assumed to have a primary adaptive function, respectively hygiene, protection of infants, and monopoly of mates. However, each could be 'used' in other ways. For example, apart from being a general expression of affiliation, grooming was also done purposefully to elicit grooming in return (e.g. when males groomed females outside oestrus), or to prevent the recipient interacting with another animal, or to gain refuge from an aggressor subordinate to the groomee. The other two behaviours, infant-interaction and consortship, are both patterns in which the male may gain temporary dominance, or some impunity from attack (Packer, 1979b). Males sometimes utilised this by initiating such interactions when they were at risk from an opponent rather than in relation to the risk to the infant or the attractiveness of the female. It has been suggested that such 'use' of infants has to be learned (6.9.6). Similarly, Packer's description of immigrant males taking refuge from residents by consorting inflating females (1979a, p.16) also implies that this tactic is learnt since it is only multiple-transfer males, who have experience of consorting, that do it. These lines of evidence suggest strongly that animals who have learnt the effects of their behaviour on others may then use the behaviour in new contexts to their own advantage.

Baboons and other primates also show considerable flexibility in their longer-term behaviour, especially in showing behaviour appropriate to their social position. For example, Post et al. (1980, p.189) suggest that low-ranking baboons may choose particular foods or feeding sites because they incur less risk of competition. Alternatively, α-male chimpanzees do not need to consort 'on safari' with swollen females, because they alone can monopolise the female in the group, but lower-rankers must attempt to consort (Tutin, 1979a). The parallel in this study was the variation in the ways that males could improve their mating success above that available from their own competitive ability: thus A2 took advantage of his agility, the prime adults used alliances, and subadults made no attempt to compete but were quick to copulate opportunistically.

These short-term and long-term variants in behaviour suggest that primates show particular social skills. Any animal who lives socially is confronted with particular problems and opportunities, and if its response to these can affect its reproductive success the evolution of more complex social skills becomes inevitable (A. Jolly, 1966). While the variations in behaviour discussed above may represent genetically programmed responses to particular circumstances, yet the multiplicity of such circumstances which are possible in a social group suggests a more parsimonious viewpoint, which is that they are the products of broader cognitive abilities not tied to particular circumstances. As Humphrey (1976) points out, an animal may benefit not just from being able to learn, but also from an ability to assess complex and changeable social situations, to predict the behaviour of others, and to anticipate the effects of its own behaviour on them. Convincing examples of this have been described in chimpanzees (Riss & Goodall, 1977; DeWaal, 1978).

It is likely that such social skills will affect eventual reproductive success, not only in chimpanzees but also baboons and other social animals. There is evidence that the matrilineal ranking system, which is maintained by complex relationships between kin (Cheney, 1977; Walters, 1980) confers reproductive advantage on high rankers (refs. in 8.5.5b) at least in macaques; social pressures on female baboons are also particularly strong during motherhood, the most critical period of their reproductive life (Altmann, 1980). Male baboons also face social problems, but of a different sort. Each male must become integrated into at least two social groups in his life: initially, his natal troop, and after that, his breeding troop in which he must establish relationships with male and female which allow him to mate. He must also learn the competitive tactics of consortship, in which the ability to assess and predict may bring immediate reproductive benefits. Males can also learn to transfer from troop to troop with greater ease (Packer, 1979a, p.18). In all, baboons demonstrate social skills which are very likely to affect their reproductive success: the fact that they have these skills strongly supports the ideas of Jolly and Humphrey (above) that responses to the social environment have been at least as important as responses to the physical environment in the evolution of primate intelligence.

REFERENCES

Adler, N.T. (1978). On the mechanisms of sexual behaviour and their evolutionary constraints. In: J.B. Hutchison (ed). Biological Determinants of Sexual Behaviour, pp.657-695. Chichester, John Wiley.

Akers, J.S. & Conaway, C.H. (1979). Female homosexual behavior in *Macaca mulatta*. Arch. Sex. Behav., 8: 63-81.

Alexander, B.K. & Bowers, J.M. (1969). Social organisation of a troop of Japanese monkeys in a two-acre enclosure. Folia primat., 10: 230-242.

Allen, M.L. & Lemmon, W.B. (1981). Orgasm in female primates. Am. J. Primatol., 1: 15-34.

Altmann, J. (1974). Observational study of behaviour: sampling methods. Behaviour, 49: 227-267.

Altmann, J. (1980). Baboon Mothers and Infants. Cambridge, Mass. Harvard University Press.

Altmann, J., Altmann, S.A. & Hausfater, G. (1978). Primate infant's effects on mother's future reproduction. Science, 201: 1028-1030.

Altmann, J., Altmann, S.A., Hausfater, G. & McCuskey, S.A. (1977). Life history of yellow baboons: physical development, reproductive parameters, and infant mortality. Primates, 18: 315-330.

Altmann, S.A. (1962). Social behavior of anthropoid primates: analysis of recent concepts. In: E.L. Bliss (ed). Roots of Behavior, pp.277-285. New York, Harper & Bros.

Altmann, S.A. (1965). Primate behavior in review. Science, 150: 1440-1442.

Altmann, S.A. (1974). Baboons, space, time, and energy. Amer. Zool., 14: 221-248.

Altmann, S.A. (1979). Baboon progressions: order or chaos? A study of one-dimensional group geometry. Anim. Behav., 27: 46-80.

Altmann, S.A. & Altmann, J. (1970). Baboon Ecology. African Field Research. Chicago, University of Chicago Press.

Altmann, S.A. & Altmann, J. (1979). Demographic constraints on behavior and social organisation. In: Bernstein, I.S. and Smith, E.O. *Primate Ecology and Human Origins*, pp.47-63. Garland STPM, N.Y. & London.

Angst, W. & Thommen, D. (1977). New data and a discussion of infant killing in Old World Monkeys and Apes. Folia primatol., *27*: 198-229.

Bachmann, C. & Kummer, H. (1980). Male assessment of female choice in hamadryas baboons. Behav. Ecol. Sociobiol., *6*: 315-321.

Baenninger, R., Estes, R.D. & Baldwin, S. (1977). Anti-predatory behaviour of baboons and impala toward a cheetah. E. Afr. Wildl. J., *15*: 327-330.

Bateman, A.J. (1948). Intra-sexual selection in *Drosophila*. Heredity, *2*: 349-368.

Beach, F.A. (1970). Coital behaviour in dogs. VIII. Social affinity, dominance, and sexual preference in the bitch. Behaviour, *36*: 131-148.

Beach, F.A. (1976). Cross-species comparisons and the human heritage. Arch. Sex. Behav., *5*: 469-485.

Beck, L.R. & Blair, W.D. (1977). Lack of spontaneous ovarian contractions in the baboon. J. Reprod. Fert., *50*: 101-102.

Bernstein, I.S. (1969). Stability of the status hierarchy in a pigtail monkey group (*Macaca nemestrina*). Anim. Behav., *17*: 452-458.

Bernstein, I.S. (1970). Primate status hierarchies. In: L.A. Rosenblum (ed). *Primate behavior*, Vol. 1: New York, Academic Press.

Bernstein, I.S. (1976). Dominance, aggression, and reproduction in primate societies. J. Theor. Biol., *60*: 459-472.

Bernstein, I.S. & Gordon, T.P. (1980). The social component of dominance relationships in rhesus monkeys (*Macaca mulatta*). Anim. Behav., *28*: 1033-1040.

Bernstein, I.S., Rose, R.M. & Gordon, T.P. (1974). Behavioral and environmental events influencing primate testosterone levels. J. Hum. Evol., 3: 517-525.

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

Bert, T., Ayats, H., Martino, A. & Collomb, H. (1967). Note sur l'organisation de la vigilance sociale chez le babouin Papio papio dans l'est Senegalais. Folia primat., 6: 44-47.

Bertrand, M. (1969). The Behavioural Repertoire of the Stumptail Macaque. Bibliotheca Primatologica, 11. Karger, Basel.

Bjornstad, A. (1976). The vegetation of Ruaha National Park, Tanzania. I. Annotated checklist of the plant species. Serengeti Research Institute Publications No.215.

Bjornstad, A. (1977). Vegetation map of Ruaha National Park; eastern central area. Serengeti Research Institute Publications No. 245.

Blurton-Jones, N.G. & Trollope, J. (1968). Social behaviour of stump-tailed macaques in captivity. Primates, 9: 365-394.

Boese, G.K. (1975). Social behavior and ecological considerations of West African baboons (Papio papio). In: R.H. Tuttle (ed). Socioecology and Psychology of Primates, pp.205-230. Mouton, The Hague.

Bolwig, N. (1959). A study of the behaviour of the chacma baboon. Behaviour, 14: 136-163.

Bowman, L.A., Dilley, S.R. & Keverne, E.G. (1978). Suppression of oestrogen-induced LH surges by social subordination in talapoin monkeys. Nature, 275: 56-58.

Bramblett, C.A. (1967). Pathology in the Darajani baboon. Am. J. phys. Anthrop., 26: 331-340.

Bramblett, C.A. (1978). Is the concept of 'control group' valid? A quantitative comparison of the behaviour of caged baboon groups. Am. J. phys. Anthrop., 49: 217-226.

Buechner, H.K., Morrison, J.A. & Leuthold, W. (1966). Reproduction in Uganda Kob with special reference to behavior. Symp. zool. Soc. Lond., 15: 69-88.

Buskirk, W.H., Buskirk, R.E & Hamilton, W.J. (1974). Troop-mobilising behavior of adult male chacma baboons. Folia primatol., 22: 9-18.

Bush, G.L., Case, S.M., Wilson, A.C. & Patton, J.L. (1977). Rapid speciation and chromosomal evolution in mammals. Proc. Natl. Acad. Sc. USA, 74: 3942-3946.

Busse, C. (1980). Female chacma baboon responses to immigrant males relative to infanticide risk. (abstr.). In: E.M. Visalberghi (ed). Abstracts of 8th Congress of International Primatological Society. Florence, Italy.

Busse, C. & Hamilton, W.J. (1981). Infant carrying by male chacma baboons. Science, 212: 1281-1283.

Bygott, J.D. (1979). Agonistic behavior, dominance, and social structure in wild chimpanzees of the Gombe National Park. In: D.A. Hamburg & E.R. McCown (eds). The Great Apes, pp.405-427 Menlo Park. Benjamin/Cummings.

Byles, R.F. & Sanders, M.F. (1980). Morphological variation in a population of Kenyan olive baboons. Am. J. phys. Anthrop., 52: p.210 (abstract).

Carpenter, C.R. (1942a). Social behavior of free-ranging Rhesus monkeys (Macaca mulatta). 1. Specimens, procedures and behavioral characteristics of estrus. J. comp. Psychol. 33: 133-142.

Carpenter, C.R. (1942b). Sexual behavior of free ranging rhesus monkeys (Macaca mulatta). II. Periodicity of estrus, homosexual, auto-erotic and non-conformist behavior. J. comp. Psychol., 33: 142-162.

Carpenter, C.R. (1952). Social behaviour of non-human primates. In: C.R. Carpenter (ed). Naturalistic Behavior of Nonhuman Primates, pp.365-385. Pennsylvania State Univ. Press.

Chalmers, N.R. (1968). The social behaviour of free living mangabeys in Uganda. Folia primat., 8: 228-281.

Chalmers, N.R. & Rowell, T.E. (1971). Behaviour and female reproductive cycles in a captive group of mangabeys. Folia primat., 14: 1-14.

Chapais, B. & Schulman, S.R. (1980). An evolutionary model of female dominance relations in primates. J. Theor. Biol., 82: 47-89.

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

Cheney, D.L. (1978). Interactions of immature male and female baboons with adult females. Anim. Behav., 26: 389-408.

Cheney, D.L. & Seyfarth, R.M. (1977). Behaviour of adult and immature male baboons during inter-group encounters. Nature, 269: 404-406.

Chevalier-Skolnikoff, S. (1974). Male-female, female-female, and male-male sexual behavior in the stumptail monkey, with special attention to the female orgasm. Arch. Sex. Behav., 3: 95-116.

Chevalier-Skolnikoff, S. (1976). Homosexual behavior in a laboratory group of stumptail monkeys (Macaca arctoides): forms, contexts, and possible social functions. Arch. Sex. Behav., 5: 511-527.

Christopher, S.B. (1972). Social validation of an objective measure of dominance in captive monkeys. Behav. Res. Meth. & Instru., 4: 19-20.

Clutton-Brock, T.H. & Harvey, P.H. (1976). Evolutionary rules and primate societies. In: P.P.G. Bateson and R.A. Hinde (eds). Growing Points in Ethology, pp.195-238. Cambridge Univ. Press.

Clutton-Brock, T.H. & Harvey, P.H. (1977). Primate ecology and social organisation. J. Zool., Lond., 183: 1-39.

Clutton-Brock, T.H. & Harvey, T.H. (1978). Mammals, resources and reproductive strategies. Nature, 273: 191-195.

Clutton-Brock, T.H., Albon, S.D. & Harvey, P.H. (1980). Antlers, body size, and breeding group size in the Cervidae. Nature, 285: 565-567.

Collins, D.A. (1978). Why do some baboons have red bottoms? New Sci., 78 (1097): 12-14.

Conaway, C.H. & Koford, C.B. (1964). Estrous cycles and mating behavior in a free-ranging band of rhesus monkeys. J. Mammal., 45: 577-588.

Cox, C.R. & LeBoeuf, B.J. (1977). Female incitation of male competition: a mechanism in sexual selection. Am. Nat., 111: 317-335.

Crankshaw, O.S. (1979). Female choice in relation to calling and courtship songs in Acheta domesticus. Anim. Behav., 27: 1274-1275.

Crook, J.H. (1972). Sexual selection, dimorphism, and social organisation in the primates. In: B. Campbell (ed). Sexual Selection and the Descent of Man, pp.231-281. London, Heinemann.

Crook, J.H. & Aldrich-Blake, F.P.G. (1968). Ecological and behavioral contrasts between sympatric ground-dwelling primates in Ethiopia. Folia primat., 8: 192-227.

Crowder, M.J. (1978). Beta-binomial Anova for proportions. Applied Statistics, 27: 34-37.

Curtin, R.A. (1980). Strategy and tactics in gray langur reproduction (abstr.). Am. J. Phys. Anthrop., 52: 218.

Darwin, C. (1871). The Descent of Man, and selection in relation to sex. London, John Murray.

Davies, N.B. & Halliday, T.R. (1979). Competitive mate searching in male common toads, Bufo bufo. Anim. Behav., 27: 1253-1267.

Deag, J.M. (1974). A study of the social behaviour and ecology of the wild Barbary macaque, Macaca sylvanus L. Univ. of Bristol, Ph.D. Thesis.

Deag, J.M. (1977). Aggression and submission in monkey societies. Anim. Behav., 25: 465-474.

Deag, J.M. (1980). Interactions between males and unweaned barbary macaques: testing the agonistic buffering hypothesis. Behaviour, 75: 54-81.

Deag, J.M. & Crook, J.H. (1971). Social behaviour and 'agonistic buffering' in the wild barbary macaque Macaca sylvana L. Folia primat., 15: 183-200.

Defler, T.R. (1978). Allogrooming in two species of macaque (Macaca nemestrina and Macaca radiata). Primates, 19: 153-167.

Deputte, B.L. & Goustard, M. (1980). Copulatory vocalisations of female macaques (Macaca fascicularis): variability factors analysis. Primates, 21: 83-99.

DeVore, I. (1963). Mother-infant relations in free-ranging baboons. In: H.L. Reingold (ed). Maternal Behavior in Mammals, pp. 305-335. New York, Wiley.

DeVore, I. (1965). Male dominance and mating behavior in baboons. In: F.A. Beach (ed). Sex and Behavior, pp.266-289. New York, John Wiley.

DeVore, I. & Hall, K.R.L. (1965). Baboon ecology. In: I. DeVore (ed). Primate Behavior, pp.20-52. New York; Holt, Rinehart, & Winston.

DeVore, I. & Washburn, S.L. (1963). Baboon ecology and human evolution. In: F.C. Howell & F. Bourliere (eds). African Ecology and Human Evolution, pp.335-367. Chicago, Aldine.

DeWaal, F.B.M. (1977). The organisation of agonistic relations within two captive groups of Java-monkeys (Macaca fascicularis). Z. Tierpsychol., 44: 225-282.

DeWaal, F.B.M. (1978). Exploitative and familiarity-dependent support strategies in a colony of semi-free living chimpanzees. Behaviour, 66: 268-312.

Dittus, W.P. (1979). The evolution of behaviors regulating density and age-specific sex ratios in a primate population. Behaviour, 69: 265-302.

Dixson, A.F. (1977). Observations on the displays, menstrual cycles and sexual behaviour of the "Black ape" of Celebes (Macaca nigra). J. Zool., Lond., 182: 63-84.

Downhower, J.F. (1976). Darwin's finches and the evolution of sexual dimorphism in body size. Nature, 263: 558-563.

Drickamer, L.C. (1974a). Social rank, observability, and sexual behaviour of rhesus monkeys (Macaca mulatta). J. Reprod. Fert., 37: 117-120.

Drickamer, L.C. (1974b). A ten-year summary of reproductive data for free-ranging Macaca mulatta. Folia primat., 21: 61-80.

Drickamer, L.C. (1975). Quantitative observation of behavior in free-ranging *Macaca mulatta*: methodology and aggression. Behaviour, 55: 209-236.

Drickamer, L.C. & Vessey, S.H. (1973). Group changing in free-ranging male rhesus monkeys. Primates, 14: 359-368.

Dunbar, R.I.M. (1976). Some aspects of research design and their implications in the observational study of behaviour. Behaviour, 58: 78-98.

Dunbar, R.I.M. (1977). Feeding ecology of gelada baboons: a preliminary report. In: T.H. Clutton-Brock (ed). *Primate ecology: feeding and ranging behaviour of lemurs, monkeys, and apes*, pp.254-275. London, Academic Press.

Dunbar, R.I.M. (1978a). Sexual behaviour and social relationships among gelada baboons. Anim. Behav., 26: 167-178.

Dunbar, R.I.M. (1978b). Life with geladas: a battle of the sexes. New Sci., 79 (1110): 28-30.

Dunbar, R.I.M. (1980). Determinants and evolutionary consequences of dominance among female gelada baboons. Behav. Ecol. Sociobiol., 7: 253-265.

Dunbar, R.I.M. & Dunbar, E.P. (1975). Social dynamics of gelada baboons. Contrib. Primatol. Vol. 6. Basel, S. Karger.

Dunbar, R.I.M. & Dunbar, E.P. (1977). Dominance and reproductive success among female gelada baboons. Nature, 266: 351-352.

Duvall, S.W., Bernstein, I.S. & Gordon, T.P. (1976). Paternity and status in a rhesus monkey group. J. Reprod. Fert., 47: 25-31.

Eaton, G.G. (1974). Male dominance and aggression in Japanese macaque reproduction. In: W. Montagna & W.A. Sadler *Reproductive Behavior*, pp.287-297. New York, Plenum Publ. Co.

Eaton, G.G. (1976). The social order of Japanese macaques. Scient. Am., 235: 96-106.

Eaton, G.G. (1978). Longitudinal studies of sexual behavior in the Oregon Troop of Japanese macaques. In: T.E. McGill, D.A. Dewsbury, B.D. Sachs (eds). *Sex and Behavior*, pp.35-59. New York, Plenum Press.

Emory, G.R. (1976). Aspects of attention, orientation, and status hierarchy in mandrills (Mandrillus sphinx) and gelada baboons (Theropithecus gelada). Behaviour, 59: 70-87.

Enomoto, T. (1978). On social preference in sexual behavior of Japanese monkeys (Macaca fuscata). J. Hum. Evol., 7: 283-293.

Erikson, L.B. (1967). Relationship of sexual receptivity to menstrual cycles in adult rhesus monkeys. Nature, 216: 299-301.

Evans, R.G. (1974). Factors affecting the social and sexual interactions of the rhesus monkey and anubis baboon. Univ. of London, Ph.D. Thesis, Institute of Psychiatry.

Fairbanks, L.A. (1980). Relationships among adult females in captive vervet monkeys: testing a model of rank-related attractiveness. Anim. Behav., 28: 853-859.

Farr, J.A. (1980). Social behaviour patterns as determinants of reproductive success in the guppy, Poecilia reticulata Peters (Pisces: Poeciliidae). Behaviour, 74: 38-91.

Fedigan, L.M. & Gouzoules, H. (1978). The consort relationship in a troop of Japanese monkeys. In: D.J. Chivers & J. Herbert (eds). Recent Advances in Primatology, Vol. I: Behaviour, pp.493-496. London, Academic Press.

Fisher, R.A. (1930). The Genetical Theory of Natural Selection. Oxford, Clarendon Press.

Fox, C.A., Wolff, H.S. & Baker, J.A. (1970). Measurement of intra-vaginal and intra-uterine pressures during human coitus by radiotelemetry. J. Reprod. Fert., 22: 243-251.

Freeland, W.J. (1976). Pathogens and the evolution of primate sociality. Biotropica, 8: 12-24.

Frisch, R.E. & McArthur, J.W. (1974). Menstrual cycles: fatness as a determinant of minimum weight for height necessary for their maintenance or onset. Science, 185: 949-951.

Gartlan, J.S. (1964). Dominance in east african monkeys. Proc. E. Afr. Acad., II: 75-79.

Gartlan, J.S. (1968). Structure and function in primate society. Folia primat., 8: 89-120.

Geist, V. (1971). Mountain Sheep. Chicago University Press.

Gibson, R.M. & Guinness, F.E. (1980). Behavioural factors affecting male reproductive success in red deer (Cervus elaphus). Anim. Behav., 28: 1163-1174.

Gillman, J. (1937). The cyclical changes in the vaginal smear in the baboon and its relationship to perineal swelling. S. Afr. J. Med. Sci., 2: 44-56.

Gillman, J. (1940). Effect of multiple injections of progesterone on the turgescent perineum of the baboon (Papio porcarius). Endocrinology, 26: 80-87.

Gillman, J. & Gilbert, C. (1946). The reproductive cycle of the chacma baboon (Papio ursinus) with special reference to the problems of menstrual irregularities as assessed by the behaviour of the sex skin. S. Afr. J. Med. Sci. 11: Biol. Supp. 1-54.

Gilmore, H.A. (1977). The evolution of agonistic buffering in baboons and macaques. Manuscript of a paper presented to American Assoc. of Physical Anthropologists. Seattle, Washington.

Goldfoot, D.A., Westerborg-van Loon, H., Groeneveld, W. & Slob, A.K. (1980). Behavioral and physiological evidence of sexual climax in the female stump-tailed macaque (Macaca arctoides). Science, 208: 1477-1479.

Goodall, J. Van Lawick- (1968). The behaviour of free-living chimpanzees in the Gombe Stream area. Anim. Behav. Monogr., 1: 161-311.

Goodall, J. Van Lawick- (1975). The behaviour of the chimpanzee. In: I. Eibl-Eibesfelt (ed). Hominisation und Verhalden, pp.56-100. Stuttgart, Gustav Fischer Verlag.

Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., Pierce, A. & Riss, D. (1979). Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: D.A. Hamburg & E.R. McCown (eds). The Great Apes, pp.12-53. Menlo Park, Calif., Benjamin/Cummings.

Goss-Custard, J.D., Dunbar, R.I.M. & Aldrich-Blake, F.P.G. (1972). Survival, mating and rearing strategies in the evolution of primate social structure. Folia primat., 17: 1-19.

Gouzoules, H. (1974). Harassment of sexual behavior in stumptail macaque, Macaca arctoides. Folia primatol., 22: 208-217.

Grubb, P. (1974). The rut and behaviour of Soay rams. In: P.A. Jewell, C. Milner, J.M. Boyd. Island Survivors, pp.195-223. London, Athlone Press.

Hagino, N. (1974). Follicular maturation, ovulation, luteinisation, and menstruation in the baboon. In: E.M. Coutinho & F. Fuchs Physiology and Genetics of Reproduction, Part A, pp.323-342. New York & London, Plenum Press.

Hall, K.R.L. (1962). The sexual, agonistic and derived social behaviour patterns of the wild chacma baboon, Papio ursinus. Proc. Zool. Soc. Lond., 139: 283-327.

Hall, K.R.L. (1963). Variations in the ecology of the chacma baboon, Papio ursinus. Symp. zool. Soc. Lond., 10: 1-28.

Hall, K.R.L. (1964). Aggression in monkey and ape societies. In: J.D. Carthy & F.J. Ebling (eds). The Natural History of Aggression, pp.51-64. London, New York, Academic Press.

Hall, K.R.L. (1965a). Behaviour and ecology of the wild patas monkey, Erythrocebus patas, in Uganda. J. Zool. Lond., 148: 15-87.

Hall, K.R.L. (1965b). Ecology and behavior of baboons, patas, and vervet monkeys in Uganda. In: H. Vagtborg (ed). The Baboon in Medical Research, Vol. 1, pp.43-61. Austin, University of Texas.

Hall, K.R.L. (1967). Social interactions of the adult male and adult females of a patas monkey group. In: S.A. Altmann (ed). Social Communication among Primates, pp.261-280. University of Chicago Press, Chicago.

Hall, K.R.L. & DeVore, I. (1965). Baboon social behavior. In: I. DeVore (ed). Primate Behavior, pp.53-110. New York; Holt, Rinehart & Winston.

Hamilton, W.D. (1971). Geometry for the selfish herd. J. Theor. Biol., 31: 295-311.

Hamilton, W.J. III & Arrowood, P.C. (1978). Copulatory vocalisations of chacma baboons (Papio ursinus), gibbons (Hylobates hoolock), and humans. Science, 200: 1405-1409.

Hamilton, W.J. III, Buskirk, R.E. & Buskirk, W.H. (1975). Chacma baboon tactics during intertroop encounters. J. Mammal., 56: 857-870.

Hamilton, W.J. III & Busse, C. (1980). Male transfer and offspring protection in chacma baboons (abstr.). In: E.M. Visalberghi (ed). Abstracts of the 8th Congress of the International Primatological Society. Florence, Italy.

Hanby, J.P. (1974a). The social nexus: problems and solutions in the portrayal of primate social structures. Symp. 5th Cong. Int'l. Primat. Soc., pp.25-42.

Hanby, J.P. (1974b). Male-male mounting in Japanese monkeys. Anim. Behav., 22: 836-849.

Hanby, J.P. (1976). Sociosexual development in primates. In: P.P.G. Bateson and P.H. Klopfer (eds). Perspectives in Ethology, Vol. 2, pp.1-67. New York, Plenum Press.

Hanby, J.P. & Brown, C.E. (1974). The development of sociosexual behaviours in Japanese macaques, Macaca fuscata. Behaviour, 49: 152-196.

Hanby, J.P., Robertson, L.T. & Phoenix, C.H. (1971). The sexual behaviour of a confined troop of Japanese macaques. Folia primat., 16: 123-143.

Harcourt, A.H., Harvey, P.H., Larson, S.G. & Short, R.V. (in press). Testis weight, body weight and breeding system in primates. Nature, in press.

Harcourt, A.H., Stewart, K.S. & Fossey, D. (1976). Male emigration and female transfer in wild mountain gorilla. Nature, 263: 226-227.

Harcourt, A.H. & Stewart, K.J. (1977). Apes, sex, and societies. New Sci., 76: 160-162.

Harding, R.S.O. (1977). Patterns of movement in open country baboons. Am. J. phys. Anthrop., *47*: 349-354.

Harvey, P.H., Kavanagh, M. & Clutton-Brock, T.H. (1978). Canine tooth size in female primates. Nature, *276*: 817-818.

Hausfater, G. (1975). Dominance and reproduction in baboons (*Papio cynocephalus*). Contrib. Primatol., Vol. 7. Basel, S. Karger.

Heape, W. (1900). The sexual season of mammals and the relation of pro-oestrum to menstruation. Quant. J. Microsc. Sci., *44*: 1-70.

Hendrickx, A.G. (1967). The menstrual cycle of the baboon as determined by the vaginal smear, vaginal biopsy, and perineal swelling. In: H. Vagtborg (ed). *The Baboon in Medical Research*, Vol. II, pp.437-459. Austin, University of Texas Press.

Hendrickx, A.G. & Kraemer, D.C. (1969). Observations on the menstrual cycle, optimal mating time, and preimplantation embryos of the baboon, *P*. *anubis* and *P*. *cynocephalus*. J. Reprod. Fert., suppl.6: 119-128.

Hendrickx, A.G., Kraemer, D.C. (1971). Reproduction. In: A.G. Hendrickx (ed). *Embryology of the Baboon*, pp.3-30. Chicago, London, University of Chicago Press.

Hill, W.C. Osman (1970). *Primates; Comparative anatomy and taxonomy*. 8: Cynopithecinae. Edinburgh, University Press.

Hinde, R.A. (1974). *Biological bases of human social behaviour*. New York McGraw-Hill.

Hinde, R.A. (1975). The concept of function. In: G. Baerends, C. Beer, A. Manning (eds). *Function and Evolution in Behaviour*, pp.3-15. Oxford, Clarendon Press.

Hinde, R.A. (1976). Interactions, relationships and social structure. Man, *11*: 1-17.

Hinde, R.A. (1978). Dominance and role - two concepts with dual meanings. J. Social Biol. Struct., *1*: 27-38.

Hinde, R.A. & Proctor, L.P. (1977). Changes in the relationships of captive rhesus monkeys on giving birth. Behaviour, *61*: 304-321.

Hinde, R.A. & Rowell, T.E. (1962). Communication by postures and facial expression in the rhesus monkey Macaca mulatta. Proc. Zool. Soc. Lond., 138: 1-21.

Hladick, C.M. (1975). Ecology, diet and social patterns in Old and New World primates. In: R. Tuttle (ed). Socioecology and Psychology of Primates, pp.3-35. The Hague, Mouton.

Holm, R.A. (1979). Effects of parental risk and prenatal stress on pregnancy outcome. In: G.C. Ruppenthal (ed). Nursery Care of Nonhuman Primates, pp.21-26. New York, Plenum Press.

Homewood, K.M. (1975). Monkey on a riverbank. Natural History; Jan. 1975; 68-73.

Hoogstraal, H. (1956). African Ixodoidea. 1. Ticks of the Sudan. Research Report N.M. 005 050.29.07. U.S. Naval Medical Research Unit No.3. Cairo, Egypt.

Hrdy, S.B. (1976). Care and exploitation of nonhuman primate infants by conspecifics other than the mother. Adv. Study. Behav. 6: 101-158.

Hrdy, S.B. (1977). The Langurs of Abu. London, Harvard University Press.

Hrdy, S.B. (1978). Allomaternal care and abuse of infants among hanuman langurs. In: D.J. Chivers & J. Herbert (eds). Recent Advances in Primatology, Vol.1: Behaviour, pp.169-172. London, Academic Press.

Hrdy, S.B. (1979a). The evolution of human sexuality: the latest word and the last. Quart. Rev. Biol., 54: 309-314.

Hrdy, S.B. (1979b). Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethol. Sociobiol., 1: 13-40.

Hrdy, S.B. & Hrdy, D.B. (1976). Hierarchical relations among female hanuman langurs (Primates: Colobinae, Presbytis entellus). Science, 193: 913-915.

Huffman, S.L., Chowdhury, A.K.M.A. & Mosley, W.H. (1978). Postpartum amenorrhea: how is it affected by maternal nutritional status? Science, 200: 1155-1157.

Humphrey, N.K. (1976). The social function of intellect. In: P.P.G. Bateson & R.A. Hinde (eds). Growing Points in Ethology, pp.303-317. Cambridge Univ. Press.

Hutchins, M. & Barash, D.P. (1976). Grooming in primates: implications for its utilitarian function. Primates, 17 (2): 145-150.

Imanishi, K. (1963). Social behavior in Japanese monkeys, Macaca fuscata. In: C.H. Southwick (ed). Primate Social Behavior, pp.68-81. Princeton, N.J., Van Nostrand.

Jay, P.C. (1965). The common langur of North India. In: I. DeVore (ed). Primate Behavior, pp.197-249. New York, Holt, Rinehart and Winston.

Jenni, D.A. (1974). Evolution of polyandry in birds. Amer. Zool., 14: 129-144.

Jochle, W. (1975). Current research in coitus-induced ovulation: A review. J. Reprod. Fert., Suppl. 22: 165-207.

Jolly, A. (1966). Lemur social behavior and primate intelligence. Science, 153: 501-506.

Jolly, A. (1967). Breeding synchrony in wild Lemur catta. In: S.A. Altmann (ed). Social Communication among Primates, pp.3-14. University of Chicago Press.

Jolly, A. (1972). The Evolution of Primate Behavior. New York, London, Macmillan.

Jolly, C.J. (1966). Introduction to the Cercopithecoidea, with notes on their use as laboratory animals. Symp. Zool. Soc. Lond., 17: 427-457.

Jolly, C.J. & Brett, F.L. (1973). Genetic markers and baboon biology. J. med. Prim., 2: 85-99.

Judge, D.S., Rodman, P.S. (1976). Macaca radiata: intragroup relations and reproductive status of females. Primates, 17: 535-539.

Kaplan, J.R. (1977). Patterns of fight interference in free-ranging rhesus monkeys. Am. J. phys. Anthrop., 47: 279-288.

Kaplan, J.R. (1978). Fight interference and altruism in rhesus monkeys. Am. J. phys. Anthrop., 49: 241-250.

Kaufmann, J.H. (1965). A three-year study of mating behavior in a free-ranging band of rhesus monkeys. Ecology, 46: 500-512.

Katzberg, A. (1967). The histology of the vagina and uterus of the baboon. In: H. Vagtborg (ed). The baboon in medical research, Vol.II: 235-270. Austin, Univ. of Texas Press.

Kawai, M. (1958). On the system of social ranks in a natural troop of Japanese monkeys: 1: Basic rank and dependent rank. In: S. Altmann (ed). Japanese monkeys: a collection of translations. Published by the editor, 1965.

Kawamura, S. (1958). The matriarchal social order in the Minoo-B group. Primates, 1: 149-158.

Keverne, E.B. (1976). Sexual receptivity and attractiveness in the female rhesus monkey. Adv. Study Behav., 7: 155-200.

Kleiman, D.G. (1977). Monogamy in mammals. Quart. Rev. Biol., 52: 39-69.

Koford, C.B. (1963). Rank of mothers and sons in bands of rhesus monkeys. Science, 141: 356-357.

Kolata, G.B. (1976). Primate behavior: sex and the dominant male. Science, 191: 55-56.

Koyama, N. (1967). On dominance rank and kinship of a wild Japanese monkey troop in Arashiyama. Primates, 8: 189-216.

Kummer, H. (1967). Tripartite relations in hamadryas baboons. In: S.A. Altmann (ed). Social Communication among Primates, pp.63-71. Chicago, University of Chicago Press.

Kummer, H. (1968). Social Organisation of Hamadryas Baboons. Chicago University Press.

Kummer, H. (1969). Spacing mechanisms in social behavior. In: J.F. Eisenberg, W.S. Dillon (eds). Man and Beast: Comparative Social Behaviour, pp.221-234. Washington, D.C., Smithsonian Institution Press.

Kummer, H. (1973). Dominance versus possession. In: E. Menzel (ed). Symp. IVth Int. Congr. Primat., Vol.1, pp.226-231. Precultural Primate Behavior. Basel, S. Karger.

Kummer, H., Abegglen, J.-J., Bachmann, C.H., Falett, J. & Sigg, H. (1978). Grooming relationships and object competition among hamadryas baboons. In: D.J. Chivers & J. Herbert (eds). Recent Advances in Primatology, Vol.1: Behaviour, pp.31-38. London, Academic Press.

Kummer, H. Gotz, W. & Angst, W. (1970). Cross-species modifications of social behaviour in baboons. In: J.R. Napier & P.H. Napier (eds). Old World Monkeys, pp.353-363. N.Y. & Lond., Academic Press.

Kummer, H., Gotz, W. & Angst, W. (1974). Triadic differentiation: an inhibitory process protecting pair bonds in baboons. Behaviour, 49: 62-87.

Kummer, H. & Kurt, F. (1965). A comparison of social behavior in captive and wild hamadryas baboons. In: H. Vagtborg (ed). The Baboon in Medical Research, Vol.1, pp.65-80. Austin, University of Texas Press.

Kuntz, R.E. & Myers, B.J. (1967). Parasites of the Kenya baboon: arthropods, blood protozoa, and helminths (Kenya, 1966). Primates, 8: 75-82.

Kurland, J.A. (1977). Kin selection in the Japanese monkey. Contrib. Primatol., Vol.12. Basel, S. Karger.

Lack, D. (1966). Population studies of birds. Oxford, Clarendon Press.

LeBoeuf, B.J. (1974). Male-male competition and reproductive success in elephant seals. Amer. Zool., 14: 163-176.

LePere, R.H., Benoit, P.E., Hardy, R.C. & Goldzieher, J.W. (1965). The origin and function of the ovarian nerve supply in the baboon. In: H. Vagtborg (ed). The Baboon in Medical Research, Vol.1, pp.243-248. Austin, University of Texas Press.

Lee, P.C. & Oliver, J.I. (1979). Competition, dominance, and the acquisition of rank in juvenile yellow baboons, (Papio cynocephalus). Anim. Behav., 27: 576-585.

Lindburg, D.G. (1971). The rhesus monkey in North India: an ecological and behavioral study. In: L.A. Rosenblum (ed). Primate Behaviour, Vol.2, pp.1-106. New York and London, Academic Press.

Lindburg, D.G. (1973). Grooming behavior as a regulator of social interactions in rhesus monkeys. In: C.R. Carpenter (ed). Behavioral Regulators of Behavior in Primates, pp.124-148. Lewisburg, Bucknell University Press.

Lindburg, D.G. (1975). Mate selection in the rhesus monkey, Macaca mulatta. Paper presented at 44th annual meeting of the American Society of Physical Anthropologists, Denver, Colorado.

Lorenz, K. (1966). On Aggression. London, Methuen.

Lott, D.F. (1979). Dominance relations and breeding rate in mature male american bison. Z. Tierpsychol., 49: 418-432.

Loy, J. (1971). Estrous behaviour of free-ranging rhesus monkeys (Macaca mulatta). Primates, 12: 1-31.

Loy, J. & Loy, K. (1977). Sexual harassment among captive patas monkeys (Erythrocebus patas). Primates, 18: 691-699.

MacLennan, A.H., Harris, J.A. & Wynn, R.M. (1971). Menstrual cycle of the baboon. II. Endometrial ultrastructure. Obstet. Gynec., 38: 359-374.

MacLennan, A.H. & Wynn, R.M. (1971). Menstrual cycle of the baboon. I. Clinical features, vaginal cytology and endometrial histology. Obstet. Gynec., 38: 350-358.

Maples, W.R. & McKern, T.W. (1967). A preliminary report on classification of the Kenya baboon. In: H. Vagtborg (ed). The Baboon in Medical Research, Vol.2, pp.13-22. Austin, University of Texas.

Marais, E.N. (1939). My Friends the Baboons. London, Blond & Briggs.

Marsden, H.M. (1968). Agonistic behaviour of young rhesus monkeys after changes induced in the social rank of their mothers. Anim. Behav., 16: 38-44.

Mason, W.A. (1978). Ontogeny of social systems. In: D.J. Chivers & J. Herbert. Recent Advances in Primatology, Vol.1, pp.5-14. London, Academic Press.

Maslow, A.H. (1936a). The role of dominance in the social and sexual behaviour of infra-human primates. 1. Observations at Vilas Park Zoo. J. Genet. Psychol., 48: 261-277.

Massey, A. (1977). Agonistic aids and kinship in a group of pigtail macaques. Behav. Ecol. Sociobiol., 2: 31-40.

Maxim, P.E. & Buettner-Janusch, J. (1963). A field study of the Kenya baboon. Amer. J. phys. Anthrop., 21: 165-180.

Maynard Smith, J. (1958). Sexual selection. In: S.A. Barnett (ed). A Century of Darwin, pp.231-244. London, Heinemann.

Maynard Smith, J. & Price, G.R. (1973). The logic of animal conflict. Nature, 246: 15-18.

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

Mazur, A. (1976). Effects of testosterone on status in primate groups. Folia primatol., 26: 214-226.

McGonigle, B.O. & Chalmers, M. (1977). Are monkeys logical? Nature, 267: 694-696.

McLaren, I.A. (1967). Seals and group selection. Ecology, 48: 104-110.

Michael, R.P. & Keverne, E.B. (1968). Pheromones and the communication of sexual status in primates. Nature, 218: 746-749.

Michael, R.P. & Saayman, G.S. (1967). Sexual performance and the timing of ejaculation in male rhesus monkeys. J. Comp. Physiol. Psychol., 64: 213-218.

Michael, R.P., Zumpe, D., Keverne, E.B. & Bonsall, R.W. (1972). Neuroendocrine factors in the control of primate behavior. Rec. Prog. Horm. Res., 28: 665-706.

Missakian, E.A. (1972). Genealogical and cross-genealogical dominance relations in a group of free-ranging rhesus monkeys (Macaca mulatta) on Cayo Santiago. Primates, 13: 169-180.

Moore, J. (1978). Dominance relations among free-ranging female baboons in Gombe National Park, Tanzania. In: D.J. Chivers & J. Herbert. Recent Advances in Primatology, Vol.1: Behaviour, pp.67-70. London, Academic Press.

Mori, A. (1979). In: M. Kawai (ed). Ecological and Sociological Studies of Gelada Baboons. Contrib. Primatol. (16). Basel, Karger.

Myers, R.E. (1972). The pathology of the rhesus monkey placenta. In: Diczfalusy and C.C. Standley (eds). The Use of Non-Human Primates in Research on Human Reproduction, pp.221-256. Stockholm, World Health Organisation.

Nagel, U. (1971). Social organisation in a baboon hybrid zone. Proc. 3rd Int. Congr. Primat. Zurich., Vol.3, pp.48-57. Basel, S. Karger.

Nagel, U. (1973). A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. Folia primat., 19: 104-165.

Napier, J.R. & Napier, P.H. (1967). A handbook of living primates. London, Academic Press.

Nash, L.T. (1973). Social behaviour and social development in baboons (Papio anubis) at the Gombe Stream National Park, Tanzania. University of California (Berkeley). Ph.D. Thesis, Ann Arbor, Mich. University Microfilms.

Nash, L.T. (1974). Parturition in a feral baboon (Papio anubis). Primates, 15: 279-285.

Nash, L.T. (1976). Troop fission in free-ranging baboons in the Gombe Stream National Park, Tanzania. Am. J. phys. Anthrop., 44: 63-77.

Nash, L.T. (1978a). The development of the mother-infant relationship in wild baboons (Papio anubis). Anim. Behav., 26: 746-759.

Nash, L.T. (1978b). Kin preference in the behavior of young baboons. In: D.J. Chivers & J. Herbert (eds). Recent Advances in Primatology, Vol.1, Behaviour, pp.71-73. London, Academic Press.

Nishida, T. (1979). The social structure of chimpanzees of the Mahale Mountains. In: D.A. Hamburg & E.R. McCown (eds). The Great Apes, pp.72-121. Menlo Park, Calif., Benjamin/Cummings.

Noe, R., DeWaal, F.B.M. & Van Hooff, J.A.R.A.M. (1980). Types of dominance in a chimpanzee colony. Folia primatol., 34: 90-110.

Nowell, L.H. & Heidrich, A.G. (1978). Factors affecting dominance relationships in adult female baboons. In: D.J. Chivers & J. Herbert (eds). Recent Advances in Primatology, Vol.1, Behaviour, pp.63-66. London, Academic Press.

O'Donald, P. (1962). The Theory of sexual selection. Heredity, 17: 541-552.

Ohsawa, H. (1979). Chapter 1 in: M. Kawai (ed). Ecological and Sociological Studies of Gelada Baboons. Contrib. Primatol., Vol.16. Basel, S. Karger.

Oki, J. & Maeda, Y. (1973). Grooming as a regulator of behavior in Japanese macaques. In: C.R. Carpenter (ed). Behavioral Regulators of Behavior in Primates, pp.149-163. Lewisburg, Bucknell University Press.

Oliver, J.I. & Lee, P.C. (1978). Comparative aspects of the behaviour of juveniles in two species of baboon in Tanzania. In: D.J. Chivers & J. Herbert (eds). Recent Advances in Primatology, Vol.1, Behaviour, pp.151-153. London, Academic Press.

Owens, N.W. (1975). A comparison of aggressive play and aggression in free-living baboons, Papio anubis. Anim. Behav., 23: 757-765.

Owens, N.W. (1976). The development of sociosexual behaviour in free-living baboons, Papio anubis. Behaviour, 57: 241-259.

Packer, C. (1975). Male transfer in olive baboons. Nature, 255: 219-220.

Packer, C. (1977a). Inter-troop transfer and inbreeding avoidance in Papio anubis in Tanzania. University of Sussex, Ph.D. Thesis.

Packer, C. (1977b). Reciprocal altruism in Papio anubis. Nature, 265: 441-443.

Packer, C. (1978). Behaviour affecting immigration of male baboons at Gombe National Park. In: D.J. Chivers and J. Herbert (eds). Recent Advances in Primatology, Vol.1, Behaviour, pp.75-77. London, Academic Press.

Packer, C. (1979a). Inter-troop transfer and inbreeding avoidance in Papio anubis. Anim. Behav., 27: 1-36.

Packer, C. (1979b). Male dominance and reproductive activity in Papio anubis. Anim. Behav., 27: 37-45.

Packer, C. (1980). Male care and exploitation of infants in Papio anubis. Anim. Behav., 28: 512-520.

Packer, C. & Pusey, A.E. (1979). Female aggression and male membership in troops of Japanese macaques and olive baboons. Folia primatol., 31: 212-218.

Parker, G.A. (1974). Courtship persistence and female-guarding as male time-investment strategies. Behaviour, 48: 157-184.

Paterson, J.D. (1973). Ecologically differentiated patterns of aggressive and sexual behavior in two troops of Ugandan baboons, Papio anubis. Am. J. phys. Anthrop., 38: 641-648.

Phoenix, C.H. (1974). The role of androgens in the sexual behaviour of adult male rhesus monkeys. In: W. Montagna & W.A. Sadler (ed). Reproductive Behavior, pp.249-258. New York, Plenum.

Poirier, F.E. (1970). Dominance structure of the nilgiri langur (Presbytis johnii) of South India. Folia primatol., 12: 161-186.

Popp, J.L. & DeVore, I. (1974). Aggressive competition and social dominance theory. Manuscript of paper presented at Burg Wartenstein Symposium No.62, The Behaviour of Great Apes. Wenner-Gren Foundation.

Popp, J.L. & DeVore, I. (1979). Aggressive competition and social dominance theory: synopsis. In: D.A. Hamburg & E.R. McCown (eds). The Great Apes, pp.317-338. Menlo Park, Benjamin/Cummings.

Portman, O.W. (1970). Nutritional requirements (NRC) of nonhuman primates. In: R.S. Harris (ed). Feeding and Nutrition of Nonhuman Primates, pp.87-116. New York, Academic Press.

Post, D.G., Hausfater, G. & McCuskey, S.A. (1980). Feeding behavior of yellow baboons (Papio cynocephalus): relationship to age, gender and dominance rank. Folia primatol., 34: 170-195.

Pusey, A.E. (1980). Inbreeding avoidance in chimpanzees. Anim. Behav., 28: 543-552.

Ralls, K. (1976). Mammals in which females are larger than males. Quart. Rev. Biol., 51: 245-276.

Ransom, T.W. (1971). Ecology and social behaviour of baboons (Papio anubis) in the Gombe National Park. University of California, Berkeley, Ph.D. Thesis.

Ransom, T.W. & Ransom, B.S. (1971). Adult male-infant relations among baboons (Papio anubis). Folia primat., 16: 179-195.

Ransom, T.W. & Rowell, T.E. (1972). Early social development of feral baboons. In: F.E. Poirier (ed). *Primate Socialisation*, pp.105-144. N.Y., Random House.

Rasmussen, D.R. (1979). Correlates of patterns of range use of a troop of yellow baboons (*Papio cynocephalus*). I. Sleeping sites, impregnable females, births and male emigrations and immigrations. Anim. Behav., *24*: 1098-1112.

Rasmussen, K.L. (1980). Consort behaviour and mate selection in yellow baboons (Papio cynocephalus). University of Cambridge, Ph.D. Thesis.

Restall, B.J. (1967). The biochemical and the physiological relationships between the gametes and the female reproductive tract. In: A. McLaren (ed). *Advances in Reproductive Physiology*, Vol.II, pp.181-212. London, Logos Press.

Rhine, R.J. (1975). The order of movement of yellow baboons (*Papio cynocephalus*). Folia primatol., *23*: 72-104.

Rhine, R.J., Forthman, D.L., Stillwell-Barnes, R., Westlund, B.J. & Westlund, H.D. (1979). Movement patterns of yellow baboons (*Papio cynocephalus*): the location of subadult males. Folia primatol., *32*: 241-251.

Rhine, R.J. & Owens, N.W. (1972). The order of movement of adult male and black infant baboons (*Papio anubis*) entering and leaving a potentially dangerous clearing. Folia primat., *18*: 276-283.

Rhine, R.J. & Westlund, B.J. (1978). The nature of a primary feeding habit in different age-sex classes of yellow baboons (*Papio* cynocephalus). Folia primatol., *30*: 64-79.

Richards, S.M. (1974). The concept of dominance and methods of assessment. Anim. Behav., *22*: 914-930.

Riss, D. & Goodall, J. (1977). The recent rise to the alpha-rank in a population of free living chimpanzees. Folia primatol., *27*: 134-151.

Roberto Frisancho, A., Sanchez, J., Pallardel, D. & Yanez, L. (1973). Adaptive significance of small body size under poor socio-economic conditions in Southern Peru. Am. J. phys. Anthrop., *39*: 255-262.

Rose, M.D. (1977). Positional behaviour of olive baboons (Papio anubis) and its relation to maintenance and social activities. Primates, 18: 59-116.

Rose, R.M., Gordon, T.P. & Bernstein, I.S. (1972). Plasma testosterone levels in male rhesus: influences of sexual and social stimuli. Science, 178: 643-645.

Rose, R.M., Holaday, J.W. & Bernstein, I.S. (1971). Plasma testosterone, dominance rank, and aggressive behaviour in male rhesus monkeys. Nature, 231: 366-368.

Rosenblum, L.A., Kaufman, I.C. & Stynes, A.J. (1966). Some characteristics of adult social and autogrooming patterns in two species of macaque. Folia primat., 4: 438-451.

Rowell, T.E. (1966a). Forest living baboons in Uganda. J. Zool., London, 149: 344-364.

Rowell, T.E. (1966b). Hierarchy in the organisation of a captive baboon group. Anim. Behav., 14: 430-443.

Rowell, T.E. (1967a). Female reproductive cycles and the behaviour of baboons and rhesus macaques. In: S.A. Altmann (ed). Social Communication among Primates, pp.15-32. Chicago, Univ. of Chicago Press.

Rowell, T.E. (1967b). A quantitative comparison of the behaviour of a wild and caged baboon group. Anim. Behav., 15: 499-509.

Rowell, T.E. (1967c). Variability in the social organisation of primates. In: D. Morris (ed). Primate Ethology, pp.219-235. London, Morrison & Gibb.

Rowell, T.E. (1968). Grooming by adult baboons in relation to reproductive cycles. Anim. Behav., 16: 585-588.

Rowell, T.E. (1969a). Long-term changes in a population of Ugandan baboons. Folia primat., 11: 241-254.

Rowell, T.E. (1969b). Intra-sexual behaviour and female reproductive cycles of baboons (Papio anubis). Anim. Behav., 17: 159-167.

Rowell, T.E. (1970). Baboon menstrual cycles affected by social environment. J. Reprod. Fert., 21: 133-141.

Rowell, T.E. (1971). Organisation of caged groups of *Cercopithecus* monkeys. Anim. Behav., *19*: 625-645.

Rowell, T.E. (1972). Female reproduction cycles and social behavior in primates. Adv. Study Behav., *4*: 69-105.

Rowell, T.E. (1974). The concept of social dominance. Behav. Biol., *11*: 131-174.

Rowell, T.E., Din, N.A. & Omar, A. (1968). Social development of baboons in their first three months. J. Zool., Lond., *155*: 461-483.

Rowell, T.E. & Hartwell, K.M. (1978). The interaction of behavior and reproductive cycles in patas monkeys. Behav. Biol., *24*: 141-167.

Ryan, M.J. (1980). Female mate choice in a neotropical frog. Science, *209*: 523-525.

Saayman, G.S. (1970). The menstrual cycle and sexual behaviour in a troop of free ranging chacma baboons (*Papio ursinus*). Folia primat., *12*: 81-110.

Saayman, G.S. (1971a). Grooming behaviour in a troop of free-ranging chacma baboons (*Papio ursinus*). Folia primat., *16*: 161-178.

Saayman, G.S. (1971b). Behaviour of the adult males in a troop of free-ranging chacma baboons (*Papio ursinus*). Folia primat., *15*: 36-57.

Saayman, G.S. (1972a). Aggressive behaviour in free-ranging chacma baboons (*Papio ursinus*). J. Behav. Sci., *1*: 77-83.

Sade, D.S. (1965). Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. Am. J. phys. Anthrop., *23*: 1-18.

Sade, D.S. (1967). Determinants of dominance in a group of free-ranging rhesus monkeys. In: S.A. Altmann (ed). *Social Communication among Primates*, pp.99-114. Chicago & London, Univ. of Chicago Press.

Sade, D.S. (1968). Inhibition of son-mother mating among free-ranging rhesus monkeys. Science and Psychoanalysis, XII: 18-38.

Sade, D.S. (1972). Sociometrics of Macaca mulatta. 1. Linkages and cliques in grooming matrices. Folia primat., 18: 196-223.

Sade, D.S. (1972b). A longitudinal study of social behavior of rhesus monkeys. In: R. Tuttle (ed). The Functional and Evolutionary Biology of Primates, pp.378-398. Chicago, N.Y., Aldine-Atherton.

Sade, D.S., Cushing, K., Cushing, P., Dunaif, J., Figueroa, A., Kaplan, J. Lauer, C., Rhodes, D. & Schneider, J. (1977). Population dynamics in relation to social structure on Cayo Santiago. Yrbk. Phys. Anthrop., 20: 253-262.

Sadler, D.L. (1980). Adaptiveness of sexual swelling in Old World primates. Am. J. phys. Anthrop., 52: 274-275.

Saunders, C. & Hausfater, G. (1978). Sexual selection in baboons (Papio cynocephalus): a computer simulation of differential reproduction with respect to dominance rank in males. In: D.J. Chivers and J. Herbert (ed). Recent Advances in Primatology, Vol.1, Behaviour, pp.567-571. London, Academic Press.

Schulman, S.R. & Chapais, B. (1980). Reproductive value and rank-relations among macaque sisters. Am. Nat., 115: 580-593.

Scott, L.M. (1978). Mate choice by adolescent female baboons (abstract). Am. J. Phys. Anthrop., 48: 436.

Scott, J.P. & Fredericson, E. (1951). The causes of fighting in mice and rats. Physiol. Zool., 24: 273-309.

Scruton, D.M. & Herbert, J. (1970). The menstrual cycle and its effect on behaviour in the Talapoin monkey (Miopithecus talapoin). J. Zool., Lond., 162: 419-436.

Searcy, W.A. (1979). Female choice of mates: a general model for birds and its application to red-winged blackbirds (Agelaius phoeniceus). Am. Nat., 114: 77-100.

Selander, R.K. (1972). Sexual selection and dimorphism in birds. In: B. Campbell (ed). Sexual Selection and the Descent of Man, pp.180-230. London, Heinemann.

Seyfarth, R.M. (1975). The social relationships among adults in a troop of free-ranging baboons (Papio cynocephalus ursinus). University of Cambridge, Ph.D. Thesis.

Seyfarth, R.M. (1976). Social relationships among adult female baboons. Anim. Behav., 24: 917-938.

Seyfarth, R.M. (1977). A model of social grooming among adult female monkeys. J. Theor. Biol., 65: 671-698.

Seyfarth, R.M. (1978a). Social relationships among adult male and female baboons. I. Behaviour during sexual consortship. Behaviour, 64: 204-226.

Seyfarth, R.M. (1978b). Social relationships among adult male and female baboons. II. Behaviour throughout the female reproductive cycle. Behaviour, 64: 227-247.

Seyfarth, R.M. (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. Anim. Behav., 28: 798-813.

Seyfarth, R.M., Cheney, D.L. & Hinde, R.A. (1978). Some principles relating social interactions and social structure among primates. In: D.J. Chivers & J. Herbert (ed). Recent Advances in Primatology, Vol.1, pp.39-51. London, Academic Press.

Short, R.V. (1976). The evolution of human reproduction. Proc. Roy. Soc. Lond. B., 195: 3-24.

Short, R.V. (1979). Sexual selection and its component parts, somatic and genital selection, as illustrated by man and the great apes. Adv. Study Behav., 9: 131-158.

Siegel, S. (1956). Nonparametric Statistics for the Behavioral Sciences. New York, McGraw-Hill.

Sigg, H., Stolba, A., Abegglen, J.-J. & Wey, R. (in press). Life history of hamadryas baboons: physical development, reproductive parameters, infant mortality, and family relationships. Folia primatol.

Silk, J.B., Samuels, A. & Rodman, P.S. (1980). Rank, reproductive success and skewed sex ratio in Macaca radiata. (abstr.). Am. J. phys. Anthrop., 52: 279.

Simonds, P.E. (1965). The bonnet macaque in South India. In: I. DeVore (ed). Primate Behavior, pp.175-196. New York, Holt, Rinehard and Winston.

Simpson, M.J.A. (1973). The social grooming of male chimpanzees. In: R.P. Michael & J.H. Crook (eds). Comparative Ecology and Behaviour of Primates, pp.412-505. London, Academic Press.

Slob, A.K., Weigand, S.J., Goy, R.W. & Robinson, J.A. (1978). Heterosexual interactions in laboratory-housed stumptail macaques (Macaca arctoides): observations during the menstrual cycle and after ovariectomy. Horm. Behav., 10: 193-211.

Smith, C.C. (1977). Feeding behaviour and social organisation in howling monkeys. In: T.H. Clutton-Brock (ed). Primate Ecology: feeding and ranging behaviour of lemurs, monkeys and apes, pp.97-126. London, Academic Press.

Smith, D.G. (1981). The association between rank and reproductive success of male rhesus monkeys. Am. J. Primatol., 1: 83-90.

Southwick, C.H. (1967). An experimental study of intragroup agonistic behavior in rhesus monkeys. Behaviour, 28: 182-209.

Sparks, J. (1967). Allogrooming in primates: a review. In: D. Morris (ed). Primate Ethology, pp.148-175. London, Weidenfeld and Nicolson.

Stammbach, E. (1978). On social differentiation in groups of captive female hamadryas baboons. Behaviour, 67: 322-338.

Stephenson, G.R. (1973). Testing for group specific communication patterns in Japanese macaques. Symp. IVth Int. Congr. Primat., Vol.1: (ed. E. Menzel). Precultural Primate Behavior, pp.51-75. Basel, Karger.

Stephenson, G.R. (1974). Social structure of mating activity in Japanese macaques. In: S. Kondo, M. Kawai, A. Ehara & S. Kawamura (eds). Symp. 5th Cong. Int'd. Primat. Soc., pp.63-115. Tokyo, Japan Science Press.

Stevens, V.C. (1978). The use of female baboons for evaluation of immunological methods of fertility control. In: D.J. Chivers and E.H.R. Ford (eds). Recent Advances in Primatology, Vol.4, Medicine, pp.145-151. London, Academic Press.

Stevens, V.C. Sparks, S.J. & Powell, J.E. (1970). Levels of estrogens, progestogens, and luteinising hormone during the menstrual cycle of the baboon. Endocrinology, 87: 658-666.

Stoeker, J. (1974). Social behavior of baboons in a large zoo enclosure. (abstr.). Am. J. phys. Anthrop., *40*: 52.

Stoltz, L.P. (1972). The size, composition and fissioning in baboon troops (*Papio ursinus* Kerr, 1792). Zoologica Africana, *7*: 367-378.

Stoltz, L.P. & Saayman, G.S. (1970). Ecology and behaviour of baboons in the Northern Transvaal. Ann. Transvaal Mus., *26*: 99-143.

Struhsaker, T.T. (1967). Social structure among vervet monkeys (*Cercopithecus aethiops*). Behaviour, *29*: 83-121.

Struhsaker, T.T. (1975). *The Red Colobus Monkey*. Chicago Univ. Press.

Struhsaker, T.T. & Leland, L. (1979). Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. Adv. Study Behav., *9*: 159-228.

Strum, S.C. (1975). Life with the Pumphouse Gang. Nat. Geogr., *147*: 672-691.

Suarez, B. & Ackerman, D.R. (1971). Social dominance and reproductive behaviour in male rhesus monkeys. Am. J. phys. Anthrop., *35*: 219-222.

Sugawara, K. (1979). Sociological study of a wild group of hybrid baboons between *Papio anubis* and *P. hamadryas* in the Awash Valley, Ethiopia. Primates, *20*: 21-56.

Sugiyama, Y. (1971). Characteristics of the social life of bonnet macaques (*Macaca radiata*). Primates, *12*: 247-266.

Sugiyama, Y. (1976). Life history of male Japanese monkeys. Adv. Study Behav. *7*: 255-284.

Symons, D. (1978). *Play and Aggression. A Study of Rhesus Monkeys*. New York, Columbia University Press.

Szalay, F.S. & Delson, E. (1979). *Evolutionary History of the Primates*. New York, Academic Press.

Taub, D.M. (1980a). Female choice and mating strategies among wild Barbary macaques (*Macaca sylvanus* L.). In: D.G. Lindburg (ed). *The Macaques*, pp.287-344. New York, Van Nostrand Reinhold.

Taub, D.M. (1980b). Testing the "agonistic buffering" hypothesis, I. The dynamics of participation in the triadic interaction. Behav. Ecol. Sociobiol., 6: 187-197.

Tayler, C.K. & Saayman, G.S. (1972). The social organisation and behaviour of dolphins (Tursiops aduncus) and baboons (Papio ursinus): some comparisons and assessments. Ann. Cape Prov. Mus. (Nat. Hist.), 9: 11-49.

Terry, R.L. (1970). Primate grooming as a tension reduction mechanism. J. Psychol., 76: 129-136.

Thibault, C. (1972). Some pathological aspects of ovum maturation and gamete transport in mammals and man. In: E. Diczfalusy & C.C. Standley (eds). The Use of Non-Human Primates in Research on Human Reproduction, pp.59-66. Stockholm, W.H.O.

Thorington, R.W. & Groves, C.P. (1970). An annotated classification of the Cercopithecoidea. In: J.R. Napier & P.H. Napier (eds). Old World Monkeys, pp.631-647. New York, Academic Press.

Tokuda, K. (1961-62). A study on the sexual behavior in the Japanese monkey troop. Primates, 3: 1-40.

Tokuda, K., Simons, R.C. & Jensen, G.D. (1968). Sexual behavior in a captive group of pigtailed monkeys (Macaca nemestrina). Primates, 9: 283-294.

Trivers, R.L. (1972). Parental investment and sexual selection. In: B. Campbell (ed). Sexual Selection and the Descent of Man, pp.136-179. London, Heinemann.

Tutin, C.E.G. (1975). Exceptions to promiscuity in a feral chimpanzee community. In: S. Kondo, M. Kawai & A. Ehara (eds). Contemporary Primatology, pp.445-449. Basel, S. Karger.

Tutin, C.E.G. (1976). Sexual behaviour and mating patterns in a community of wild chimpanzees (Pan troglodytes schweinfurthii). University of Edinburgh, Ph.D. Thesis.

Tutin, C.E.G. (1979a). Mating patterns and reproductive strategies in a community of wild chimpanzees (Pan troglodytes schweinfurthii). Behav. Ecol. Sociobiol., 6: 29-38.

Tutin, C.E.G. (1979b). Responses of chimpanzees to copulation, with special reference to interference by immature individuals. Anim. Behav., 27: 845-854.

Tyler, S. (1979). Time-sampling: a matter of convention. Anim. Behav., 27: 801-810.

Vaitl, E. (1978). Nature and implications of the complexly organised social system in nonhuman primates. In: D.J. Chivers & J. Herbert (eds). Recent Advances in Primatology, Vol.1, Behaviour, pp.17-30. London, Academic Press.

Vessey, S.H. (1971). Free-ranging rhesus monkeys: behavioural effects of removal, separation and reintroduction of group members. Behaviour, 40: 216-227.

Vine, I. (1971). Risk of visual detection and pursuit by a predator, and the selective advantage of flocking behaviour. J. Theor. Biol., 30: 405-422.

Wade, T.D. (1976). The effects of strangers on rhesus monkey groups. Behaviour, 56: 194-214.

Wade, T.D. (1977). Complementarity and symmetry in social relationships of nonhuman primates. Primates, 18: 835-847.

Wade, T.D. (1978). Status and hierarchy in nonhuman primate societies. In: P.P.G. Bateson and P.H. Klopfer. Perspectives in Ethology, Vol.3, pp.109-134. New York, Plenum Press.

Walters, J. (1980). Interventions and the development of dominance relationships in female baboons. Folia primatol., 34: 61-89.

Walters, J. (1981). Inferring kinship from behaviour: maternity determinations in yellow baboons. Anim. Behav., 29: 126-136.

Washburn, S.L. & DeVore, I. (1961). The social life of baboons. Scient. Am., 204: 62-71.

Weatherhead, P.J. & Robertson, R.J. (1979). Offspring quality and the polygyny threshold: "the sexy son hypothesis". Am. Nat. 113: 201-208.

Wheatley, B.P. (1980). Malaria as a possible selective factor in the speciation of macaques. J. Mammal., 61: 307-311.

Wildt, D.E., Doyle, L.L. Stone, S.C. & Harrison, R.M. (1977). Correlation of perineal swelling with serum ovarian hormone levels, vaginal cytology, and ovarian follicular development during the baboon reproductive cycle. Primates, 18: 261-270.

Wiley, R.H. (1974). Evolution of social organisation and life-history patterns among grouse. Quart. Rev. Biol., 49: 201-227.

Wilkinson, P.F. & Shank, C.C. (1976). Rutting-fight mortality among musk oxen on Banks Island, Northwest Territories, Canada. Anim. Behav., 24: 756-758.

Williams, D.A. (1975). The analysis of binary responses from toxicological experiments involving reproduction and teratogenicity. Biometrics, 31: 949-952.

Williams, G.C. (1975). Sex and Evolution. Princeton Univ. Press.

Wilson, M.E., Gordon, T.P. & Bernstein, I.S. (1978). Timing of births and reproductive success in rhesus monkey social groups. J. med. Primatol., 7: 202-212.

Wilson, A.P. & Vessey, S.H. (1968). Behavior of free-ranging castrated rhesus monkeys. Folia primat., 9: 1-14.

Wolfe, L. (1979). Behavioral patterns of estrous females of the Arashiyama West troop of Japanese macaques (*Macaca fuscata*). Primates, 20: 525-534.

Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. Behaviour, 75: 262-300.

Wright, S. (1940). Breeding structure of populations in relation to speciation. Am. Nat., 74: 232-248.

Zuckerman, S. (1931). The menstrual cycle of the primates. III. The alleged breeding season of primates, with special reference to the chacma baboon (*Papio porcarius*). Proc. Zool. Soc. Lond., : 325-343.

Zuckerman, S. (1932). The social life of monkeys and apes. London, Kegan Paul.

Zuckerman, S. & Parkes, A.S. (1932). The menstrual cycle of the primates. V. The cycle of the baboon. Proc. Zool. Soc. Lond. : 139-191.

Zumpe, D. & Michael, R.P. (1968). The clutching reaction and orgasm in the female rhesus monkey (Macaca mulatta). J. Endocrinol., 40: 117-123.

Zumpe, D. & Michael, R.P. 1977). Effects of ejaculation by males on the sexual invitations of female rhesus monkeys (Macaca mulatta). Behaviour, 60: 260-277.

Appendix I

Definitions of behaviours

Premiss: In the following, the terms approach and leave are used to describe one animal's moving into or out of arms reach of another.

A. GROOMING

(i) Groom-present: The donor, within arm's reach, presents part of the body (other than the rear) to another.
(ii) Groom: The donor picks through the fur of the recipient, with one or both hands. (Note: Self-grooming, or Autogrooming, was not recorded).

B. AGONISTIC BEHAVIOURS: (broad definition)

- Non-aggressive agonism; between males only:

(iii) Replace: When one male vacates a position (feeding or nesting site, grooming partner), a nearby male moves to occupy it immediately afterwards.
(iv) Pass: A male approaches and leaves another without stopping or exchanging gestures.
(v) Male contact: A male approaches, exchanges non-aggressive gestures with, and leaves another (e.g. arm-round, stand in contact, cheekchew etc. but excluding mounts).

- Non-aggressive agonism between any animals

Excludes any interaction with threat or more intense aggression.
(vi) Avoidance: One animal walks towards another who moves out of the line of travel of the first before they are within arm's reach.
(vii) Supplant: The donor approaches the recipient who leaves within five seconds, or within five seconds of the cessation of gestural exchange.

- Aggression

Any interaction including gestures of threat or more intense aggression (as defined in Hall and DeVore, 1965). Aggressive interactions were classified on a continuum of increasing intensity, and only the most intense of the following was recorded.
(viii) Threat: Any of a number of stereotyped gestures - head-bob, eyebrow raise, slapping ground, yawn canine-threat (i.e. directed yawn), sweeps ground, etc.

(ix) Chase: Directed running pursuit of another.

(x) Attack: Any aggressive contact, including grappling, hitting, grabbing, biting, throwing to ground etc. Often reciprocal.

(xi) Agonistic alliance: Agonistic interactions simultaneously involving two or more animals against a third, either in attack or defence. Any pair of animals simultaneously directing aggression toward a third are referred to as allies.

- Interactions between male and infant

Interactions between either an adult or subadult male and a black or brown infant were subdivided as one of:

(xii) Interest: The male approaches the infant and looks closely at it without contact; usually while the infant is on the mother.

(xiii) Manipulation: The male touches the infant: trying to pull it from its mother; or if it is off the mother, grooming, holding, or restraining it, excluding (xiv).

(xiv) Carrying: The male travels while bearing the infant, either supporting it with one hand while walking tripedal, or with the infant clinging ventral or dorsal.

(xv) Use of infant: All cases where a male was carrying an infant (or manipulating an infant off the mother) while interacting with another male, either as donor or recipient.

C. SOCIOSEXUAL AND SEXUAL BEHAVIOUR:

(xvi) Present (rear-present): This was only recorded when given by female to male. The female directs her rear toward a male, either by taking up a stance, or during travel by inclining her rear toward, or cocking her tail away from, a male whom she is passing. There is no distance criterion: the female often looks at the male.

(xv) Rear-oriented behaviours: Males' responses to presents, or unsolicited gestures directed at a female's rear.

(a) Negative: (i) Avoidance. A male turns his head away, or leaves, when a female presents.
(ii) Ignores. The male shows no visible response to a present.

(b) Greets rear: (i) Touches rear. With or without a present, the male touches the rump, perineum, belly, or flanks of the female, from behind, but without inspecting. (ii) The male may nip the female's flanks.

(c) Inspects: The male moves his nostrils to within three inches of the female's perineum. This category subsumes any of (i) above if an inspect occurred.

(xvi) Mounting: A contact interaction in which the mounter moves the pubic region to the body of another, usually the rear. Mounters stand bipedally with hands on hips or flanks of mountees, often clasping the ankles with their hind feet (= footclasp). Mounts were subdivided as follows:

(a) Attempt-mount: The mounter does not reach the full mounted position, either through inability, or because the recipient evades, or due to interruption by harassment.

(b) Half-mount: The mounter begins to mount (i.e. with forefeet clear of the ground) but desists before reaching the full mount position.

(c) Mount: A complete mount, without intromission, classified according to: (a) orientation: whether the mount was correctly oriented (i.e. sagittally at the rear) or wrongly oriented, and (b) presence or absence of pelvic thrusting by the mounter. Thrusting without intromission was shallow and usually rapid.

(d) Intromitted mount: A correctly oriented mount with penile intromission. Intromission was either seen directly, or inferred from the presence of slow deep thrusting by the mounter.

(xvii) Components of intromitted mounts: For all intromitted mounts for which it was possible to observe clearly was recorded the following:

(a) Male pause: The male ceases thrusting and stays rigid for a few seconds before dismounting. Considered indicative of ejaculation.

(b) Female vocal response: Ranging from 0 - none heard, through 1 - audible vocalisation, but not the distinctive copulation grunt, to 2 - recognisable copulation grunt.

(c) Female locomotory response: Ranging from 0 - the female moves no more than two paces when the male dismounts, through 1 - the female walks or trots, usually less than 5 metres, to 2 - the female runs forward, often beyond 5 metres.

(d) Onlookers' response: Nearby animals would sometimes
    (i) walk or run towards the mounted pair, or
    (ii) harass - direct aggressive gestures at the pair.

(xviii) Classes of intromitted mount: On the presence of absence of the male's pause, the member of the pair which terminated the mount, and the response of onlookers, mounts with intromission were judged to be:

(1) Incomplete mounts (i.e. without pause), terminated voluntarily by the male or by the female.

(2) Interrupted mounts (without pause), terminated when the male dismounts in response to the behaviour of onlookers, e.g. harassment.

(3) Complete intromitted mounts: the male pauses before dismounting.

D. POSSESSIVE AND CONSORT BEHAVIOUR:

Interactions defined by gesture and/or context when shown by male to female.

(xix) Stands or sits next: The male approaches and stands or sits within arms reach of the female. Often directly behind her. In movement, classified as following the female.

(xx) Coercion: The male interacts forcibly with the female, by pushing, cuffing, nipping her skin, or pulling her rear. May precede mounting. If elicited by the presence of a rival, included as possessive interaction (below).

(xxi) Possessiveness: Behaviours whereby the male appears to reduce the likelihood that a female will interact with another animal. Distinguished by their contexts: at the arrival of another male nearby; when the female moves towards such a male; or (occasionally) at the proximity of another troop. Characterised by the urgency of the male's performance.

(a) Herding: The male pushes or cuts in front of the female to divert her from her line of travel towards another male.

(b) Shielding: The male interposes himself between the female and a nearby male, but without touching her. Blocking, intermediate between (a) and (b), is when a male stands to block the female's travel toward another male.

(c) Other behaviours sometimes judged from context to be possessive were male mounting, chasing, hurrying close to, and sometimes grooming the female:

For all interactions in these categories, the apparent stimulus was recorded: e.g. other troop seen/male nearby/chasing nearby, etc.

E. CONSORTSHIPS:

Pairs were defined as 'in consort' on the following criteria (criteria judged to be obvious also to rival males): any two were sufficient.

(a) the male consistently travels after the female whenever she moves.

(b) the male shows possessive behaviour to the female against other males.

(c) the male persistently grooms the female.

The start and finish of each consortship was classified, if seen, as:

(1) Non-agonistic: (a) Finds: a male and female, both of whom seen previously not in consort, start to consort.

(b) Deserts: a male desists from consorting without any evidence of competition from other males.

(2) Agonistic: (a) Displacement: the consort male deserts the female in apparent response to the presence of a nearby male who immediately assumes consortship, but no aggression is exchanged. It was not possible to record attempted displacements.

(b) Aggressive: the consort male gives up consortship of a female during aggressive exchanges with animals other than the female. Subdivided as solo if the consort male had only one antagonist (although he might have an ally in defence), and as allied if the aggression involved the consort pair and animals in addition to one male opponent. These were usually other males.

Aggression directed from adult or subadult males to a consort pair were considered to be attempts to gain consortship of the female.

Appendix II

Additional tables of data

Contents

Tables

Table 6.XXVII : Male-male alliance compared with proximity.

	Allies											
Subjects	A 1	A 2	A 3	A 4	A 5	S 1	A 6	A 7	A 8	S 2	S 3	S 4
A 1		1 137 9.4	2 120 13.5	0 133 3.7	3 121 8.9	1 85 2.9	1 122 5.6	0 141 3.9	1 136 9.2	0 143 12.8	1 141 11.5	0 143 13.6
A 2	1 99 6.8		0 99 5.8	0 102 1.6	1 90 5.6	0 48 1.6	0 88 3.5	0 99 4.2	0 102 3.2	0 99 6.9	0 104 5.7	0 101 8.2
A 3	2 142 16	0 122 7.1		11 161 14.9	34 119 23.9	2 82 4.9	2 132 5.7	3 149 13.9	2 182 16	5 177 29.3	0 180 16.7	2 178 17.7
A 4	0 105 2.5	0 112 1.7	11 99 9.6		14 80 5	3 71 6.9	6 89 4.1	7 103 5	5 110 4.8	1 112 11.8	0 117 9.5	0 119 8.2
A 5	3 188 13.7	1 198 12.3	34 172 32.1	14 201 11.5		4 107 8.8	15 159 10.5	22 181 18.7	8 211 12.5	5 214 27.1	1 219 35.8	2 224 29.4
S 1	1 43 1.5	0 44 1.5	2 44 2.7	3 43 4.3	4 35 3.1		3 42 2.1	0 44 1.1	1 45 1.5	2 34 1.9	0 46 3.7	0 42 3
A 6	1 43 2	0 49 1.9	2 43 1.9	6 39 1.9	15 28 2.6	3 35 1.8		4 38 2.4	2 47 1.7	2 45 3.9	0 50 3.0	0 50 4.1
A 7	0 81 2.3	0 81 3.4	3 73 6.9	7 72 3.6	22 66 8.1	0 46 1.2	4 54 3.3		1 94 4	2 93 4.4	0 91 5.3	2 93 4.7
A 8	1 28 2	0 37 1.2	2 35 3.2	5 28 i.4	8 23 1.8	1 20 0.7	2 29 1.1	1 36 1.5		2 27 1.9	0 34 3	0 37 2.4
S 2	0 52 4.7	0 53 3.7	5 50 8.9	1 56 5.9	5 52 7.0	2 29 1.6	2 50 4.3	2 55 2.6	2 52 3.5		0 56 7.6	1 52 7.1
S 3	1 44 3.7	0 48 2.6	0 48 4.4	0 48 3.9	1 46 7.6	0 26 2.1	0 38 2.3	0 48 2.8	0 48 4.3	0 47 6.4		3 41 4.1
S 4	0 57 5.4	0 57 4.6	2 57 5.8	0 60 4.1	2 58 7.8	0 35 2.5	0 51 4.1	2 58 3	0 60 3.9	1 56 7.6	3 51 5	

Each cell records the number of alliances (top left), the remainder of the subject's aggression (top right) and the expected number of alliances (lower left) derived from the total of the other two scores in proportion to time in proximity.

Table 7.XVII: Number of intromitted mounts to each female in each cycle state, by males of each class (Imm - immature: Sub - subadult: Ad - Adult). Brackets = pooled for χ^2.

	Inflation			Full			Deflation		
Females:	Imm.	Sub.	Ad.	Imm.	Sub.	Ad.	Imm.	Sub.	Ad.
F 1	(27	9	2)	7	1	28			
F 5	(7	1	8)	21	5	73	14	6	4
F 6	49	14	8	22	11	73	13	3	3
F 7	26	9	8	43	19	73	7	3	7
F13	44	2	3	19	10	17			
F17	46	20	2	18	8	7	4	0	0
	χ^2 23.54			χ^2 71.93			no test		
	df 8; $p < .001$			df. 10; $p < .01$					

Table 7.XVIII: Number of intromitted mounts to each female by males of each class in which the ejaculatory pause was present (+) or absent (-). All cycle states are pooled.

	Immature		Subadult		Adult	
Females:	-	+	-	+	-	+
F 1	15	1	3	0	10	4
F 5	13	8	4	3	17	30
F 6	21	3	5	1	15	18
F 7	14	3	10	3	13	1
F13	28	7	2	3	7	6
F17	25	5	15	2	3	1

Table 7.XXI: Differences between females in their responses to particular male classes in inflation and full swelling. Vocal responses graded 0 > 1 > 2. Brackets = pooled for χ^2.

Females:	With subadults in inflation			With adults at full swelling		
	0	1	2	0	1	2
F 1	8	16	3	0	3	4
F 5	3	2	2	1	3	7
F 6	1	8	40	0	3	19
F 7	1	9	16	2	1	40
F13	10	29	5	1	13	5
F17	11	32	3	0	14	4

With subadults in inflation	With adults at full swelling
χ^2 92.45	χ^2 49.29
df. 8; $p < .001$	df. 4; $p < .001$

Legend to Tables 7.XXII, XXIII, XXIV, XXV, and XXVI.

The following tables contain a large number of 2 x 2 matrices. Each matrix compares two variables which are listed at the head of the table. Each matrix is of the form:

	c	d
a		
b		

The test in each case is to compare the ratio between a and b in each column c and d. The proportion of b in column d is compared with that in column c, and marked as greater (+), less than (–), or equal (=). For example, the matrices in Table 7.XXII show the number of ejaculatory mounts with the ejaculatory pause (b) and without it (a) for subadult males in column c, and adult males in column d.

Each table compares two variables concerning intromitted mounts. The conditions of the other variables for each matrix are indicated by the following abbreviations in terms of:

The female's identity: F1, F5, F6, F7, F13, or F17.

Female cycle state: Inf (inflating), Ful (fully swollen) or Def (deflating).

Female vocal response to copulation: 0, 1, or 2.

Class of male mounter: Ad (adult), Sub (subadult) or Imm (immature).

Ejaculatory pause: as present (poz) or absent (nil).

All matrices with any data have been filled in, but only those marked + or – contributed to the analyses in section 7.

Table 7.XXIIa. The proportion of intromitted mounts with and without the ejaculatory pause (Poz & Nil respectively): adult and subadults compared. Other abbreviations as listed above.

e.g.

	Sub	Ad.
Nil		
Poz		

Vocal resp.:	0	1	2		0	1	2
F 1				F 5			
Inf.	0 2 0 0	3 0 0 0			1 4 0 3+		
Ful.			0 8 0 4		0 1 0 2	0 5 1 2–	0 6 2 20–
Def.					2 1 0 0	1 0 0 0	0 0 0 3
F 6				F 7			
Inf.	1 2 0 0	0 1 0 0	2 1 0 2+		1 4 0 0	2 2 0 0	2 0 1 0
Ful.	0 1 0 0	0 1 0 0	2 9 1 15+			1 0 0 0	4 4 2 1–
Def.			0 0 0 1			0 3 0 0	
F13				F17			
Inf.	1 2 0 0	0 1 0 0			3 0 0 0	5 0 0 0	1 0 0 0
Ful.	0 1 0 0	0 2 1 3–	1 1 2 3+		1 1 0 0	5 0 0 0	0 2 1 1–
Def.							

Table 7.XXIIb. The proportion of intromitted mounts with and without ejaculatory pause (Poz & Nil respectively): subadults and immature males compared. Abbreviations listed above.

e.g.

	Imm	Sub
Nil		
Poz		

Vocal resp.:	0	1	2		0	1	2
F 1				F 5			
Inf.	5 2 0 0	8 0 1 0	1 0 0 0		3 4 0 3+	2 0 0 0	0 0 1 0
Ful.			1 8 0 4+		0 1 1 2–	0 5 0 2	5 6 2 20+
Def.					3 1 0 0	0 0 1 0	0 0 2 3
F 6				F 7			
Inf.	1 2 0 0	6 1 0 0	18 1 1 2+		1 4 0 0	1 2 0 0	3 0 0 0
Ful.	0 1 0 0	0 1 0 0	2 9 2 15+		2 0 0 0		6 4 1 1+
Def.		1 0 0 0	1 0 0 1+			0 3 0 0	1 0 2 0
F13				F17			
Inf.	8 2 0 0	8 1 3 0–	1 0 1 0		7 0 2 0	15 0 1 0	0 0 1 0
Ful.	1 1 0 0	4 2 2 3+	2 1 1 3+		0 1 0 0	2 0 1 0	0 2 0 1
Def.						1 0 0 0	

Table 7.XXIIIa. The proportion of intromitted mounts with and without the ejaculatory pause (Poz & Nil respectively) compared between inflation and full swelling. Abbreviations as above.

e.g.

	Inf	Ful
Nil		
Poz		

Vocal resp.:		0	1	2		0	1	2
	F 1				F 5			
Imm.		5 0 0 0	8 0 0 0	1 1 0 0		3 0 0 1+	2 0 0 0	0 5 1 2–
Sub.			3 0 0 0			1 0 0 0	0 0 0 1	0 0 0 2
Ad.		2 0 0 0		0 8 0 4		4 1 3 2+	0 5 0 2	0 6 0 20
	F 6				F 7			
Imm.		1 0 0 0	6 0 0 0	10 2 1 2+		1 2 0 0	1 0 0 0	3 6 0 1+
Sub.		1 0 0 0		2 2 0 1+		1 0 0 0	2 1 0 0	2 4 1 2=
Ad.		2 1 0 0	1 1 0 0	1 9 2 15–		4 0 0 0	2 0 0 0	0 4 0 1
	F13				F17			
Imm.		8 1 0 0	8 4 3 2+	1 2 1 1–		7 0 2 0	15 2 1 1+	0 0 1 0
Sub.		1 0 0 0	0 0 0 1	0 1 0 2		3 1 0 0	5 5 1 0–	1 0 0 1+
Ad.		2 1 0 0	1 2 0 3+	0 1 0 3		0 1 0 0		0 2 0 1

Table 7.XXIIIb. The proportion of intromitted mounts with and without the ejaculatory pause (Poz & Nil respectively) compared between full swelling and deflation. Abbreviations as above.

e.g.

	Ful	Def
Nil		
Poz		

Vocal resp.:	0		1		2		0		1		2	
	F 5						F 6					
Imm.	0	3	0	0	5	0			0	1	2	1
	1	0–	0	1	2	2+			0	0	2	0–
Sub.	0	2	0	1	0	0					2	0
	0	0	1	0–	2	0					1	0
Ad.	1	1	5	0	6	0	1	0	1	0	9	0
	2	0–	2	0	20	3+	0	0	0	0	15	1+
	F 7						F17					
Imm.	2	0			6	1			2	1		
	0	0			1	2+			1	0–		
Sub.			1	0	4	0	1	0	5	0	0	0
			0	0	2	0	0	0	0	0	1	0
Ad.			0	3	4	0	1	0			2	0
			0	0	1	0	0	0			1	0

Table 7XXIVa. The proportion of intromitted mounts with incomplete (0 or 1) and complete (2) vocal response according to whether the mounter was adult or subadult male.

e.g.

	0+1	2
Sub:		
Ad:		

Cycle State:		Inf		Ful		Def			Inf		Ful		Def	
	F 1							F 5						
Nil:		3	0	0	0				1	0	0	0	3	0
		2	0	0	8				4	0	6	6	1	0
Poz:				0	0				0	0	1	2	0	0
				0	4				3	0	4	20+	0	3
	F 6							F 7						
Nil:		1	2	0	2				3	2	1	4	0	0
		3	1-	2	9-				6	0-	0	4+	3	0
Poz:		0	0	0	1	0	0		0	1	0	2		
		0	2	0	15	0	1		0	0	0	1		
	F13							F17						
Nil:		1	0	0	1				6	1	6	0		
		3	0	3	1-				0	0	1	2+		
Poz:				1	2				1	0	0	1		
				3	3-				0	0	0	1		

Table 7.XXIVb. The proportionof intromitted mounts with incomplete (0 or 1) or complete (2) vocal response according to whether the mounter was an adult or an immature male.

e.g.

	0+1	2
Imm		
Ad		

Cycle state:	Inf	Ful	Def		Inf	Ful	Def
F 1				F 5			
Nil:	13 1 2 0–	0 1 0 8			5 0 4 0	0 5 6 6–	3 0 1 0
Poz:	1 0 0 0	0 0 0 4			0 1 3 0–	1 2 4 20+	1 2 0 3+
F 6				F 7			
Nil:	7 10 3 1–	0 2 1 9–	1 1 0 0		2 3 6 0–	2 6 0 4+	0 1 3 0–
Poz:	0 1 0 2	0 2 0 15	0 0 0 1			0 1 0 1	0 2 0 0
F13				F17			
Nil:	16 1 3 0–	5 2 3 1+			22 0 0 0	2 0 1 2+	1 0 0 0
Poz:	3 1 0 0	2 1 3 3+			3 1 0 0	1 0 0 1+	

Table 7.XXVa. The proportion of intromitted mounts with incomplete (0 or 1) or complete (2) vocal response: inflation compared with full swelling.

e.g.	0+1	2
Inf.		
Ful.		

Male class:	Imm		Sub		Ad.			Imm		Sub		Ad.	
F 1							F 5						
Nil:	13	1	3	0	2	0		5	0	1	0	4	0
	0	1+	0	0	0	8+		0	5+	0	0	6	6+
Poz:	1	0			0	0		0	1	0	0	3	0
	0	0			0	4		1	2–	1	2	4	20+
F 6							F 7						
Nil:	7	10	1	2	3	1		2	3	3	2	6	0
	0	2+	0	2+	2	9+		2	6+	1	4+	0	4+
Poz:	0	1	0	0	0	2		0	0	0	1	0	0
	0	2	0	1	0	15		0	1	0	2	0	1
F13							F17						
Nil:	16	1	1	0	3	0		22	0	8	1	0	0
	5	2+	0	1+	3	1+		2	0	6	0–	1	2
Poz:	3	1	0	0	0	0		3	1	1	0	0	0
	2	1+	1	2	3	3		1	0–	0	1+	0	1

Table 7XXVb. The proportion of intromitted mounts with incomplete (0 or 1) or complete (2) vocal response: full swelling compared with deflation.

e.g.	0+1	2
Full		
Def.		

Male class:		Imm	Sub	Ad.		Imm	Sub	Ad.
	F 5				F 6			
Nil:		0 5	0 0	6 6		0 2	0 2	2 9
		3 0–	3 0	1 0–		1 1–	0 0	0 0
Poz:		1 2	1 2	4 20		0 2	0 1	0 15
		1 2=	0 0	0 3+		0 0	0 0	0 1
	F 7				F17			
Nil:		2 6	1 4	0 4		2 0	6 0	1 2
		0 1+	0 0	3 0–		1 0	0 0	0 0
Poz:		0 1	0 2	0 1		1 0	0 1	0 1
		0 2	0 0	0 0		0 0	0 1	0 0

Table 7.XXXVI. The proportion of intromitted mounts with and without ejaculatory pause (Poz & Nil respectively); in mounts with partial (0 + 1) or full (2) vocal response.

e.g.	0+1	2
Nil		
Poz		

Cycle state:		Inf		Ful		Def			Inf		Ful		Def	
	F 1							F 5						
Imm:		13	1	0	1				5	0	0	5	3	0
		1	0–	0	0				0	1+	1	2–	1	2+
Sub:		3	0						1	0	0	0	3	0
		0	0						0	0	1	2	0	0
Ad:		2	0	0	8				4	0	6	6	1	0
		0	0	0	4				3	0	4	20+	0	3+
	F 6							F 7						
Imm:		7	10	0	2	1	1		2	3	2	6	0	1
		0	1+	0	2	0	0		0	0	0	1+	0	2
Sub:		1	2	0	2				3	2	1	4		
		0	0	0	1				0	1+	0	2+		
Ad:		3	1	2	9	0	0		6	0	0	4	3	0
		0	2+	0	15+	0	1		0	0	0	1	0	0
	F13							F17						
Imm:		16	1	5	2				24	0	2	0	1	0
		3	1+	2	1+				3	1+	1	0	0	0
Sub:		1	0	0	1				8	1	6	0		
		0	0	1	2–				1	0–	0	1+		
Ad:		3	0	3	1						1	2		
		0	0	3	3+						0	1+		

Appendix III

Some behavioural differences between baboons at Ruaha and Gombe

The present study was preceded by observations of olive baboons at Gombe between 1972 and 1975. Some obvious differences between them are here listed.

1. Supplanting Oliver and Lee (1978) showed that Ruaha juveniles supplanted adult females, and were supplanted by adult males much more than at Gombe. This suggests that feeding competition at Ruaha was more intense.

2. Mounting Compared with baboons at Gombe, the Ruaha animals showed more frequent mounts between females (discussed in 5.7.3b), and in copulation a higher proportion of series-mounts (7.10.4).

3. Harassment At Ruaha, only 2.74% of 261 intromitted mounts were harassed at all. In contrast, at Gombe 10% of 79 such mounts were interrupted by harassment, and many more were harassed (unpubl. data).

4. Vocalisations Although no tape recordings were made, some vocalisations obviously differed.

4a. The two-phase bark (Hall & DeVore, 1965), or wahoo.
This was given at Gombe by (i) lost baboons, as a contact call; (ii) adult males, often preceded by the humm/roargrunt sequence (Ransom, 1971); at intervals when in or apart from the troop; at night in choruses, possibly as an intertroop spacing call; (iii) by adult males during or after intertroop interactions with chasing back of females. These contexts are as reported for Kenyan olive baboons by Hall & DeVore (*ibid*.). Although at Ruaha it was given as in (i) above, it was very rarely given by males as in (ii). Most interestingly, while it was given during intertroop interactions as in (iii), it was not then given as isolated calls but rather interspersed within a sequence of the two-phase pantgrunt (= roaring, Hall & DeVore, 1965) while chasing-back females. In this respect it is more like the context of *wahoo* reported for chacmas, where males give it during attacks on other males or on females (Hall, 1963, p.9). Hamilton *et al*. (1975) also report it

in chacmas during intertroop interactions, and at night as in (ii).

4b. The roar (Hall & DeVore, 1965) or pantgrunt.

Gombe males used this in aggression to one another, as do Kenyan olive baboons (Hall & DeVore *ibid*.). During male-male aggression the Ruaha males used the pantgrunt much less, but more often screamed (e.g. with tail up, apparently to solicit aid). In this respect they resemble chacmas, which do not pantgrunt according to Hall and DeVore (*ibid*.).

4c. The copulation call. At Ruaha the copulation call was similar to that heard at Gombe but of longer duration. It was given in 62% of intromitted mounts, which compares with 10-30% for olive baboons, 90-100% for chacmas (7.10.4).